

Chaos in One-Predator, Two-Prey Models: General Results from Bifurcation Theory

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ABSTRACT

We show that chaos is the expected outcome of the dynamics of a class of one-predator, two-prey models. This generalizes results of previous studies of Lotka–Volterra models. We examine dynamics near a state in which a high codimension bifurcation occurs, considering all possible nearby dynamics in both parameter and state space by doing an unfolding analysis of the model's normal form. In this way, we argue that realistic predator–prey systems that can be closely modeled by the general models discussed here must exhibit chaotic dynamics.

1. INTRODUCTION

Following early work by May [6, 7], ecologists have searched for chaotic dynamics in both field and theoretical investigations [4]. In theoretical investigations, the primary approach has been to specify a particular model and then look for chaotic dynamics for “reasonable” parameter values [4]. This program has proceeded from May's [6] initial investigations of discrete-time single-species models through a succession of more complex models, including continuous-time models of simple three-species food webs such as the one-predator, two-prey

model investigated by Gilpin [1] or the three-species food chain model investigated by Hastings and Powell [3].

The Lotka–Volterra one-predator, two-prey model first investigated by Gilpin [1] has received further attention. Gilpin demonstrated the existence of chaos by looking at numerical solutions for particular parameter values. More complete numerical studies of this model, including Poincaré sections, were performed by Schaffer and Kot [8]. More recently, Schnabl et al. [9] performed even more extensive numerical studies and constructed bifurcation diagrams showing how the solutions of Gilpin and Schaffer connected up with other chaotic solutions of the same model (in a different form) also studied by Vance [10].

Yet the studies of this one-predator, two-prey model suffer from a lack of generality, which is endemic to the general research program of investigating specific models for reasonable parameter values. Even the use of bifurcation diagrams typically covers only a subset of the high dimensional space of all possible parameter values. Left unanswered is the extent to which the existence of chaotic dynamics depends on the particular model chosen as well as on the particular parameter combinations chosen.

In [5], we took one step in the direction of showing that chaotic dynamics are a more general consequence of simple food web interactions using a bifurcation analysis to show that chaotic dynamics are expected in three-species food chain models. This analysis consisted of extending the work of Guckenheimer and Holmes [2] to account for constraints imposed by the biology and showing the presence of heteroclinic trajectories in the rz plane of a cylindrical coordinate system in an unfolding near the bifurcation point where the two lower trophic levels (represented by r in the polar coordinate plane) go through a Hopf bifurcation and the growth rate of the top trophic level (represented by z) changes from negative to positive. The existence of this heteroclinic trajectory implies the existence of chaotic solutions. (More precisely, the heteroclinic trajectory implies the existence of horseshoes, which implies the existence of, at least, chaotic transient behavior and invariant chaotic sets. True chaotic behavior is a likely outcome.)

Our approach in the current paper is to extend this way to analyzing chaotic dynamics to the one-predator, two-prey model. Our goal is to demonstrate that chaotic dynamics in this simple food web are expected and do not depend on the specifics of the model chosen. We proceed by embedding the Lotka–Volterra model initially studied by Gilpin [1] in a more complex model that allows for more realistic nonlinear functional responses. In [5] we pointed out that by examining a system in a structurally unstable state (i.e., a state that will undergo radical qualitative change with any minute change in the parameters), the researcher can determine the realm of possible local dynamics without a complete

study of the dynamic variables. To this end, we now seek degenerate states of our model that are attainable by the real system. If the real system can attain a degenerate state, one must consider all possible perturbations from this degenerate state. To do this, we first transform the model to a standardized and simplified form called its *normal form*. This analysis is a local one centered about a degenerate equilibrium point, and the normal form is a model whose vector field is represented by a Taylor series expanded about the equilibrium. Finally, we introduce terms (in the power series) originally absent in the normal form but still biologically viable in order to attain any possible state that a real system could be expected to attain. Since such an analysis had not been carried on this otherwise extensively studied model, we set out to complete the analysis. We also explain why the embedding is necessary to complete the analysis. We then use the same bifurcation analysis approach we used earlier (see [5]) to show that in this more general setting, chaotic dynamics are the expected result.

2. THE LOTKA-VOLTERRA MODEL

Gilpin [1] and later Schaffer and Kot [8] studied the one-predator, two-prey Lotka-Volterra type model,

$$\frac{dN_i}{dT} = N_i \left(R_i - \sum_{j=1}^3 \alpha_{ij} N_j \right), \quad i = 1, 2, 3, \quad (1)$$

where N_1 and N_2 represent prey while N_3 is the predator and

$$\alpha_{ij} > 0 \quad \text{for } i = 1, 2; \quad j = 1, 2, 3; \\ \alpha_{ij} < 0 \quad \text{for } i = 3; \quad j = 1, 2; \quad (2a)$$

$$\alpha_{33} = 0; \quad (2b)$$

and

$$R_i > 0 \quad \text{for } i = 1, 2; \quad R_3 < 0. \quad (2c)$$

They reported that quasi-periodic behavior as well as chaotic dynamics could occur. Schnabl et al. [9] later studied the same model (but presented in a different form earlier by Vance [10]) much more extensively, again using most of the usual indicators of chaotic dynamics.

In our approach, we find it useful to first rescale the Gilpin model to reduce the dimension of the parameter space. The resulting system is shown below with the change of variable given in Table 1.

$$\dot{n}_1 = n_1(r_1 - a_{11}n_1 - a_{12}n_2 - n_3), \quad (3a)$$

$$\dot{n}_2 = n_2(r_2 - a_{21}n_1 - a_{22}n_2 - a_{23}n_3), \quad (3b)$$

$$\dot{n}_3 = n_3(-1 + n_1 + n_2). \quad (3c)$$

TABLE 1

Values of Rescaled Parameters and Variables in Gilpin's Model Using Gilpin's Choices of Parameters as an Example*

Rescaled parameters	Original parameters	Numerical values
a_{11}	$-\alpha_{11}/\alpha_{31}$	0.2
a_{12}	$-\alpha_{12}/\alpha_{32}$	2.0
a_{21}	$-\alpha_{21}/\alpha_{31}$	0.3
a_{22}	$-\alpha_{22}/\alpha_{32}$	2.0
a_{23}	α_{23}/α_{13}	0.1
r_1	$-R_1/R_3$	1.0
r_2	$-R_2/R_3$	1.0
n_1	$(\alpha_{31}/R_3)N_1$	$200N_1$
n_2	$(\alpha_{32}/R_3)N_2$	$2000N_2$
n_3	$-(\alpha_{13}/R_3)N_3$	$100N_3$
t	R_3T	T

* $\alpha_{11} = \alpha_{12} = \alpha_{22} = \alpha_{23} = 0.001$; $\alpha_{21} = 0.0015$; $\alpha_{13} = 0.01$; $\alpha_{31} = -0.005$; $\alpha_{32} = -0.0005$; $\alpha_{33} = 0.0$; $R_1 = R_2 = -R_3 = 1.0$.

All parameters are necessarily nonnegative by this rescaling. We should point out that there are many possible useful rescalings. We chose this one to best simplify the predator equation and later simplify some algebra in the analysis. We next present some results of a basic stability analysis of this model as a preliminary to the bifurcation analysis.

3. ANALYSIS OF THE GILPIN MODEL

3.1. PRELIMINARY ANALYSIS

We begin our analysis with a discussion of the equilibria and their stability. System (3) has seven equilibria:

$$(0, 0, 0), \quad (4)$$

$$(0, r_2/a_{22}, 0), \quad (5)$$

$$(r_1/a_{11}, 0, 0), \quad (6)$$

$$(0, 1, (r_2 - a_{22})/a_{23}), \quad (7)$$

$$(1, 0, r_1 - a_{11}), \quad (8)$$

$$\left(\frac{a_{22}r_1 - a_{12}r_2}{a_{11}a_{22} - a_{12}a_{21}}, \frac{a_{11}r_2 - a_{21}r_1}{a_{11}a_{22} - a_{12}a_{21}}, 0 \right), \quad (9)$$

and

$$\left(\frac{a_{12}a_{23} - a_{22} - a_{23}r_1 + r_2}{a_{21} - a_{22} - a_{11}a_{23} + a_{12}a_{23}}, \frac{a_{21} - a_{11}a_{23} + a_{23}r_1 - r_2}{a_{21} - a_{22} - a_{11}a_{23} + a_{12}a_{23}}, \right. \\ \left. \frac{a_{11}a_{22} - a_{12}a_{21} + (a_{21} - a_{22})r_1 + (a_{12} - a_{11})r_2}{a_{21} - a_{22} - a_{11}a_{23} + a_{12}a_{23}} \right). \quad (10)$$

The most interesting behavior occurs at the nontrivial equilibria, so we are most interested in studying the fixed point in (10). However, the analysis can be greatly simplified by recognizing that the nontrivial equilibrium in (10) arises (by varying the parameters) from the more trivial equilibria. For example, setting

$$a_{21} - a_{22} = 1, \quad a_{12} - a_{11} = 0, \quad (11)$$

(8) and (10) are equivalent. Thus, we can just as easily study the behavior near (10) by studying the behavior near (8) when the equilibria split. We do precisely that.

The Jacobian matrix corresponding to equilibrium (8) is of the form

$$\begin{pmatrix} -a_{11} & -a_{12} & -1 \\ 0 & r_2 - a_{23}(r_1 - a_{11}) - a_{21} & 0 \\ r_1 - a_{11} & r_1 - a_{11} & 0 \end{pmatrix}. \quad (12)$$

We must have

$$a_{11} = 0 \quad (13)$$

and

$$r_2 = a_{21} + a_{23}r_1 \quad (14)$$

so that the eigenvalues of the Jacobian all have zero real part, that is, so that the equilibria (8) and (10) coalesce. We will focus on this case in the rest of our analysis.

3.2. BIFURCATION ANALYSIS

With the restrictions (13) and (14), we can find a normal form that can conveniently be transformed to cylindrical coordinates by the usual transformation,

$$x = r \cos \theta; \quad y = r \sin \theta; \quad z = z. \quad (15)$$

We can compute the normal form to any desired degree, but degree 3 is sufficient for our analysis. In cylindrical coordinates, the normal form is

$$\begin{aligned}\dot{r} &= \gamma_1 r z + \gamma_2 r z^2, \\ \dot{z} &= \gamma_3 z^2 + \gamma_4 z^3,\end{aligned}\tag{16}$$

where the azimuthal term (not shown) can be omitted since all velocities are independent of θ in normal form. The reader should note that the linear terms are absent since equilibrium (8) (now the origin) is degenerate. Comparing the normal form to the normal form for an arbitrary model sharing the same Jacobian (again disregarding the azimuthal term and writing to degree 3),

$$\begin{aligned}\dot{r} &= a_1 r z + a_2 r^3 + a_3 r z^2, \\ \dot{z} &= b_1 r^2 + b_2 z^2 + b_3 r^2 z + b_4 z^3\end{aligned}\tag{17}$$

(see Wiggins [11]), we note the absence of three terms in (16). The r^2 term missing in the z -velocity equation must be absent because $z = 0$ is invariant. However, the absence of the other terms is simply a consequence of the relative simplicity of this model. As we show next, by using nonlinear functional responses, all possible terms are present in the normal form.

Due to the absence of the r^3 term in the r -velocity equation, we are likely to have a highly degenerate bifurcation at this fixed point for the chosen region in parameter space. We knew from the restrictions that gave all of the eigenvalues zero real part that the bifurcation has codimension greater than or equal to 2. Furthermore, previous experience tells us that an r^3 term in the r -velocity equation accounts for complicated dynamics in the original system, while without it complicated dynamics cannot be accounted for (without considering higher order terms.) Thus, we expect that the bifurcation is at least codimension 3 (using the definition given by Wiggins [11]).

The usual next step in a normal form analysis is to perturb the normal form by introducing additional terms. By doing so, we hope to determine all of the possible local behavior of the model. To ease the job of finding a perturbation, we generalize our original system by using Type II rather than linear functional responses. The generalized model is

$$\frac{dN_1}{dT} = R_1 N_1 - \frac{R_1}{K_1} N_1^2 - \alpha_{12} N_1 N_2 - \frac{\alpha_1 N_1 N_3}{1 + \beta_1 N_1}, \tag{18a}$$

$$\frac{dN_2}{dT} = R_2 N_2 - \frac{R_2}{K_2} N_2^2 - \alpha_{21} N_1 N_2 - \frac{\alpha_2 N_2 N_3}{1 + \beta_2 N_2}, \tag{18b}$$

$$\frac{dN_3}{dT} = \frac{C_1 \alpha_1 N_1 N_3}{1 + \beta_1 N_1} + \frac{C_2 \alpha_2 N_2 N_3}{1 + \beta_2 N_2} - D_1 N_3, \tag{18c}$$

which becomes

$$\dot{x} = x - x^2 - a_{12}xy - \frac{a_1xz}{1+b_1x}, \quad (19a)$$

$$\dot{y} = \rho y - ky^2 - a_{21}xy - \frac{a_2yz}{1+b_2y}, \quad (19b)$$

$$\dot{z} = \frac{a_1xz}{1+b_1x} + \frac{a_2yz}{1+b_2y} - mz, \quad (19c)$$

where the change of variable is given in Table 2.

We focus on the fixed point corresponding to (8),

$$(\bar{x}, 0, \bar{z}) = \left(\frac{m}{a_1 - b_1m}, 0, \frac{a_1 - b_1m - m}{(a_1 - b_1m)^2} \right), \quad (20)$$

where $a_1 - b_1m - m \geq 0$. The Jacobian matrix evaluated at this fixed point is of the form

$$\begin{pmatrix} j_{11} & j_{12} & j_{13} \\ 0 & j_{22} & 0 \\ j_{31} & j_{32} & 0 \end{pmatrix}, \quad (21)$$

TABLE 2

Values of Rescaled Parameters and Variables in the Generalized Model*

	a_{12}	a_{21}	a_1	a_2	b_1	b_2	
	$\frac{\alpha_{12}C_1K_1}{C_2R_1}$	$\frac{\alpha_{21}K_1}{R_1}$	$\frac{\alpha_1C_1K_1}{R_1}$	$\frac{\alpha_2C_1K_1}{R_1}$	β_1K_1	$\frac{\beta_2C_1K_1}{C_2}$	
(a)	1	1.5	5	0.5	0	0	
(b)	1	1.5	5	0.5	1.1	0	
	ρ	k	m	x	y	z	t
	$\frac{R_2}{R_1}$	$\frac{C_1K_1R_2}{C_2K_2R_1}$	$\frac{D_1}{R_1}$	$\frac{N_1}{K_1}$	$\frac{C_2}{C_1K_1}N_2$	$\frac{N_3}{C_1K_1}$	R_1T
(a)	1	1	1	0.001 N_1	0.001 N_2	0.002 N_3	T
(b)	1	1	1	0.001 N_1	0.001 N_2	0.002 N_3	T

*The rescaled model is equivalent to the Gilpin model if $R_1 = R_2 = D_1 = 1$; $K_1 = K_2 = 1000$; $\alpha_{12} = 0.001$; $\alpha_1 = 0.01$; $\alpha_{21} = 0.0015$; $\alpha_2 = 0.001$; $C_1 = C_2 = 0.5$; and (a) $\beta_1 = \beta_2 = 0$. However, in order to study the fixed point of interest for the generalized model, we must set $\beta_1 > 0.001$. In (b), we set $\beta_1 = 0.0011$ as an example.

which has the corresponding eigenvalues

$$\lambda_1 = j_{22}; \quad \lambda_2, \lambda_3 = \frac{j_{11} \pm \sqrt{j_{11}^2 + 4j_{13}j_{31}}}{2}. \quad (22)$$

In particular,

$$j_{11} = \frac{b_1}{a_1} - \frac{m(a_1 + b_1 m)}{a_1(a_1 - b_1 m)}, \quad j_{12} = \frac{-a_{12}m}{a_1 - b_1 m}, \quad j_{13} = -m, \quad (23a)$$

$$j_{22} = \frac{a_2 m}{(a_1 - b_1 m)^2} - \frac{a_2 + a_{21}m}{a_1 - b_1 m} + \rho, \quad (23b)$$

$$j_{31} = \frac{a_1 - b_1 m - m}{a_1}, \quad (23c)$$

$$j_{32} = \frac{a_2(a_1 - b_1 m - m)}{(a_1 - b_1 m)^2}. \quad (23d)$$

Thus, in order to attain a bifurcation of at least codimension 2, we must set

$$j_{11} = 0, \quad j_{22} = 0. \quad (24)$$

In terms of the parameters, condition (24) becomes

$$m = \frac{a_1(b_1 - 1)}{b_1(b_1 + 1)}, \quad \rho = \frac{2a_1a_{21}(b_1 - 1) + a_2(b_1 + 1)^2}{4a_1b_1}. \quad (25)$$

After computing the normal form subject to (25), we get (disregarding the azimuthal term) the following two equations in cylindrical coordinates,

$$\begin{aligned} \dot{r} &= \gamma_1 r z + \gamma_2 r z^2 + \gamma_3 r^3, \\ \dot{z} &= \gamma_4 z^2 + \gamma_5 r^2 z + \gamma_6 z^3, \end{aligned} \quad (26)$$

where the γ 's are complicated nonlinear functions of the parameters a_1 , a_2 , a_{12} , a_{21} , b_1 , b_2 , and k . Only γ_3 can easily be seen to be negative. The other parameters apparently take either sign depending on parameter values. The reader should note that (26) is in the same form as the general normal form (17) with the exception of the r^2 term in the z -velocity equation. As already mentioned, the r^2 term is absent because of the biological constraint that extinct populations remain so. Thus, by perturbing the original model (1) by nonlinear functional responses, we can see which higher order terms to consider when unfolding system

(16). We rescale (26) again by letting

$$u = \alpha r; \quad v = \beta z \quad (27)$$

and then choosing $\beta = \gamma_1$ and $\alpha^2 = -\gamma_3$. This yields the rescaled normal form

$$\begin{aligned} \dot{u} &= uv + auv^2 - u^3, \\ \dot{v} &= bv^2 + cu^2v + dv^3. \end{aligned} \quad (28)$$

It is easy to choose a two-parameter unfolding by rescaling the linear part of the system near the bifurcation. The unfolded normal form is

$$\begin{aligned} \dot{u} &= \mu_1 u + uv + auv^2 - u^3, \\ \dot{v} &= \mu_2 v + bv^2 + cu^2v + dv^3, \end{aligned} \quad (29)$$

which is equivalent to the system in [5] where we showed that chaotic dynamics will typically occur near the bifurcation. In particular, the planar system (29) undergoes global bifurcations with both heteroclinic and homoclinic orbits near (in phase-parameter space) the degenerate equilibrium (20). By reconsidering the azimuthal equation, we find that homoclinic and heteroclinic orbits result in horseshoe dynamics for the full three-dimensional system. In fact, system (29) has lots of interesting dynamics near the degenerate equilibrium (20). There are five fixed points arbitrarily close to the origin in the rz plane [corresponding to (20)]: $(r_0, 0), (r_1, z_1), (r_2, z_2), (0, z_3), (0, z_4)$. The fixed points off the r axis correspond to limit cycles, while the fixed point on the z axis corresponds to a nontrivial equilibrium for the full system. Pitchfork, transcritical, and saddle-node bifurcations all occur for planar system (29), implying all of the same for the full system plus bifurcations of limit cycles. In addition, Hopf bifurcations can occur in the planar system, resulting in quasi-periodic behavior for the full system. These results were reported in greater detail in [5].

Since the results come from analyzing the normal form, we recognize that these results follow for numerous models that share the same normal form. Great care should be taken in determining what values of γ_i are feasible, and thus in determining which behavior predicted by the normal form analysis can be attained by the original model. However, we stress that due to limitations of the mathematical model (e.g., it does not account for spatial structure, genetics, seasonality, etc.), it is possible that the real system may in fact exhibit behavior predicted by the normal form analysis regardless of whether the model does. The idea behind our argument is that if the real system being modeled can attain a state near the degenerate equilibrium, then the real system is just a perturbation of the model, and thus the real system must exhibit at least

a subset of the behaviors exhibited by the unfolding analysis. Thus, not only can the generalized Gilpin model including nonlinear functional responses exhibit chaos, but in fact one expects that other similar models also will exhibit chaotic dynamics.

4. NUMERICAL RESULTS

By using a bifurcation diagram, we can show that the chaotic solutions that we predict based on the normal form analysis occur near the high codimension bifurcation for the model with nonlinear functional responses. Figure 1 shows a bifurcation diagram for model (19). We set $b_2 = 0$ and chose b_1 as the bifurcation parameter since $b_1 = 0$ yields Gilpin's model. The diagram shows local maxima in z for b_1 between 0 and 3.3. Due to the positivity constraint on the biologically mean-

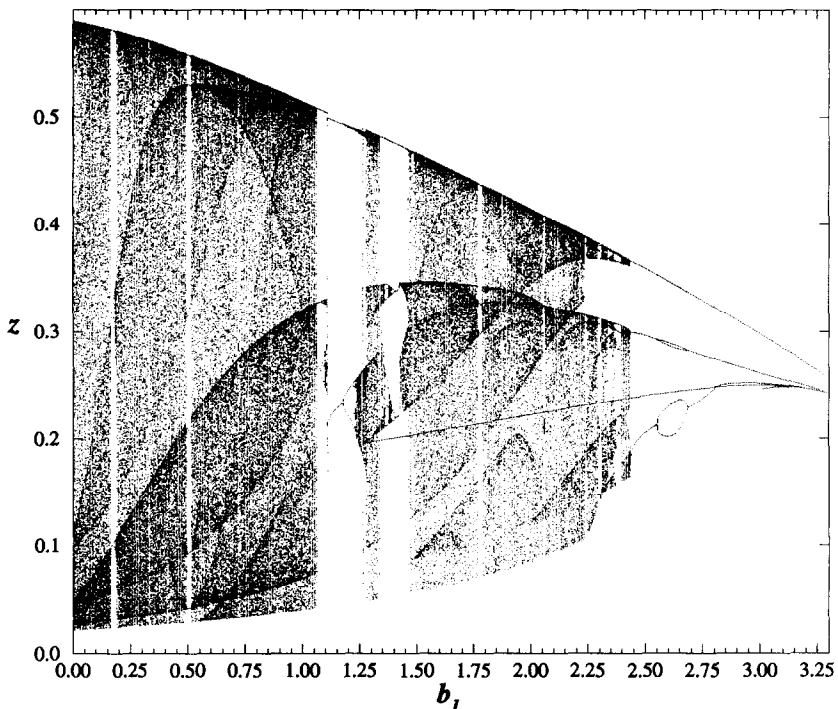


FIG. 1. Bifurcation diagram for model (18), using b_1 as the bifurcation parameter. We graph local maxima of z versus b_1 .

ingful parameters, Equation (25) implies that $b_1 > 1$ in order for the high codimension bifurcation to occur. We see that there is still the possibility of finding a chaotic attractor here, but it diminishes with increasing b_1 . Of course, the bifurcation diagram does not represent dynamics at the high codimension bifurcation but instead near it. The dynamics at bifurcation are uninteresting.

There are a couple of important points to make regarding the bifurcation diagram in Figure 1. First and foremost, it gives yet another way to argue that Gilpin's model is chaotic. It is apparent from the diagram that except for a few visible period-doubling windows, small b_1 implies chaos. Second, using an unfolding analysis of the generalized Gilpin model also implies chaos, and we can see this in the diagram for $b_1 \geq 1$. Furthermore, the behavior for $b_1 \approx 1$ is qualitatively the same as for $b_1 = 0$.

The next point is a curious one. In [5] we showed how decreasing the functional response could drive a food chain into a chaotic state. In the generalized Gilpin model, we varied the same parameter in the functional response but found that when the functional response decreased, the system ultimately stabilized and ended up with a unique stable equilibrium. This apparent contradiction is explained upon closer examination. In the food chain model studied in [5], the functional response was of y on x . Decreasing y 's predation on x enabled x to grow to higher densities and amplified the xy oscillations. Meanwhile, a once relatively stable relationship z on y was offset by the change in the xy interaction. Meanwhile, in the generalized Gilpin model, the functional response in question is that of z on x . Thus, just as expected, we see a decrease in the relative maxima of z as b_1 increases (i.e., as the xz functional response decreases.) Furthermore, it is easy to show that when $z = 0$, there is a stable nontrivial equilibrium for x and y . Thus as z decreases, the stabilizing affect of the prey's interaction acts to stabilize the once chaotic system.

We should remark that since the unfolding analysis is centered at the fixed point (8) in which $y = 0$, changing b_2 had no effect on the model in the preceding analysis. On the other hand, it should be clear that both functional responses indeed play a role in the dynamics. Due to the parameter choices made by Gilpin [1], the functional response of z on x is more substantial than that of y on x . (Compare the ten-fold difference of a_1 and a_2 in Table 2.) As a result, it takes much greater changes in b_2 to have an effect similar to small changes in b_1 . So, while the yz predation relationship is not as sensitive to small changes in parameters as is the xz relationship, it is still important. We are not disregarding this importance, but instead we are simplifying our study

by recognizing the symmetry in the model and arbitrarily taking the xz relationship as our focus of study.

5. CONCLUSIONS

There are two simple three-species food webs that have been extensively studied by theoretical ecologists: a three-trophic-level food chain and the one-predator, two-prey web that is the subject of the analysis we present here. The results we present here show that the appearance of chaos (or more precisely, chaotic transients and chaotic invariant sets) in a one-predator, two-prey web does not depend critically on the choice of the model used to describe the dynamics. This result, coupled with the analogous result for food chains contained in [5], shows the plausibility of chaotic dynamics in simple food webs in general. Moreover, our work quickly shows combinations of parameter values (those near the bifurcation point) for which chaotic dynamics are likely.

Although the results we present here are phrased in terms of a food web with only three species, we can argue from these results about the plausibility of chaos in webs with more species. If we focus on parameter values where there is a simultaneous Hopf bifurcation and a saddle-node bifurcation corresponding to a change in the growth rate of a rare species from negative to positive, we again will be looking at a bifurcation of codimension greater than 1—in fact, a bifurcation whose linear part and unfolding will essentially be similar to those of the bifurcation analyzed here and in [5]. Thus, once again, we expect that chaotic dynamics will be present. Moreover, as the numerical work here and in [5] has shown, the chaotic solutions arising near the high codimension bifurcation point can exhibit all the dynamical possibilities that appear in the model, even for other parameter values.

The work presented here thus should add further support to the view expressed in Hastings et al. [4] that studies of ecological models have demonstrated the plausibility of chaos, justifying further detailed studies of time series from natural and experimental systems in order to determine how important chaos is in natural systems. In fact, our results imply that if chaos is not common in natural systems, we would require an explanation as to why the chaos that is apparently common in all but the simplest food web models is not reflected in nature.

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