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CHAOS IN A THREE-SPECIES FOOD CHAIN

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Abstract. A continuous time model of a food chain incorporating nonlinear functional
(and numerical) responses exhibits chaotic dynamics in long-term behavior when biologi-
cally reasonable parameter values are chosen. The appearance of chaos in this model
suggests that chaotic dynamics may be common in natural food webs.

Key words: chaos; dynamics; food chain; food web; functional response; predation.

INTRODUCTION

The classical ecological models of interacting pop-
ulations typically have focussed on two species (e.g.,
May 1973, Hassell 1978). They have been applied to
plant and animal systems in aquatic and terrestrial
environments, and across many taxa (e.g., Roughgar-
den et al. 1989). However, it has long been recognized
that the limited "caricature" of ecological systems by
two interacting species can account for only a small
number of the phenomena that are commonly exhib-
itied in nature. This is particularly true in community
studies where the essence of the behavior of a complex
system may only be understood when the interactions
among a large number of species are incorporated

One approach to the study of an ecological com-
munity begins with an important object: its food web.
Theoretical studies of food webs must contend with
the question of how to couple the large number of
interacting species. One line of investigation assumes
that the "building blocks" are species interacting in
pairwise fashion (see the influential books of May 1973,
Pimm 1982). Behavior of the entire community is then
assumed to arise from the coupling of these strongly
interacting pairs. The approach has the substantial
virtue that it is tractable to theoretical analysis. Moreover,
the considerable intuition that investigators have
developed over decades with two-species models may be
applied to community food web questions.

Note, however, that important behavior that may
be critical to community function may arise only
through the interaction of three or more species. Price
et al. (1980) present a strong case that understanding
of plant-insect interactions must be based on threetrophi-level schemes. In marine intertidal com-
nunities the influential studies of Paine (1966) demon-
strated the importance of the strong coupling of higher
trophic levels to lower ones in the food web. Similar
results have emerged from experiments in freshwater
plankton communities (Carpenter and Kitchell 1984,
Carpenter et al. 1987). Mathematical developments
also suggest that community models involving only
two species as the basic building blocks may miss im-
portant ecological behavior. For example, results that
are much more complicated than those seen in two-
species models appeared in early theoretical studies
(Rosenzweig 1973, Wollkind 1976) of three-species, or
three-trophic-level, models based on local stability
analyses. These analyses considered only linear ap-
proximations to the nonlinear equations that ecologists
conventionally assume apply to these more complex
situations.

More importantly, two-species continuous time
models have only two basic patterns: approach to an
equilibrium or to a limit cycle (Segel 1984). In contrast,
simple discrete time models of even a single species
can exhibit chaotic behavior (e.g., May 1974, 1976).
But research of the last 15 yr (e.g., Gilpin 1979, Guck-
enheimer and Holmes 1983, Schaffer 1985) demonstra-
tes the very complex dynamics that can arise in
model systems (in continuous time) with three or more
species. The terms chaos, strange attractor, and fractal
are becoming familiar to many, if not all, ecologists
(Schaffer and Kot 1986a). The key feature of chaotic
dynamics is the sensitive dependence on initial con-
ditions. Even a very small change in initial conditions
can lead to different results. Indeed, the divergence
between results grows exponentially in time for vir-
tually all pairs of starting conditions. Several of the
early mathematical investigations of chaos were of eco-
logical models (e.g., May 1974). An investigation by
Gilpin (1979) showed that a system of one predator
and two competing prey can exhibit chaotic behavior.
Schaffer and collaborators (e.g., Schaffer and Kot 1985b)
have been especially persuasive in their view that chaos
may be a much more important phenomenon than
ecologists had earlier believed. In particular, a number
of simple ecological and epidemiological systems with
seasonality in contact rates unequivocally demonstrate
chaos (Schaffer and Kot 1986b). Schaffer and Kot
(1985a) and Olsen et al. (1988) show that measles in

1 Manuscript received 14 May 1990; accepted 20 August
1990; final version received 14 September 1990.
species \( X \)
\[ \]
species \( Y \)
\[ \]
species \( Z \)
\[ \]
\[ \text{FIG. 1. The feeding relationships in the food chain. Arrows go from prey to predators.} \]

New York, Baltimore, and Denmark may be a specific example of this behavior.

We investigate here perhaps the simplest three-species continuous time model, a three-level food chain. We demonstrate that, for biologically reasonable choices of parameters, chaotic dynamics result. These dynamics cannot arise in two-species models. We discuss the biologically significant implications that the presence of chaotic dynamics may have for more general food web models.

**Model Formulation**

Simple models for three-species food chains that incorporate a functional response in both of the consumer species have been studied previously (e.g., Rosenzweig 1973, Wollkind 1976). Following these efforts, we let \( X \) be the numbers of the species at the lowest level of the food chain, \( Y \) the numbers of the species that preys upon \( X \), and \( Z \) the numbers of the species that preys upon \( Y \). We use the letters \( X, Y, Z \) as both the names and variables. (We later introduce lower case letters as scaled measures of population size.) The food chain that this system models is illustrated diagrammatically in Fig. 1.

Incorporating “type II” saturating functional responses in both species (see Murdoch and Oaten 1975), the model takes the form:

\[
\begin{align*}
\frac{dX}{dT} &= R_0 \frac{X(1 - X/K_0)}{X} - C_1 F_1(X)Y \\
\frac{dY}{dT} &= F_1(X)Y - F_2(Y)Z - D_1 Y \\
\frac{dZ}{dT} &= C_2 F_2(Y)Z - D_2 Z
\end{align*}
\]

(1)

with

\[
F_i(U) = A_i U/(B_i + U) \quad \text{for } i = 1, 2
\]

(2)

representing the functional response. Here \( T \) is time. The constant \( R_0 \) is the “intrinsic growth rate,” and the constant \( K_0 \) is the “carrying capacity” of species \( X \). The constants \( C_1^{-1} \) and \( C_2 \) are conversion rates of prey to predator for species \( Y \) and \( Z \), respectively; \( D_1 \) and \( D_2 \) are constant death rates for species \( Y \) and \( Z \), respectively. The constants \( A_i \) and \( B_i \), for \( i = 1, 2 \) parametrize the saturating functional response; \( B_i \) is the prey population level where the predation rate per unit prey is half its maximum value.

The model we have just specified has 10 parameters, which makes analysis difficult. To reduce the number of parameters and to determine which combinations of parameters control the behavior of the system, we nondimensionalize the system (see the discussion in Lin and Segel 1974 or Nisbet and Gurney 1982). We choose

\[
\begin{align*}
x &= X/K_0, \\
y &= C_1 Y/K_0, \\
z &= C_2 Z/(C_2 K_0), \\
t &= R_0 T.
\end{align*}
\]

(3)

Making these substitutions and simplifying yields the following system of equations, where the variables \( x, y, z \) are now scaled (nondimensional) measures of population size, and \( t \) is a new (nondimensional) time variable. We obtain:

\[
\begin{align*}
\frac{dx}{dt} &= x(1 - x) - f_1(x)y \\
\frac{dy}{dt} &= f_1(x)y - f_2(y)z - d_1 y \\
\frac{dz}{dt} &= f_2(y)z - d_2 z
\end{align*}
\]

(4)

with

\[
f_i(u) = a_i u/(1 + b_i u).
\]

(5)

The six nondimensional parameters in terms of the original parameters are listed in Table 1.

**Analysis and Results**

The only choice for investigating the global dynamical behavior of the system (Eq. 4) is numerical integration. (A stability analysis and determination of Hopf bifurcations for this system is a relatively straightforward procedure but would not shed light on the global behavior we are interested in.) We employed a package developed by Hindmarsh (1980) that implements an algorithm due to Gear. Our choice of parameters was guided by two factors: first, we wanted to investigate biologically reasonable food chains, and second, we wanted to determine if chaotic dynamics were likely. Accordingly, we chose parameters for which the natural time scale of the interaction between \( Y \) and \( Z \), i.e., at the higher trophic levels, was substantially longer than that between \( X \) and \( Y \), that is, \( d_i \) much larger than \( d_i \). Further, one of the ways to generate chaos is to “periodically force” nonlinear systems that

| Table 1. Nondimensional parameters and values of the parameters used in the simulations. |
|----------------------------------|-------------------------------|----------------------|
| Nondimensional parameters | Dimensional parameters | Parameter values used in the simulations |
| \( a_1 \) | \((K_0 A_1)/(R_4 B_4)\) | 5.0 |
| \( b_1 \) | \(K_0/B_1\) | varied from 2.0 to 6.2 |
| \( a_2 \) | \((C_1 A_1 K_0)/(C_1 R_0 B_3)\) | 0.1 |
| \( b_2 \) | \(K_0/(C_2 B_3)\) | 2.0 |
| \( d_1 \) | \(D_1/R_0\) | 0.4 |
| \( d_2 \) | \(D_1/R_0\) | 0.01 |
already exhibit limit cycle behavior. We chose parameter values that would lead to cycling in the pair of species $X$ and $Y$, with $Z$ absent, and also, with $X$ constant, the pair $Y$ and $Z$. The values of the parameters chosen using these guidelines are listed in Table 1. Since the parameter space is large, we concentrated our investigations on varying $b_1$, holding the other parameters fixed. Earlier investigations (e.g., Murdoch and Oaten 1975) showed that the half saturation constant, which is proportional to $b_1^{-1}$, was a key parameter in determining stability in predator–prey models. As we demonstrate below in this section, for different values of $b_1$, the system (Eq. 4) exhibited stability, limit cycle behavior, and chaos.

Our initial investigations consisted of letting the system run for 10,000 time steps, and examining only the last 5000 time steps to eliminate transient behavior. We studied the behavior of the system by examining plots of each species against time, as well as a three-dimensional phase plot (eliminating the explicit dependence on the time variable) of all three species against each other. Dynamics that have the irregular behavior suggestive of chaos are illustrated in Fig. 2. Note that this irregular behavior, e.g., varying number of secondary maxima between primary maxima for species $X$ and $Y$, is not the result of a transient, but represents the behavior on the attractor. (An attractor is the [possibly very complex] smallest set of points in three dimensions [the numbers of the three species] that is approached from nearby initial conditions.) The attractor in Fig. 2D resembles the surface of an upside-down teacup, although the solutions of the system (Eq. 4) do not lie on a surface.

The dynamics within the attractor are given roughly as follows. Starting in the “handle” of the “teacup,” the system moves to the wide part of the teacup and then spirals along the teacup to the narrow end, entering the handle again. In terms of the species behavior, the top predator $Z$ crashes, allowing wide swings in the population levels of $X$ and $Y$. As $Z$ increases in numbers, the swings in $X$ and $Y$ become damped, until $Z$ causes the levels of $Y$ to crash. This leads to a crash in $Z$, and an outbreak in $X$, starting the process again. The sequence of events, in terms of species numbers, always follows the same general pattern. What is unpredictable is the timing. One way to express this is that the time between crashes of species $Z$ varies in an erratic fashion. Also, the number of peaks in species $Y$ between major crashes varies, and the population size at the peaks varies. The sensitive dependence of future dynamics on the current state, the signature of chaos, is apparent from the fact that all the trajectories in the “handle” of the “teacup” are very close together.

Thus a small change in initial conditions may lead to different dynamic behavior. We have illustrated this behavior by comparing the trajectories generated by very slightly different initial conditions for the set of parameter values that led to the chaotic dynamics il-

![Fig. 2. Chaotic dynamics for the model system. Trajectories are plotted for the parameter values in Table 1, with $b_1 = 3.0$. Plots of $x$ vs. time, $y$ vs. time, and $z$ vs. time are given in (A), (B), and (C), respectively. A three-dimensional phase plot is given in (D).](image-url)
Fig. 3. Divergence of trajectories when the model system exhibits chaotic dynamics. Trajectories of species $x$ are plotted for two different initial conditions (--- and ····), differing only by 0.01 in $x$ with $y$ and $z$ unchanged, for the parameter values in Table 1, with $b_1 = 3.0$.

illustrated previously in Fig. 2. One set of initial conditions is on the attractor, the other set differs from the first by changing $x$ by 0.01. As shown in Fig. 3, the numbers of species $X$ remain similar for the two initial conditions for a short time, but after two “crashes” of species $Z$ the two different initial conditions lead to dynamics that are essentially uncorrelated (although, of course, restricted to the attractor). Note that in Fig. 3 the choice of $R_0 \approx 1/d$, a common value for reproductive rates of lower trophic level organisms, would imply that after $\approx 300$ d (1 yr) the system would be indeterminate. Similarly, even a slight perturbation in species numbers, as would occur naturally, may lead to unpredictable results through time.

We then proceeded to a more systematic investigation of the dynamics, as a function of changes in $b_1$, by constructing a bifurcation diagram. As noted in Glass and Mackey (1988), a compelling diagnostic test for chaos is the appearance in a bifurcation diagram of one of the typical routes to chaos. We found a sequence of period doublings as exhibited by one-dimensional difference equations such as the logistic model that has been extensively studied by May (1974) and May and Oster (1976). To construct a bifurcation diagram we integrated the system numerically using the parameter values in Table 1. Letting the system approach the attractor for each value of $b_1$ used, we then plotted successive maxima of $z$ as a function of $b_1$. We used values of $b_1$ between 2.0 and 3.2, changing $b_1$ in steps of 0.01, and values of $b_1$ from 3.2 to 6.2, changing $b_1$ in steps of 0.1. We did this both by starting with the smaller value of $b_1$ and increasing $b_1$, and also by starting with the larger value of $b_1$ and decreasing $b_1$. The bifurcation diagrams are plotted in Fig. 4. (Note that for clarity in our figures we have eliminated points due to apparent second branches for $b_1$ between 2.6 and 3.2 arising solely from the appearance of a second local maxima in the cyclic dynamics of species $Z$, as illustrated in Fig. 2C.) The values of $b_1$ (e.g., $b_1 = 2.3$) for

which there are a small number of values of $z_{max}$ in the diagram represent limit cycle behavior, while the values of $b_1$ (e.g., $b_1 = 3.0$) for which the values of $z_{max}$ form approximately an interval represent chaos. We see evidence in Fig. 4A and in more detail in Fig. 4C for period doubling leading to chaos, both as $b_1$ is increased, and as it is decreased. This is observed when: $b_1$ is increased from 2.3 to 2.4, $b_1$ is decreased from 2.55 to 2.45, $b_1$ increased from 2.437 to 2.55, and $b_1$ is increased from 2.93 to 2.96.
Also, from Fig. 4C we can deduce that for some values of \( b_i \), there are two separate attractors, one chaotic and one which is a limit cycle. This occurs both for \( b_i \) lying between 2.45 and 2.48 and between 2.53 and 2.56. Thus, the presence of chaotic dynamics may depend on the initial conditions, with some initial conditions leading to a limit cycle, and some leading to chaos.

Most striking, we see that the asymptotic behavior of the system is extremely sensitive to the value of \( b_1 \). Over ecological time scales, a population level parameter like \( b_1 \), a component of the predation rate per unit prey, which, in fact, is a composite of various individual responses, would certainly be expected to vary, perhaps significantly. From Fig. 4, it is easy to see that even small variations in \( b_1 \) may cause a shift from limit cycles to chaos or vice versa.

Although we do not present the results here, we have also examined the behavior of this system for other values of the parameter \( b_2 \). We found chaos for values of \( b_2 \) other than the one (\( b_2 = 2.0 \)) we used in the majority of our work; moreover, chaos appears more likely for larger values of \( b_2 \), similar to the dependence on \( b_1 \).

We further examined the behavior of the system for some selected values of \( b_1 \) by constructing a Poincaré map (Fig. 5). For our system, we chose a Poincaré section corresponding to a plane with \( z \) constant, in the “handle” of the teacup, where the trajectories pass through the plane from above. Thus, the Poincaré section is a set of \( x \) and \( y \) values. Moreover, for our system, as exhibited in the Fig. 5, the set of points on the Poincaré section is nearly one dimensional, i.e., it is very close to a line. Thus, we can approximate the dynamics of the Poincaré map by considering only one variable. We therefore considered \( x(n + 1) \) as a function of \( x(n) \), where \( x(n) \) is the value of \( x \) at the \( n \)th intersection of the trajectory with the Poincaré section.

(Not that we could just as easily have used the \( y \) variable.)

We illustrate in Fig. 5 these Poincaré maps for two different values of \( b_1 \) (3.0 and 6.0) for which the bifurcation diagram suggested that the behavior would be chaotic. Note that the slope of the function relating \( x(n + 1) \) to \( x(n) \) in these Poincaré maps is large in magnitude, another diagnostic feature of chaos. Recall that the quadratic map and the discrete time logistic function are single humped functions (e.g., May 1976, Guckenheimer and Holmes 1983), which lead to chaotic behavior if the functions are steep enough, i.e., if the absolute value of the slope of the function is large enough on average. However, the behavior is more complex in our food chain because there is more than a single hump in the Poincaré map. The presence of a multimodal Poincaré map indicates a variety of interesting dynamical properties for the differential equations (see, e.g., May 1979, Skjolding et al. 1983), which we will not explore further here.

**ECOLOGICAL IMPLICATIONS**

We have shown that chaos is possible for a simple, biologically reasonable, continuous-time, food chain model. The specific saturating forms for the consumption of prey by predators (i.e., “Type II” functional and numerical responses) are the most commonly chosen representations. Type II functional responses have been extensively used in ecological models since their introduction by Holling (1959). Since that time, applications include (but are not limited to): arthropod models (Murdoch and Oaten 1975, Hassell 1978) and models of phytoplankton competing for nutrients (Taylor and Williams 1975, Waltman et al. 1980, Smouse 1981, Tilman 1982, Powell and Richerson 1985). Further, these forms were used in the early mechanistic models of marine food chains (Steele 1974) and still form the basis for such applications (Frost 1987). Note that Table 1 and Fig. 2 show that the chaotic regime includes the region where \( b_1 \) is not far from unity. This is precisely the region of greatest biological interest. If \( b_1 \) and \( b_2 \) are much greater than unity, then the saturating Type II forms are close to constant, and the predator saturation effect (i.e., predator grazing is saturated) is eliminated. Conversely, when \( b_1 \) is small compared to one, then the Type II forms are nearly linear, and no saturation effect is seen. It is precisely the regions where “the biology” becomes important, i.e., when \( b_1 \) is \( \approx 1 \) and predators begin to saturate, that the nonlinearities of \( f_1(x) \) and \( f_2(y) \) in Eq. 5 generate chaos.

Our model suggests that chaotic behavior may be much more common in natural systems with interacting producers and consumers (predators and prey) than Hassell et al. (1976) predicted on the basis of a single-species discrete time models. It is our interpretation that chaos ultimately arises in this food chain model because of the tendency for predator–prey systems to oscillate. One predator–prey subsystem, for concreteness say \( X \) and \( Y \), oscillates at one frequency, while another, \( Y \) and \( Z \), oscillates at a different frequency; the frequencies are determined by the model parameters. In particular, the interaction at the higher trophic levels has a longer natural period because the average lifetime of the top predators is longer than the average lifetime of the consumers at the lower trophic levels. (Our simulations reflect this.) The two systems are (nonlinearly) coupled through species \( Y \) because the predator in one is the prey in the other. We conjecture that when the period of one oscillation is not some multiple of the other frequency (i.e., the frequencies are incommensurate) chaos arises, in a manner similar to the occurrence of chaos in periodically forced oscillations. Food webs depict a complex net of (nonlinearly) coupled producer–consumer interactions; accordingly, one should not be surprised to find many subsystems within a food web going through the oscillations that are a common feature of all predator-
prey systems. It seems unlikely that the frequencies of all the linked subsystems will be commensurate. Accordingly, one expects that at least some, perhaps most, of the linked predator–prey subsystems may be simultaneously undergoing chaotic oscillations.

It is instructive to compare this view with the threespecies study (a predator consuming two competing prey) of Gilpin (1979), in which chaotic behavior was identified. Typically, one does not associate oscillations with competition models based on results from two-species Lotka–Volterra competition (e.g., May 1973). However, once three or more species are allowed, oscillations can occur (May and Leonard 1975, Powell and Richerson 1985). We conjecture that food webs containing a number of competing species can also "go chaotic" in the same way as our consumer–producer food chain does.

**Consequences for food web models**

What are the implications of our results for food web models? First, our conclusions question the conventional wisdom that chaos must be rare in nature. Whenever consumers and producers are undergoing oscillations, chaotic oscillations, as we have described here, may be a strong possibility for realistic parameter values. Second, chaotic behavior, as Fig. 2 shows, need not lead to an erratic and unpatterned trajectory in time that one might infer from the usual (not mathematical) connotation of the word "chaos." Rather, the term "regular oscillations" better describes the curves.
of $x, y$, and $z$ vs. $t$ as seen in Fig. 2. As emphasized by Schaffer, detecting chaos in natural populations may be very difficult. Third, the time scales under consideration are very important. Over short time scales, say a few oscillation periods, the behavior is fairly regular. However, over many periods of oscillation the effects of sensitivity to initial conditions and unpredictability become much more important.

If a generalization from a food web model depends critically upon behavior after a long time, then the role of chaos may be much more crucial. For example, when a model formulation suggests that chaotic behavior is a strong possibility, then one might be skeptical about conclusions drawn from linear stability analyses around equilibria. This includes conclusions drawn on the basis of “return time” arguments (Pimm 1982, 1984), since “return times” are the inverses of eigenvalues of Jacobian matrices evaluated at equilibria. Moreover, the existence of chaotic behavior may depend very delicately on the exact form that terms in equations take. For example, we have not included any feedback effects of recycling through activities of the predators upon the prey. We have not examined solutions to our model suitably modified to account for these considerations. We do not know with certainty that chaotic behavior will be found.

For what ecological questions is chaotic behavior important? The answer depends on the number of species, the kinds of interactions, and the time scale. Results of our and earlier investigations certainly suggest that much more complex behavior will be seen in models of simple three-species food chains than in any two-species models. Nonetheless, a great many important results can be obtained on the basis of behavior in the nonchaotic region of parameter space. Moreover, it is much easier to develop intuition from the simpler two-species models. The geometry of strange attractors in three dimensions is exceedingly complicated (Guckenheimer and Holmes 1983). The addition of more species that “inhabit” a food web can only make analysis of models more challenging.

Acknowledgments

We profited from comments by S. Vail and C. L. Hom on earlier drafts. We are particularly indebted to W. Schaffer who pointed out an error in our earlier interpretation, and suggested the use of the bifurcation diagram and the Poincaré map. We appreciate his encouragement and enthusiasm. We appreciate the reviews of M. Kot and an anonymous referee. A. Hastings was supported by grant DE-FG03-89ER60886/A000 from the Ecological Research Division, Office of Health and Environmental Research, United States Department of Energy. This support does not constitute an endorsement of the views expressed here. T. Powell thanks NSF for support to project SUPER (NSF OCE 86-13749).

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