生物数学资料选编

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SPIRAL CHAOS IN A PREDATOR-PREY MODEL

In a recent analysis of the role of predation on prey coexistence, Vance (1978) uncovered a trajectory he termed "quasi-cyclic." In this note, I comment on this behavior and refine its classification. Vance's model used the familiar, though still surprising, Lotka-Volterra equations:

$$\frac{1}{N_i}\frac{dN_i}{dt} = r_i - \sum_j \alpha_{ij} N_j \qquad i, j = 1\text{-}3.$$
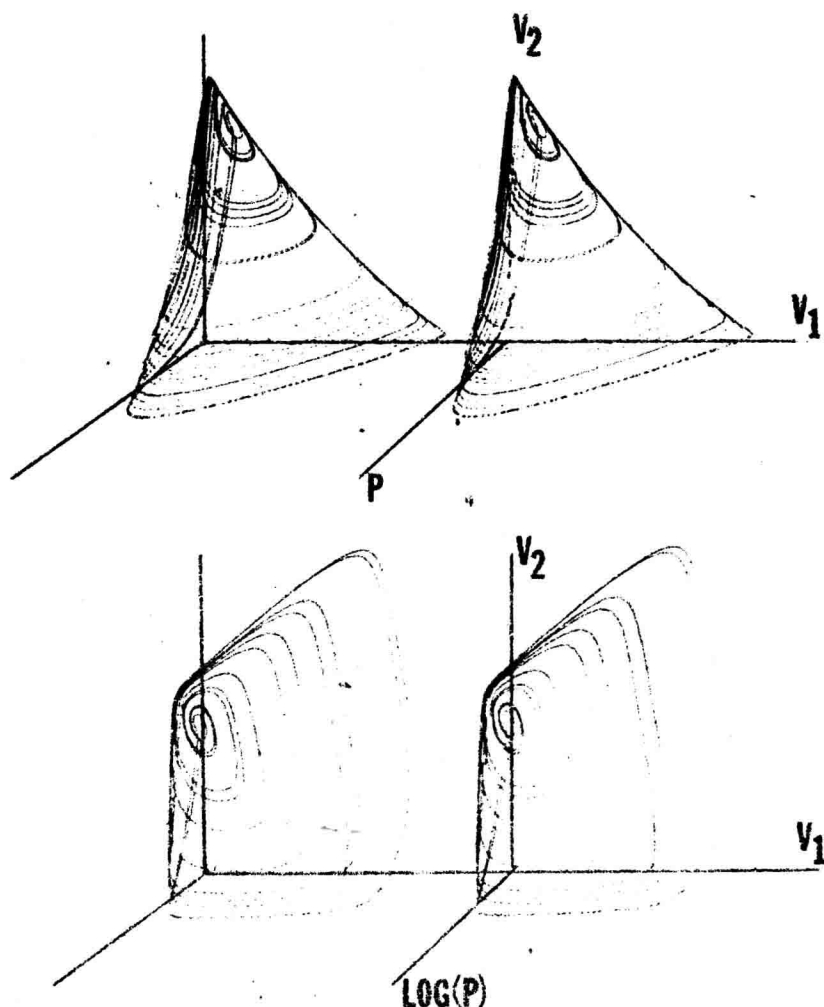
FIG. 1.— Stereoscopic state space trajectories for the two prey and one predator system. (Parameter values given in text.) Both the upper and lower plot have the same parameter values and the same initial conditions; the lower plot shows that there are no discontinuous behaviors at low predator densities that might have arisen as computer artifacts; the trajectory is dashed where it moves most rapidly.

The behavior occurred for the parameter values $r_1 = r_2 = -r_3 = 1$, $a_{11} = a_{12} = a_{22} = .001$, $a_{21} = .0015$, $a_{13} = .01$, $a_{23} = .001$, $a_{31} = -.005$, $a_{32} = -.0005$, $a_{33} = 0$; it is structurally stable in a neighborhood of parameter space; N_1 and N_2 are victims V_1 and V_2; and N_3 is a predator P.

Figure 1 shows this behavior as a trajectory in a three-dimensional state space. All four plots are of the same trajectory with the same starting point. In the lower plots. log P is plotted so as to reveal the behavior at low predator density. The upper and lower plots are stereographic pairs, one of which has been rotated slightly around the z-axis. If the eyes are crossed such that the left plot is studied by the right eye and vice
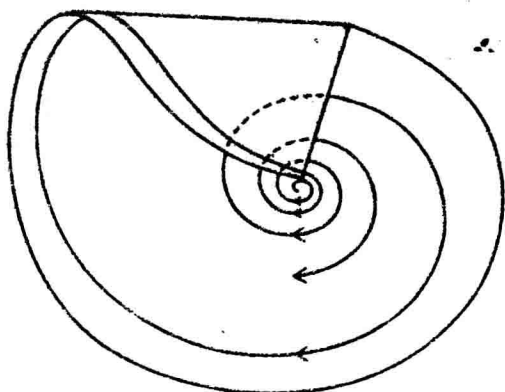
FIG. 2. Schematic diagram of the attractor manifold for the system of fig 1.

versa, the trajectory will appear three-dimensionally above the surface of the paper (your neighborhood protein chemist can probably instruct you in this art). This accomplished, it will be seen that the topology of the attractor manifold is as shown in figure 2. That is, it is a two-dimensional comma-shaped surface, the tail of which is folded over and connected to its body. In effect, the third dimension permits trajectories to be inserted "inside themselves." Otto Rössler, who has studied such "continuous chaos," classifies Vance's behavior as spiral chaos (Rössler 1976, and personal communication).

The message from this is that even the simplest possible models of community interaction require exhaustive cybernetic analysis before their repertoire of behaviors can be known, and some of these are likely to be complex. It is hardly any wonder that IBP-type models, assembled from many nonlinear component models whose parameters are necessarily inaccurate and probably improperly lumped have blown up, or as Patten (1974) puts it, "have not converged satisfactorily on measured or reasonable ecosystem behaviors." The degree to which real ecosystem behavior is chaotic is possibly the most fundamental question facing community ecology.

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Persistence and Extinction in
Three Species Lotka-Volterra Competitive Systems

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ABSTRACT

Extinction in a three species Lotka-Volterra competitive system is classified in terms of the model parameters. Necessary and sufficient conditions are given for one and two species extinction; these are, alternatively, conditions for two and one species persistence. Persistence of the system is studied assuming all pairwise interactions between species are known. An intransitive species arrangement is the only case of persistence where pairwise interactions are, by themselves, sufficient to govern persistence. No persistent arrangement can contain a pair of species that interacts in an unstable manner.

I. INTRODUCTION

Food web components may be classified as basal species [8], which are resource limited and which feed on no other species in the web; *top predators*, on which nothing else feeds; *isovores*, which feed on a single trophic level; and *omnivores*, which feed upon more than one trophic level. Some of the effects of predation on species persistence have been documented by Connell [1] and Paine [7]. The role of other food web components in determining persistence is not well documented. To facilitate understanding of the role played by species occupying the same trophic level, we study a three species Lotka-Volterra competitive system. We determine, in this elementary setting in which at least one species must survive, necessary conditions and sufficient conditions for the persistence of

two and all three species. Also, we indicate how persistence for the three species system is governed by the nature of the two species interactions for each of the three pairs of species. Finally, we discuss the relationship between persistence and stability for the system.

The mathematical model has the form

$$\frac{dx_i}{dt} = x_i\left(a_{i0} - \sum_{j=1}^{3} a_{ij}x_j\right), \qquad i = 1, 2, 3, \tag{1}$$

and may be interpreted as three basal species in competition; here, the coefficients a_{i0} and a_{ii} are assumed to be positive constants, while the remaining a_{ij} are nonnegative constants, $i,j = 1, 2, 3$. The kth species is said to go *to extinction* if there is a solution trajectory $(x_1(t), x_2(t), x_3(t))$ of (1) with positive initial position, $x_i(0) > 0$, $i = 1, 2, 3$, and asymptotic behavior $\lim_{t \to \infty} x_k(t) = 0$. [Since the coordinate planes, $x_i = 0$, are invariant manifolds for (1), and since solutions of initial value problems for (1) are unique, it follows that extinction in (1) cannot occur in a finite time. Hence any trajectory of (1) with positive initial position remains in the first octant for all time.] Persistence, on the other hand, means that no species goes extinct. In particular, persistence of the kth species means that for any choice of positive initial position, $\limsup_{t \to \infty} x_k(t) > 0$. In the first part of this article we determine inequalities involving the coefficients a_{ij} that prevent and force persistence for each possible subset of species. In the second part, we relate persistence of the whole ensemble of species to the possible resolutions of all two species competitions. In particular, there are three biologically feasible ways in which two species, x_i and x_j, can resolve competition, given the Lotka–Volterra dynamics of (1): one species, say the ith, always wins, regardless of initial population sizes (we will denote this by $x_i \gg x_j$); the species coexist in a stable manner, no matter what the initial population sizes ($x_i \leftrightarrow x_j$); or the winner of the competition depends upon the initial population sizes ($x_i \dashv x_j$).

These situations correspond respectively to the nonexistence of a positive equilibrium, the existence of an asymptotically stable positive equilibrium, and the existence of a saddle point type unstable positive equilibrium in the $x_i x_j$ plane. Geometrically, these three mutually exclusive situations are represented by different relative positions of the intersections of the sets $S_i = \{(x_i, x_j): a_{i0} - a_{ii}x_i - a_{ij}x_j = 0\}$ and $S_j = \{(x_i, x_j): a_{j0} - a_{ji}x_i - a_{jj}x_j = 0\}$ with the $x_i x_j$ plane. As is well known, the location of these x_i- and x_j-isoclines in the $x_i x_j$ plane determines the competition outcomes.

Algebraically, these two species interaction schemes are characterized in terms of inequalities involving the coefficients of (1):

$$
\begin{array}{lll}
x_i \gg x_j: & a_{i0}a_{jj} > a_{ij}a_{j0}, & a_{i0}a_{ji} > a_{ii}a_{j0}, \\
x_i \leftrightarrow x_j: & a_{i0}a_{jj} > a_{ij}a_{j0}, & a_{i0}a_{ji} < a_{ii}a_{j0}, \\
x_i \dashv x_j: & a_{i0}a_{jj} < a_{ij}a_{j0}, & a_{i0}a_{ji} > a_{ii}a_{j0}.
\end{array}
$$

We are addressing the following question. Given the competitive interaction outcome for each pair x_1x_2, x_2x_3, and x_3x_1, what can be said about persistence and extinction of the entire system?

Persistence (or the lack of extinction) is a global phenomenon. Classical approaches employing equilibrium stability analysis (Rescigno [9]) or numerical procedures (Gilpin [3]) deal with local behavior and cannot generate the general persistence conclusions we desire. Other relevant references are the articles by May and Leonard [6] and Strobeck [10], where stability and behavior aspects of Lotka-Volterra competitive systems are discussed. The paper of Grossberg [5], which appeared after our original draft of this manuscript but influenced the flavor of this revision, deserves mention. In the article [5], which does not discuss persistence per se, it is asserted that the global qualitative behavior of competitive systems can be determined by "keeping track" of which species is winning the competition at each time along each trajectory. This is interpreted geometrically in terms of the configuration of the isoplanar surfaces, and conditions are determined under which every trajectory approaches some equilibrium or, alternatively, when oscillations occur. In view of this article, our results can be obtained by checking how the isoclines are aligned in each of the coordinate planes $x_i = 0$ bounding the first octant $R_3^{+,0} = \{(x_1, x_2, x_3) : x_i > 0, i = 1, 2, 3\}$. These geometrical criteria are related to the analytical conclusions obtained by our *approach*, which was motivated by the work of Gard and Hallam [2] on persistence in simple food chains. The main distinction between these works is that the ecologically relevant problem of persistence can be attacked without having to analyze the complete trajectory structure of the system in R_3^+ (which can be complicated; see [5]); only the system behavior near the extinction boundaries need be studied.

2. EXTINCTION RESULTS

As mentioned in the introduction, it is impossible for all species to go extinct simultaneously: at least one species must survive. Indeed, since we are assuming that the parameters a_{i0}, $i = 1, 2, 3$, are positive, the fact that the equilibrium $(0, 0, 0)$ cannot attract any trajectory in $R_3^{+,0}$ follows by elementary linearization analysis of (1). The following results concerning two and one species extinction (one and two species persistence), are valid for solution trajectories $(x_1(t), x_2(t), x_3(t))$ of (1) with positive initial positions $[(x_1(0), x_2(0), x_3(0)) \in R_3^{+,0}]$.

THEOREM 1

Necessary conditions for the existence of a trajectory satisfying $\lim_{t \to \infty} x_k(t) > 0$ *and* $\lim_{t \to \infty} x_i(t) = 0$, $i \neq k$, *are*

$$a_{ik} a_{k0} \geq a_{i0} a_{k0}, \qquad i \neq k. \qquad (2)$$

-6-

Replacing the inequality in (2) *with strict inequality yields sufficient conditions for the existence of such trajectories.*

Define $b_{ij} = a_{i0}a_{jj} - a_{j0}a_{ij}$ and $c_{ij} = a_{ii}a_{jj} - a_{ij}a_{ji}$, and let

$$d_k = a_{k0} - a_{ki}\left[\frac{b_{ij}}{c_{ij}}\right] - a_{kj}\left[\frac{b_{ji}}{c_{ij}}\right], \qquad k \neq i,j, \quad i \neq j.$$

THEOREM 2

Necessary conditions for the existence of a trajectory satisfying $\lim_{t\to\infty} x_k(t) = 0$ *and* $\lim_{t\to\infty} x_i(t) > 0$, $i \neq k$, *are*

$$b_{ij}b_{ji} > 0, \qquad i \neq j, \quad i,j \neq k, \tag{3}$$

$$d_k \leqslant 0. \tag{4}$$

Again, (3) *and strict inequality in* (4) *give sufficient conditions for this type of extinction behavior.*

Before giving the proof of these results, we note that all trajectories of (1) are bounded. [For each i, $dx_i/dt \leqslant x_i(a_{i0} - a_{ii}x_i)$.]

Proof of Theorem 1. In order for the kth species to survive while the other two species go extinct, it follows from the theory of dynamical systems that $\lim_{t\to\infty} x_k(t) = a_{k0}/a_{kk}$; i.e., the trajectory approaches the equilibrium $x_k = a_{k0}/a_{kk}$, $x_i = 0$, $i \neq k$. This equilibrium can attract such a trajectory originating in $R_3^{+,0}$ only if it is not situated in either of the regions where $dx_i/dt > 0$, $i \neq k$; these are the regions below the planes $S_i = \{(x_1, x_2, x_3) : a_{i0} - \sum_{j=1}^{3} a_{ij}x_j = 0\}$. Geometrically, this means that neither plane S_i can intersect the k-axis above the equilibrium value $x_k = a_{k0}/a_{kk}$. The inequalities (2) express this condition analytically. On the other hand, if strict inequality holds in (2), then the equilibrium lies above both S_i, $i \neq k$. This guarantees that the equilibrium $x_k = a_{k0}/a_{kk}$, $x_i = 0$, $i \neq k$ has a nontrivial stable manifold that intersects $R_3^{+,0}$; i.e., there exist trajectories with the asserted behavior.

Proof of Theorem 2. As in the proof of Theorem 1, we begin by noting that when a model trajectory in $R_3^{+,0}$ represents a species which goes to extinction while the remaining two species survive, the trajectory must approach the equilibrium $x_k = 0$, $x_i = b_{ij}/c_{ij}$, $x_j = b_{ji}/c_{ij}$ [which must exist in the region $\{(x_1, x_2, x_3) : x_k = 0, x_i, x_j > 0\}$]. This implies that b_{ij} and b_{ji} must have the same sign, which is just the condition (3). Also, as in the previous proof, the equilibrium cannot be situated in the region where $dx_k/dt > 0$, the half space below S_k. Geometrically, this means that the equilibrium cannot be below the line which is the intersection of S_k and the $x_k = 0$ coordinate plane. Algebraically, this condition is the inequality (4). The

strict inequalities imply for the robust case $b_{ij} > 0$, $b_{ji} > 0$ that there exists a positive equilibrium in the $x_i x_j$ plane having a stable manifold that intersects $R_3^{+,0}$. When both b_{ij} and b_{ji} are negative, the local equilibrium structure is a saddle point. Hence, there is a single extinction trajectory of the desired type.

3. PERSISTENCE AND EXTINCTION AND TWO SPECIES COMPETITION CONFIGURATIONS

The results of the previous section are now employed to list the cases of persistence and extinction for the system (1), assuming *a priori* knowledge of all two species interactions. While these results are primarily of a bookkeeping character, they do generate some interesting theoretical hypotheses for competitive systems.

In the listings that follow $\{i,j,k\}$ can be any permutation of $\{1,2,3\}$. For any such permutation, there are sixteen different configurations for the two species interactions.

Persistence (of all species) can only occur in the following four cases:

A.1. $x_i \gg x_j$, $x_j \gg x_k$, $x_k \gg x_i$;
A.2. $x_i \leftrightarrow x_j$, $x_i \gg x_k$, $x_k \gg x_j$;
A.3. $x_i \leftrightarrow x_j$, $x_i \leftrightarrow x_k$, $x_j \gg x_k$;
A.4. $x_i \leftrightarrow x_j$, $x_j \leftrightarrow x_k$, $x_k \leftrightarrow x_i$.

In the last three of these cases additional conditions are required for persistence: A.2. $d_k \geq 0$; A.3. $d_j \geq 0$, $d_k \geq 0$; A.4. $d_i \geq 0$, $d_j \geq 0$, and $d_k \geq 0$. The species arrangement A.1 has been called nontransitive by Gilpin [3] and May and Leonard [6]. Biological occurrence of nontransitive types of interactions has been discussed in these articles. These authors also demonstrate (numerically and analytically) that an expected type of asymptotic behavior associated with nontransitive systems is bounded oscillatory motion (see [5] for the precise behavior, which is determined by a cycle graph.)

Extinction occurs in cases A.2–A.4 if the corresponding additional conditions mentioned above are violated. In particular, if $d_k < 0$, there will be trajectories with the kth species going to extinction while the others survive; and similarly for i and j in those cases where the conditions $d_i > 0$ and $d_j > 0$ are imposed for persistence.

Some extinction must occur in each of the remaining twelve cases, B.5–B.16. (See Table 1.) That is, for each of these cases there exists a region, called the region of extinction, in $R_3^{+,0}$ such that any trajectory originating in this region will possess some component species which goes to extinction. Table 1 lists these cases according to the corresponding two species competition configuration; it indicates precisely which species go to extinction and gives the additional conditions required to distinguish the extinction behavior in case the latter is not unique.

TABLE 1

Case	Interaction arrangement			Species that go to extinction in the region of extinction[a]			Conditions needed to determine mode of extinction
	x_i, x_j	x_i, x_k	x_j, x_k	x_i	x_j	x_k	
B.5	$x_i \gg x_j$	$x_i \gg x_k$	$x_j \gg x_k$	No	Yes	Yes	
B.6	$x_i \leftrightarrow x_j$	$x_i \gg x_k$	$x_j \gg x_k$	No	No	Yes	
B.7	$x_i \leftrightarrow x_j$	$x_k \gg x_i$	$x_k \gg x_j$	Yes	Yes	No	
				No	No	Cond.	$d_k < 0$
B.8	$x_i\dashv\vdash x_j$	$x_i \gg x_k$	$x_j \gg x_k$	Yes	No	Yes	
				No	Yes	Yes	
B.9	$x_i\dashv\vdash x_j$	$x_k \gg x_i$	$x_j \gg x_k$	Yes	No	Yes	
B.10	$x_i\dashv\vdash x_j$	$x_k \gg x_i$	$x_k \gg x_j$	Yes	Yes	No	
B.11	$x_i\dashv\vdash x_j$	$x_i \leftrightarrow x_k$	$x_k \gg x_j$	No	Yes	No	
B.12	$x_i\dashv\vdash x_j$	$x_i \leftrightarrow x_k$	$x_j \gg x_k$	Yes	No	Yes	
				No	Cond.	No	$d_j < 0$
B.13	$x_i\dashv\vdash x_j$	$x_i \leftrightarrow x_k$	$x_j \leftrightarrow x_k$	Cond.	No	No	$d_i < 0$
				No	Cond.	No	$d_j < 0$
B.14	$x_i\dashv\vdash x_j$	$x_i\dashv\vdash x_k$	$x_k \gg x_j$	Yes	Yes	No	
				No	Yes	Yes	
B.15	$x_i\dashv\vdash x_j$	$x_i\dashv\vdash x_k$	$x_j \leftrightarrow x_k$	No	Yes	Yes	
				No	Yes	No	
B.16	$x_i\dashv\vdash x_j$	$x_i\dashv\vdash x_k$	$x_j\dashv\vdash x_k$	Yes	Yes	No	
				Yes	No	Yes	
				No	Yes	Yes	

[a]Cond. = conditional.

For example, in case B.7 there will be trajectories originating in the region of extinction with species i, j going extinct and species k surviving, and if $d_k < 0$ there will also be trajectories along which the ith and jth species survive while the kth goes to extinction. In case B.13., precisely one of two situations develop. Either along all trajectories originating in the extinction region the ith species alone will go to extinction (if $d_i < 0$), or along all trajectories the jth species will be the single species that goes to extinction ($d_j < 0$).

We conclude this paper with a brief discussion on the relationship between persistence and the existence of an asymptotically stable equilibrium for (1) in $R_3^{+,0}$.

4. STABILITY AND PERSISTENCE

For the system (1), the persistence and asymptotic stability of a positive equilibrium are independent. The nontransitive arrangement A.1 is an example of a persistent system with an unstable positive equilibrium. This can be verified by utilizing a local stability analysis, employing the Routh-Hurwitz criterion.

Another example of a persistent system with an unstable positive equilibrium is found in the work of Strobeck [10], who developed necessary and sufficient conditions for an n-dimensional Lotka-Volterra system to have a stable positive equilibrium. He illustrates his result with a three species example in which stability is changed to instability through modifications of species growth parameters. Strobeck's stable system has coefficients

$$a_{1j}: \quad \frac{19}{3}, \frac{1}{3}, \frac{2}{3}, \frac{4}{3}$$
$$a_{2j}: \quad \frac{3}{7}, \frac{1}{18}, \frac{1}{6}, \frac{1}{3} \qquad j = 0, 1, 2, 3 \text{ respectively.}$$
$$a_{3j}: \quad 4, \frac{1}{2}, \frac{1}{3}, 1$$

This example fits the arrangement $x_1 \leftrightarrow x_2$, $x_2 \leftrightarrow x_3$, $x_1 \gg x_3$, which is case A.3 with $\{i,j,k\} = \{2,1,3\}$ in our scheme, and is persistent, since d_1 and d_3 are positive. If we multiply the a_{1j} and a_{3j} coefficients in the above example by three, we obtain Strobeck's example in which instability occurs. However, the persistence analysis is identical to that for the stability example.

The system (1) need not be persistent even if there exists an asymptotically stable positive equilibrium. Goh [4] has considered such a system with parameters

$$a_{1j}: \quad 2, 0.8, 0.5, 0.7$$
$$a_{2j}: \quad 1.5, 1, 0.2, 0.3 \qquad j = 0, 1, 2, 3 \text{ respectively.}$$
$$a_{3j}: \quad 2.1, 0.2, 1, 0.9$$

He found that the equilibrium $(1, 1, 1)$ is asymptotically stable and, by using numerical computation, also found that this system has a trajectory with the x_1 and x_3 components approaching zero. This example fits our arrangement B.2 with $\{i,j,k\} = \{1,2,3\}$, so that our classification of extinction agrees with Goh's result; note here that the second mode of extinction listed in case B.2 (i.e. trajectories along which only the 2nd species goes extinct) does not occur, since $d_2 > 0$ in this example.

5. SUMMARY AND CONCLUSIONS

The persistence-extinction theory of three dimensional Lotka-Volterra-Gause competitive models is developed. Characterizations of the two possible types of extinctions are obtained. Using these characterizations and

arrangements of two species interactions, all instances of persistence and extinction are determined.

By delineating persistence and extinction, several ecological hypotheses are generated. These include (1) the inability of a species to successfully invade a stable coexisting subcommunity (which is mathematically expressed here as $d_i < 0$) always results in a nonpersistent system: (2) no pair of competing species which interact in an unstable manner can be a component of a persistent competitive system. The results also demonstrate theoretically that knowledge of pairwise species interactions will not, in general, determine the outcome of three species competition.

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PERSISTENCE IN FOOD WEBS—I
LOTKA-VOLTERRA FOOD CHAINS

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Persistence extinction in simple food chains modelled by Lotka Volterra dynamics is governed by a single parameter which depends upon the interspecific interaction coefficients, the intraspecific interaction coefficients, and the length of the food chain. In persistent systems with nonzero carrying capacity, two new features predominate. Trophic level influence factors relate persistence on different trophic levels and determine, in conjunction with the persistence parameter, the magnitude of persistence. Equilibrium component ordering, which results in persistent systems, mandates once again that systems need to be studied on the complete ecosystem level; static field measurements reflect species location in the food chain, the total length of the food chain and assume characteristics according to these factors.

1. Introduction.   Of numerous ecosystem stability considerations, probably none affects ecosystem structure as drastically as the extinction of a biological species (e.g. Paine, 1966). Public concern about projects such as the TVA Tellico Dam Project, where the persistence of the snail darter *Percina tanasi* is in doubt (Holden, 1977) demonstrates that extinction of a biotic component of a food chain is topical as well as ecologically fundamental.

In view of the importance of persistence extinction phenomena, it is somewhat surprising that the modelling and analysis of ecosystems have not concentrated foremost upon species survival. The influence of stability developments in the engineering and mathematical communities was, undoubtedly, initially too inviting and overwhelming.

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Ecosystem stability considerations are maturing and evolving with practicality and realism in focus (Holling, 1973; May, 1974; Maynard Smith, 1974; Patten, 1974); however, a generally applicable theory of stability for ecosystems is, at best, in infancy.

Goodman (1975) states that "minimally, stability means persistence." In this article, we initiate a study of the fundamental aspect of ecosystem stability, persistence-extinction, with emphasis upon developing techniques which might be applicable in a general setting.

Persistence attributes of simple deterministic food chains of arbitrary length which are modelled by Lotka–Volterra dynamics are investigated. Here a simple food chain has trophic levels which are functionally regarded as a single species. The dynamics of each trophic level is governed by the adjoining trophic levels which immediately precede or succeed it. Persistence is, in general, a global property of a dynamical system; it is not dependent upon interior solution space structure but is dependent upon solution behavior near extinction boundaries.

Equilibrium analysis used in conjunction with linearization techniques has been a principal tool used for studying the survival problem (Freedman and Waltman, 1977; May, 1974; Rescigno and Jones, 1972; Saunders and Bazin, 1975). Such approaches have not been particularly fruitful for higher dimensional food chains basically due to intrinsic complex analytical and topological problems; for example, classification of recurrent solutions of higher dimensional dynamical systems is, at best, difficult. Other techniques, for example, graph theoretical ones, have been of some utility in higher dimensional food chains (Yorke and Anderson, 1973).

The qualitative approach employed here introduces the concept of a persistence or extinction function, which is essentially an appropriate system transformation in the Liapunov tradition. This technique yields (global) persistence or extinction results from the system structure without *a priori* information of the asymptotic character of the model solutions.

2. *Preliminary Terminology and Techniques.* Let R_+ denote the non-negative real numbers and R^n_+ the non-negative cone in R^n; that is, $R^n_+ = \{x \in R^n : x = (x_1, \ldots, x_n)$ where $x_i \in R_+, i = 1, 2, \ldots, n\}$. The positive cone in R^n is $R^{n0}_+ = \{x \in R^n_+ : x = (x_1, \ldots, x_n), x_i > 0\}$.

The models considered here are of the form

$$x'_i = x_i f_i(x_1, x_2, \ldots, x_n), \quad i = 1, 2, \ldots, n; \quad ' = d/dt; \tag{1}$$

where each f_i is a continuous function from R^n_+ to R and is sufficiently smooth to guarantee that initial value problems for (1), with the initial

13·

position having non-negative components, have unique solutions.

The primary theme develops persistence of a food chain modelled by (1) in the following sense.

Definition 1.   System (1) is *persistent* if each solution $\phi = \phi(t)$ of (1) with $\phi(0) \in R^n_+$ satisfies lim sup$_{t \to \tau} \phi_i(t) > 0$ for all i, $1 \leq i \leq n$, and $\tau \in (0, T_\phi]$ where $[0, T_\phi)$ is the maximal interval of existence of ϕ. If (1) is *not persistent*, then there is a solution ϕ with $\phi(0) \in R^{n_0}_+$ where some component, say ϕ_j, satisfies lim$_{t \to \tau} \phi_j(t) = 0$ for some τ in $(0, T_\phi]$. As we shall be concerned with persistence of the complete food chain, any solution of (1) considered subsequently will tacitly have initial value in $R^{n_0}_+$.

If it is known that the maximal interval of existence of all solutions of (1) is $[0, \infty)$, (that is, $T_\phi = \infty$) then it follows from the assumed uniqueness of solutions of initial value problems that persistence of (1) is determined by using only $\tau = \infty$ in Definition 1.

In the sequel, the well known **comparison technique is employed**. It is convenient to categorize the differential equations employed as comparison equations in the following terms. Let ω be a continuous function from R_+ into R. The differential equation

$$u' = \omega(u) \tag{2}$$

is of *persistent type* provided any solution $\psi = \psi(t)$ of (2) with $\psi(0) > 0$ satisfies lim sup$_{t \to \tau} \psi(t) > 0$ for all $\tau \in (0, \infty]$. The equation (2) is of *extinction type* provided any solution ψ of (2) with $\psi(0) = 0$ satisfies lim$_{t \to \tau} \psi(t) = 0$ for some τ in $(0, \infty]$. For example, if the right side of (2) is $\omega(u) = \alpha u$, then (2) is of persistent type whenever $\alpha \geq 0$ and of extinction type if $\alpha < 0$.

The concept of a persistence (extinction) function is now introduced. It is tacitly required that the functions ρ and ε used subsequently be continuous functions from R^n_+ to R_+ which are continuously differentiable on $R^{n_0}_+$.

Definition 2.   A function ρ is called a *persistence function for system* (1) if the following are satisfied:

(i) $\rho(x_1, x_2, \ldots, x_n) \to 0$ if $x_i \to 0$ for some i, $i = 1, 2, \ldots, n$;

(ii) ρ satisfies the differential inequality $\dot\rho \geq \omega(\rho)$ wherein

$$\dot\rho(x_1, x_2, \ldots, x_n) \equiv \sum_{i=1}^{n} \frac{\partial \rho}{\partial x_i} x_i f_i(x_1, x_2, \ldots, x_n); \tag{3}$$

and the associated comparison differential equation $u' = \omega(u)$ is of persistent type.

Definition 3. A function ε is an *extinction function for* (1) if the following are satisfied:

(iii) $\varepsilon(x_1, x_2, \ldots, x_n) \to 0$ only if some $x_i \to 0$, $i = 1, 2, \ldots, n$;

(iv) ε satisfies the differential inequality $\dot{\varepsilon} \leq \omega(\varepsilon)$ where $\dot{\varepsilon}$ is defined as in (3) and the associated comparison differential equation $u' = \omega(u)$ is of extinction type.

If $\omega(\rho) \geq 0$ (resp. $\omega(\varepsilon) \leq 0$), then $-\rho$ (resp. ε) is a Liapunov function in the sense of **LaSalle** (1976). The existence of a persistence (extinction) function for (1) implies the persistence (nonpersistence; i.e., extinction of a component species) of system (1).

THEOREM 1. *Let ρ be a persistence function for system* (1). *Then, for any solution $\phi = (\phi_1, \phi_2, \ldots, \phi_n)$ of* (1) *with maximal interval of existence $[0, T_\phi)$, $\limsup_{t \to \tau} \phi_i(t) > 0$ for each $\tau \in (0, T_\phi]$ and each $i, i = 1, 2, \ldots, n$; that is, system* (1) *is persistent.*

Example 1. The function $\rho(x_1, x_2) = x_1 x_2 / (1 + x_1)$ is a persistence function for the symbiotic model

$$x_1' = x_1(\tfrac{1}{2} - \tfrac{1}{2}x_1 + 2x_2 + x_1 x_2 - x_1^2),$$
$$x_2' = x_2(1 + x_1 - 2x_2);$$

here, ρ satisfies the equation $\dot{\rho} = \rho(3/2 - \rho)$ which is of persistent type and the condition $\rho(x_1, x_2) \to 0$ if $x_i \to 0$ follows by noting that $x_1 \to 0$ and $x_2 \to \infty$ are incompatible.

The extinction analogue of Theorem 1 is our next result.

THEOREM 2. *Let ε be an extinction function for* (1). *Then, for any solution $\phi = (\phi_1, \phi_2, \ldots, \phi_n)$ there exists an $i, i = 1, 2, \ldots n$ and a $\tau, 0 < \tau \leq \infty$, such that $\lim_{t \to \tau} \phi_i(t) = 0$; that is,* (1) *is not persistent and extinction of some component species results.*

Proof of Theorem 1. Suppose that system (1) is not persistent; then, there exists a $\tau \in (0, T_\phi]$ and a $j, 1 \leq j \leq n$, such that $\limsup_{t \to \tau} \phi_j(t) \leq 0$. Condition (i) leads to the conclusion that $\lim_{t \to \tau} \rho(\phi(t)) = 0$. This conclusion is not consistent with the assumption that the comparison equation $u' = \omega(u)$ has no solution which approaches zero since, from elementary differential inequalities, it follows that $\rho(\phi(t)) \geq \psi(t)$, where $\psi(t)$ is the solution of the initial value problem $u' = \omega(u)$, $\psi(0) = \rho(\phi(0))$.

The proof of Theorem 2 is similar to that above and is omitted.

115.

Example 2. The system

$$x_1' = x_1(1 + ax_1), \quad a > 0$$

$$x_2' = -x_2(1 + bx_2), \quad b > 0$$

shows that considerations of the maximal interval of existence in the above theorems are necessary. The function $\rho(x_1, x_2) = x_1 x_2 (1 + ax_1 + bx_2)$ satisfies $\dot\rho = 0$ and is a persistence function. Solutions of $x_2' = -x_2(1 + bx_2)$ with positive initial conditions approach zero as t approaches infinity; however, solutions of the system exist only on a finite interval.

As will be demonstrated below, the persistence of (1) can sometimes be verified even if the persistence function does not satisfy the differential inequality throughout the entire region R^n, but only a slab of the form $\{(x_1, x_2, \ldots, x_n) \in R^n; 0 < x_n \leq \lambda$ and some $\lambda > 0\}$. The conclusion in these circumstances is the establishment of a component hierarchy structured by the dominance of the species which survive the struggle for existence.

To illustrate, in an elementary setting, our technique for determining species survival, we consider the quadratic model:

$$x_1' = x_1(a + bx_1 + cx_2)$$

$$x_2' = x_2(e + fx_1 + gx_2)$$

where $a, b, c, e, f,$ and g are constants (not necessarily positive). Define $\rho(x_1, x_2) = x_1 x_2$; then

$$\dot\rho = \rho[(a + e) + (b + f)x_1 + (c + g)x_2].$$

Suppose we know, *a priori*, that solutions are bounded. If $a + e > 0$, $b + f > 0$ and $c + g > 0$ then $\dot\rho \geq (a + e)\rho$ and it follows that the system is persistent. Whenever $a + e > 0$ and $b + f > 0$, then species x_1 survives since $\dot\rho > 0$ on the slab $\{(x_1, x_2); x_1 \in R^1, 0 < x_2 < (a + e)/(c + g)\}$. Similarly, when $a + e > 0$ and $c + g > 0$, species x_1 survives. These results are, admittedly, not sharp. They are presented only to demonstrate a technique utilized subsequently in a more elaborate setting.

3. Lotka-Volterra Food Chains.

By employing the techniques developed in the previous section, we now classify persistence in a simple food chain modelled by Lotka Volterra dynamics. The results, which depend upon the interspecific and intraspecific interaction coefficients and the length of the predator-prey system, determine persistence-extinction up to a single parameter (bifurcation) value. The presence or absence of a carrying capacity for the food chain resource (lowest trophic level) has an interest-

·16·