PERSISTENCE IN FOOD WEBS.

I. LOTKA-VOLTERRA FOOD CHAINS

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PERSISTENCE IN FOOD WEBS:

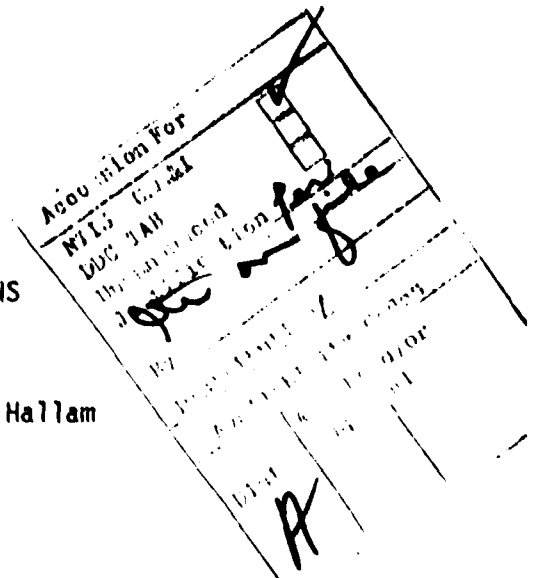## I. LOTKA-VOLTERRA FOOD CHAINS

Thomas C. Gard and Thomas G. Hallam

INTRODUCTION

Of numerous ecosystem stability considerations, none probably affects ecosystem structure as drastically as the extinction of a biological species (e.g., Paine, 1966). As demonstrated by public concern about projects such as the TVA Tellico Dam Project where the persistence of the snail darter Percina tanasi is vascillating (Holden, 1977), extinction of a biotic component of a food chain is topical as well as ecologically fundamental.

Viewing 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 eventuation in the engineering and mathematical communities was, undoubtedly, initially too inviting and overwhelming.

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

Goodman (1975) states that "minimally, stability means persistence." In this article, we initiate a study of this fundamental aspect of ecosystem stability, persistence-extinction, with emphasis upon development of a general theory. Persistence attributes of simple deterministic

food chains of arbitrary length and modelled by Lotka-Volterra dynamics are determined. Here a simple food chain has a single species composing each trophic level with its dynamics governed by the levels immediately preceding and succeeding. Persistence is, in general, a global property of a dynamical system; it is not solution structure or configuration oriented. 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). 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. The conclusions are sharp and depend only upon the model parameter and food chain length.

PRELIMINARY TERMINOLOGY AND TECHNIQUES

Let R_+ denote the nonnegative real numbers and R_+^n the nonnegative 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

$$x_i' = x_i f_i(x_1, x_2, \ldots, x_n), \qquad i = 1, 2, \ldots, n; \quad ' = d/dt; \qquad (1)$$

where each f_i is a continuous function from R_+^n to R and is sufficiently smooth to guarantee that initial value problems for equation (1) with the initial position $x_i(0) > 0$, $i = 1, 2, \ldots, n$, have unique solutions.

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

Definition 1. System (1) is <u>persistent</u> if each solution $\phi = \phi(t)$ of (1) with $\phi(0) \in R_+^{n0}$ satisfies $\lim\sup_{t \to \tau} \phi(t) > 0$ for all $\tau \in (0, T_\phi]$ where $[0, T_\phi)$ is the maximal interval of existence of ϕ. If (1) is <u>not persistent</u>, then there is a solution ϕ with $\phi(0) \in R_+^{n0}$ 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_+^{n0}.

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 <u>persistent type</u> provided any solution $\psi = \psi(t)$ of (2) with

$\psi(0) > 0$ satisfies $\lim\limits_{t \to \tau} \sup \psi(t) > 0$ for all $\tau \in (0,\infty]$. The equation

(2) is of <u>extinction type</u> provided any solution $v = v(t)$ of the initial

value problem (2) with $v(0) > 0$ satisfies $\lim\limits_{t \to \tau} v(t) = 0$ 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 intro-

duced. 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_+^{n0}.

<u>Definition 2.</u> A function ρ is called a <u>persistence function for</u>

<u>system</u> (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 per-

sistent type.

<u>Definition 3.</u> A function ϵ is an <u>extinction function for</u> (1) if

the following are satisfied:

(iii) $\epsilon(x_1, x_2, \ldots, x_n) \to 0$ 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.

The existence of a persistence (extinction) function for (1) implies the persistence (nonpersistence; i.e., extinction of a component species) of system (1).

<u>Theorem</u> 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 $[0, T_\phi)$, $\displaystyle\limsup_{t \to \tau} \phi_i(t) > 0$ for each $\tau \in (0, T_\phi]$ and each i, i = 1, 2, ..., n; that is, system (1) is persistent.

<u>Example</u> 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 $\dot{\rho} = \rho(\tfrac{3}{2} - \rho)$ which is of persistent type and the condition $\rho(x_1, x_2) \to 0$ if $x_1 \to 0$ 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.

<u>Theorem</u> 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, ..., n and a τ, $0 < \tau \leq \infty$, such that $\displaystyle\lim_{t \to \tau} \phi_i(t) = 0$; 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, $1 \le j \le n$, such that $\lim\sup\limits_{t \to \tau} \phi_j(t) \le 0$. Condition (i) leads to the conclusion that $\lim\limits_{t \to \tau} \rho(\phi(t)) = 0$. 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 $\rho(\phi(t)) \ge u(t)$, where $u(t)$ is the solution of the initial value problem $u' = \omega(u)$, $u(0) = \rho(\phi(0))$.

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

Example 2. The system

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

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

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_+^{n0} but only a slab of the form $\{(x_1, x_2, \ldots, x_n) \in R_+^{n0}, 0 < x_j \le \lambda_j\}$ for some j, $j = 1, 2, \ldots, n$

and some $\lambda_j > 0$. 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 $\rho(x_1,x_2) = x_1x_2$; then

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

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_2 survives since $\dot{\rho} > 0$ on the slab $\{(x_1,x_2) : x_1 \in R_+^{10}, \ 0 < x_2 < (a + e)/(c + g)\}$. 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.

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 intra-specific 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 interesting effect upon the character of the persistence criterion. The model considered here is

$$x_1' = x_1(a_{10} - a_{11}x_1 - a_{12}x_2)$$

$$x_2' = x_2(-a_{20} + a_{21}x_1 - a_{23}x_3)$$

$$\vdots \qquad \vdots \qquad\qquad\qquad (4)$$

$$x_{n-1}' = x_{n-1}(-a_{n-1,0} + a_{n-1,n-2}x_{n-2} - a_{n-1,n}x_n)$$

$$x_n' = x_n(-a_{n0} + a_{n,n-1}x_{n-1}).$$

In (4), all a_{ij} are positive constants with the exception of a_{11} which is nonnegative. Before proceeding with our main result for (4) with nonzero carrying capacity we note that limitations on the resource level are propagated throughout the food chain.

Theorem 3. All solutions of (4) with positive initial conditions are bounded provided $a_{11} > 0$.

Proof. From the first equation in (4), it follows that $x_1' < x_1(a_{10} - a_{11}x_1)$. The comparison principle establishes the bound

$x_1(t) \leq \max \{x_1(0), a_{10}/a_{11}\}$ for $t \in R_+$.

We now define the function u by

$$u = \sum_{j=1}^{n} (\prod_{i=1}^{j-1} a_{i,i+1} \prod_{k=j}^{n-1} a_{k+1,k}) x_j$$

wherein any improperly indexed product is defined to be one. From (4) it follows that

$$u' = \prod_{k=1}^{n-1} a_{k+1,k} \; x_1(a_{10} - a_{11}x_1 - a_{12}x_2)$$

$$+ \sum_{j=2}^{n-1} (\prod_{i=1}^{j-1} a_{i,i+1} \prod_{k=j}^{n-1} a_{k+1,k}) x_j (-a_{j,0} + a_{j,j-1}x_{j-1} - a_{j,j+1}x_{j+1})$$

$$+ \prod_{i=1}^{n-1} a_{i,i+1} x_n (-a_{n0} + a_{n,n-1}x_{n-1})$$

$$\leq -mu + b$$

where

$$m = \min_{1 \leq j \leq n} a_{j0}, \; b = \max_{x_1} |x_1(2a_{10} - a_{11}x_1)| \prod_{k=1}^{n-1} a_{k+1,k}.$$

Application of the comparison principle leads to

$$u(t) \leq u(0) \exp(-mt) + b/m;$$

this implies x_i, $i = 2, \ldots, n$, is bounded and completes the proof of the theorem.

For system (4), the next theorem classifies persistence in terms
of a single parameter μ. Writing the food chain length n as 2m + 1
if n is odd or 2m if m is even, we define

$$\mu = a_{10} - \sum_{j=1}^{m} a_{2j,0} \prod_{i=1}^{j} \frac{a_{2i-2,2i-1}}{a_{2i,2i-1}}$$

$$- \sum_{\ell=1}^{m} a_{2\ell+1,0} \prod_{i=1}^{\ell} \frac{a_{2i-1,2i}}{a_{2i+1,2i}}.$$

Theorem 4. Suppose the resource level in (4) has a positive
carrying capacity $(a_{11} > 0)$. Then, the food chain as modelled by system
(4) is persistent provided $\mu > 0$; it is not persistent if $\mu < 0$.

Proof. First, we review some appropriate properties of the
dynamical system (4). Bounding hyperplanes of R_+^{n0} of the form
$H_j = \{(x_1, x_2, x_3, \ldots, x_n) \in R_+^n : x_j = 0\}$ are invariant manifolds for
(4). The intersection of the ω-limit set Ω_ϕ of a solution ϕ (which
is bounded by Theorem 3) with such a hyperplane is therefore a compact
invariant set which contains a minimal compact invariant set (Nemytskii
and Stepanov, 1960). A classical result of Birkhoff implies that every
trajectory in this minimal set is recurrent. When extinction of some
constituent of the food chain represented by (4) occurs, its model equiva-
lent is a trajectory approaching a bounding hyperplane. This extinction
trajectory converges as $t \to \infty$ (since, as previously remarked, finite
extinction time is not possible) to a set containing recurrent solutions.

Suppose now that $\mu < 0$ and, for the purpose of contradiction, that
system (4) has a solution $\phi = (\phi_1, \phi_2, \ldots, \phi_n)$ with $\phi(0) \in R_+^{n0}$ which

satisfies $\lim_{t\to\infty} v_j(t) = 0$ for some minimal index j. This assumption can be rephrased as $H_j \cap \Omega_v \neq \emptyset$. We claim that any recurrent solution in this intersection lies in some minimal subsurface:

$$H^{k0} = \{(x_1, x_2, \ldots, x_n) : x_i > 0, 1 \leq i \leq k - 1, x_i = 0, i \geq k\}.$$

That is, the solution is in H^{k0} but not in any subsurface on which $x_i = 0$ for some i, $1 \leq i \leq k - 1$. The trivial solution $(0, 0, \ldots, 0)$ cannot be such a recurrent solution since it is of hyperbolic type; hence, it is not in Ω_v. Now, if the claim is false, there is a recurrent solution $v(t) = (v_1(t), \ldots, v_n(t))$ satisfying, for some indices ι and m, $v_\iota(t) \equiv 0$ and $v_m(t) \neq 0$. If ι is the largest index with $v_\iota(t) \equiv 0$ the function $v_{\iota+1}$ satisfies the differential equation

$$v'_{\iota+1} = v_{\iota+1} \, (-a_{\iota+1,0} \, v_{\iota+1} - a_{\iota+1,\iota+2} \, v_{\iota+2}).$$

Thus, $v'_{\iota+1} < 0$ for all t, a fact which is not possible for a recurrent solution. The minimality of H_k^0 is ascertained.

We shall now show that v cannot have its assumed asymptotic behavior. This is accomplished by showing that for some $r_i > 0$, $i = 1, 2, \ldots, n$, and for some $\lambda_j > 0$, $j = k, \ldots, n$,

$$\rho \equiv \prod_{i=1}^{n} x_i^{r_i}$$ is a persistence function on the hyperrectangular slab

$$S = \{(x_1, x_2, \ldots, x_n) \in R_+^n : 0 < x_j \leq \lambda_j, j \geq k\}.$$

The asymptotic condition required for ρ to be a persistence function follows readily from Theorem 3 and the definition of ρ. It remains to show that ρ

is a solution of a differential inequality whose comparison equation is of persistent type.

From (4), we obtain

$$\dot{\rho} = [r_1(a_{10} - a_{11}x_1 - a_{12}x_2) + \sum_{j=2}^{n-1} r_j(-a_{j0} + a_{j,j-1}x_{j-1} - a_{j,j+1}x_{j+1})$$

$$+ r_n(-a_{n0} + a_{n,n-1} x_{n-1})]$$

$$= \rho[r_1a_0 - \sum_{j=2}^{n} r_ja_{j0} + (r_2a_{21} - r_1a_{11})x_1$$

$$+ \sum_{j=3}^{n}(r_ja_{j,j-1} - r_{j-2}a_{j-2,j-1})x_{j-1} - r_{n-1}a_{n-1,n}x_n].$$

$$(5)$$

Now, choose the r_j's, $1 \le j \le k$, so that

$$r_2/r_1 = a_{11}/a_{21} \text{ and}$$

$$r_j/r_{j-2} = a_{j-2,j-1}/a_{j,j-1}, \quad j = 3, 4, \ldots, k.$$

Using these relationships to determine the quotient r_j/r_1 as a function of the coefficients, we find if j is even and $4 \le j \le k$,

$$\frac{r_j}{r_1} = \frac{a_{11}}{a_{21}} \prod_{i=2}^{j/2} \frac{a_{2i-2,2i-1}}{a_{2i,2i-1}}; \qquad (6a)$$

while if j is odd and $3 \le j \le k$,

$$\frac{r_j}{r_1} = \prod_{i=1}^{(j-1)/2} \frac{a_{2i-1,2i}}{a_{2i+1,2i}} . \tag{6b}$$

Substitution of (6) into (5) leads to

$$\dot{\rho} = \rho[r_1\mu_k - \sum_{j=k+1}^{n} r_j a_{j0} + \sum_{j=k+1}^{n} (r_j a_{j,j-1} - r_{j-2} a_{j-2,j-1})x_{j-1}$$
$$\tag{7}$$
$$- r_{n-1} a_{n-1,n} x_n]$$

where if k is odd (k = 2p + 1) or even (k = 2p), μ_k is given by

$$\mu_k = a_{10} - \sum_{j=1}^{p} a_{2j,0} \prod_{i=1}^{j} \frac{a_{2i-2,2i-1}}{a_{2i,2i-1}}$$

$$- \sum_{\ell=1}^{p} a_{2\ell+1,0} \prod_{i=1}^{\ell} \frac{a_{2i-1,2i}}{a_{2i+1,2i}} .$$

Since, by hypothesis, μ is positive, μ_k is positive. To establish that $\dot{\rho} > 0$ in S, we select the remaining r_i, i = k + 1, k + 2, ..., n, and the λ_j, i = k, k + 1, ..., n sufficiently small so that the magnitude of the remaining terms is less than $r_1\mu_1$. The expression in the square brackets in (7) is positive on S so $\dot{\rho} > 0$ and as previously remarked, extinction cannot occur. This contradiction establishes that $\mu > 0$ is sufficient for the persistence of (4).

To demonstrate that $\mu < 0$ implies extinction, the extinction function $\varepsilon = \varepsilon(x_1, x_2, ..., x_n) = \prod_{i=1}^{n} x_i^{r_i}$, where all of the r_i's are chosen according to the scheme (6) used above, is employed. Then, from (4), it follows that

ϵ satisfies the inequality

$$\dot{\epsilon} = \epsilon[r_1\mu - r_{n-1}a_{n-1,n}x_n] \le r_1\mu\epsilon,$$

with a comparison equation of extinction type. Theorem 2 implies that the food chain is not persistent.

We now consider a food chain modelled by (4) in which the resource level has no carrying capacity; that is, $a_{11} = 0$. In this setting, the persistence parameter μ_0 depends more intricately on the dimension of the system than the previous case with nonzero carrying capacity. If the food chain length n is either $2m + 1$ or $2m + 2$ for some positive integer m then $\mu_0 = a_{10} - \sum_{j=1}^{m} a_{2j+1,0} \prod_{i=1}^{j} \frac{a_{2i-1,2i}}{a_{2i+1,2i}}$.

Theorem 5. Let $a_{11} = 0$. The food chain modelled by system (4) is persistent provided $\mu_0 > 0$; it is not persistent if $\mu_0 < 0$.

Proof. Theorem 3, which established the boundedness of solutions of (4) assuming $a_{11} > 0$, was required in the proof of Theorem 4. The analogous lemma employed here is that any solution ϕ of (4) with $\phi(0) \in R_+^{n0}$ such that $\lim_{t\to\infty} \phi_j(t) = 0$ for some j, is bounded. To establish this, we first note that $\lim_{t\to\infty}\phi_j(t) = 0$ implies $\lim_{t\to\infty}\phi_i(t) = 0$ for $i \ge j$. From (4) it follows that for t sufficiently large

$$\phi'_{j+1}(t) = \phi_{j+1}(t)[-a_{j+1,0} + a_{j+1,j}\phi_j(t) - a_{j+1,j+2}\phi_{j+2}(t)]$$

$$\le \phi_{j+1}(t)[-a_{j+1,0}/2].$$

Thus, $\lim_{t\to\infty}\phi_{j+1}(t) = 0$; an induction completes the argument.

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It, then, suffices to prove the assertion in the case that ϕ
is such that $\lim_{t\to\infty}\phi_n(t) = 0$. To this end, we use the classical Lotka-
Volterra auxiliary function $v(x_1, x_2, \ldots, x_n) = \sum_{i=1}^{n} \alpha_i(x_i - \beta_i - \beta_i \ell n\, x_i/\beta_i)$,
where α_i, β_i are positive parameters to be chosen later. Boundedness of
ϕ will follow if it is shown that $v(t) = v(\phi(t))$ is eventually nonincreasing.
Employing (4) with some rearrangement leads to

$$\dot{v}(x_1, x_2, \ldots, x_n) = \sum_{i=1}^{n-1} [-\alpha_i a_{i,i+1} + \alpha_{i+1} a_{i+1,i}](x_i - \beta_i)(x_{i+1} - \beta_{i+1})$$

$$+ \alpha_1(x_1 - \beta_1)(a_{10} - a_{12}\beta_2)$$

$$+ \sum_{i=2}^{n-1} \alpha_i(x_i - \beta_i)(-a_{i0} + a_{i,i-1}\beta_{i-1} - a_{i,i+1}\beta_{i+1})$$

$$+ \alpha_n(x_n - \beta_n)(-a_{n0} + a_{n,n-1}\beta_{n-1}).$$

The parameters α_i, $i = 1, \ldots, n$ are selected so that the first
sum of $n - 1$ terms vanishes. If n is even, it is possible to choose the
β_i so that each of the remaining terms is zero; thus, in this case,
α_i, β_i exist so that $\dot{v} \equiv 0$ from which the boundedness of ϕ follows.
Whenever n is odd, we can choose the β_i parameters in such a way that all
terms vanish with the exception of the last one; hence,

$$\dot{v} = \alpha_n(x_n - \beta_n)(-a_{n0} + a_{n,n-1}\beta_{n-1})$$

$$= \alpha_n(x_n - \beta_n)\mu_0 \prod_{i=1}^{m} \frac{a_{2i+1,2i}}{a_{2i-1,2i}}.$$

This leads to

$$\dot{v}(t) = \alpha_n \mu_0 \prod_{i=1}^{m} \frac{a_{2i+1,2i}}{a_{2i-1,2i}} (\phi_n(t) - \beta_n)$$

which, since $\mu_0 > 0$, satisfies $\dot{v}(t) < 0$ for all t sufficiently large. Therefore, any solution which does not persist is bounded.

The remainder of the proof is the same as that of Theorem 4 up through the calculation of $\dot{\rho}$; from (5) with $a_{11} = 0$ we obtain

$$\dot{\rho} \geq \rho[r_1(a_{10} - \sum_{i=2}^{n} \frac{r_i}{r_1} a_{i0})$$

$$+ \sum_{i=3}^{m} (r_i a_{i,i-1} - r_{i-2}a_{i-2,i-1})x_{i-1} - r_{n-1}a_{n-1,n}x_n]. \tag{8}$$

Now let k be written as $k = \ell = 2p + 1$ or $k = \ell + 1 = 2p + 2$ where ℓ is an odd integer. We choose r_{2j+1}, $j = 1, 2, \ldots, p$ as in (6b):

$$\frac{r_j}{r_1} = \prod_{i=1}^{(j-1)/2} \frac{a_{2i-1,2i}}{a_{2i+1,2i}}.$$

Since $\mu_0 > 0$, it follows that

$$a_{10} - \sum_{j=1}^{p} a_{2j+1,0} \frac{r_{2i+1}}{r_1} > 0.$$

Select the remaining r_{2j}, $j = 1, \ldots, p$ (or $p + 1$ if $k = 2p + 2$) so that

$$a_{10} - \sum_{j=2}^{k} r_j/r_1 \, a_{j0} > 0, \tag{9}$$

If q is the largest even index, $q \leq k$, we now adjust r_2, r_4, ..., r_q sequentially (to bound successive terms on the right side of (8) while preserving inequality (9)) according to the following scheme. Choose r_{q-2} possibly smaller than the original choice so that

$$r_q / r_{q-2} \geq a_{q-2,q-1} / a_{q,q-1}.$$

In a similar manner, choose r_{q-4} smaller if necessary so that

$$r_{q-2} / r_{q-4} \geq a_{q-4,q-3} / a_{q-2,q-3}.$$

Continue adjusting r_{2i} until r_2 is revised.

We now have

$$\dot{\rho} \geq \rho [r_1 (a_{10} - \sum_{i=2}^{k} (r_i/r_1) a_{i0}) - \sum_{i=k+1}^{n} r_i a_{i0}$$

$$+ \sum_{i=k+1}^{n} (r_i a_{i,i-1} - r_{i-2} a_{i-2,i-1}) x_{i-1} - r_{n-1} a_{n-1,n} x_n].$$

Proceeding as in Theorem 4, we can select the remaining r_i's and the λ_i's so that the expression in the brackets remains nonnegative on S. This leads to the desired conclusion that $\mu_0 > 0$ implies system persistence.

The proof that $\mu_0 < 0$ implies nonpersistence is analogous to the similar portion of the proof of Theorem 4. As an extinction function use $\epsilon(x_1, x_2, \ldots, x_n) = \prod_{i=1}^{p} x_{2i-1}^{r_{2i-1}}$ where r_i are determined by (6b). Then, when n is odd, the differential equation

$$\dot{\varepsilon} = r_1 \mu_0 \varepsilon$$

results; if n is even, we obtain

$$\dot{\varepsilon} = \varepsilon[r_1 \mu_0 - r_{n-1} a_{n-1,n} x_n],$$

from which nonpersistence follows.

COMMENT AND COMPARISON

While the above results are independent of system equilibrium considerations, the conclusions have a positive correlation with the location of the equilibrium points when they exist. For convenience in demonstrating these and other relationships, we restrict consideration to food chains of length four with nonzero resource carrying capacity:

$$x_1' = x_1(a_{10} - a_{11}x_1 - a_{12}x_2)$$

$$x_2' = x_2(-a_{20} + a_{21}x_1 - a_{23}x_3)$$

$$x_3' = x_3(-a_{30} + a_{32}x_2 - a_{34}x_4) \tag{10}$$

$$x_4' = x_4(-a_{40} + a_{43}x_3).$$

The equilibrium points of (10) are indicated in Figure 1.

TROPHIC LEVEL COORDINATES AND INFLUENCE FACTOR

$$1 \longrightarrow \frac{a_{11}}{a_{12}} \qquad 2 \longrightarrow \frac{a_{12}a_{21}}{a_{11}a_{23}} \qquad 3 \longrightarrow \frac{a_{11}a_{23}a_{32}}{a_{12}a_{21}a_{34}} \longrightarrow 4$$

	x_1	x_2	x_3	x_4
I:	0	0	0	0
II:	$\dfrac{a_{10}}{a_{11}}$	0	0	0
III:	$\dfrac{a_{20}}{a_{21}}$	$\dfrac{a_{10}}{a_{12}} - \dfrac{a_{11}a_{20}}{a_{12}a_{21}}$	0	0
IV:	$\dfrac{a_{10}}{a_{11}} - \dfrac{a_{12}a_{30}}{a_{11}a_{32}}$	$\dfrac{a_{30}}{a_{32}}$	$\dfrac{a_{20}}{a_{23}} + \dfrac{a_{10}a_{21}}{a_{11}a_{23}} - \dfrac{a_{12}a_{21}a_{30}}{a_{11}a_{23}a_{32}}$	0
V:	$\dfrac{a_{20}}{a_{21}} + \dfrac{a_{23}a_{40}}{a_{21}a_{43}}$	$\dfrac{a_{10}}{a_{12}} - \dfrac{a_{11}a_{20}}{a_{12}a_{21}} - \dfrac{a_{11}a_{23}a_{40}}{a_{12}a_{21}a_{43}}$	$\dfrac{a_{40}}{a_{43}}$	$-a_{30} + \dfrac{a_{10}a_{32}}{a_{12}a_{34}} - \dfrac{a_{11}a_{20}a_{32}}{a_{12}a_{21}a_{34}} + \dfrac{a_{11}a_{23}a_{40}a_{32}}{a_{12}a_{21}a_{43}a_{34}}$

Figure 1

If we designate the $i\underline{th}$ coordinate of equilibrium point I by x_i^I, II by x_i^{II}, etc., the persistence Theorem 4 may be phrased as (10) is persistent if the coordinate equilibriums satisfy the inequalities

$$x_1^V < x_1^{IV} \text{ (with the sequential ordering } x_1^V < x_1^{IV} > x_1^{III} < x_1^{II} > 0);$$

or equivalently,

$$x_2^V > x_2^{IV} \text{ (with the sequential ordering } x_2^V > x_2^{IV} < x_2^{III} > 0);$$

or equivalently,

$$x_3^V < x_3^{IV}, \ (x_3^V < x_3^{IV} > 0);$$

or equivalently,

$$x_4^V > 0.$$

The last inequality is just a restatement of the persistence inequality $\mu > 0$. Analogously, if the coordinate ordering is reversed, nonpersistence results.

This equilibrium coordinate ordering indicates that introduction of a new top predator into an ecosystem would result in an order interchange of equilibrium populations on an alternating scheme. For example, in an aquatic system with trophic levels composed of phytoplankton, herivores, and primary carnivores, the model conclusion predicts that the addition of a secondary carnivore reduces the equilibrium levels

of the phytoplankton and primary carnivores while increasing the herbivore population.

The component ordering also indicates that the persistence-extinction mechanism is mathematically one of bifurcation associated with the parameter μ; essentially the equilibrium V for (10) "splits" off from IV as the parameters transact from the extinction ($\mu < 0$) to persistence range ($\mu > 0$).

In the case of a persistent system, the resource transfer is modulated by trophic level influence factors which determine to some extent the magnitude of persistence. These factors are indigenous to the specific trophic level and relate persistence in the food chain hierarchy. If the model is interpreted as nutrient flow, energy flow, etc., componentwise throughout the system, trophic level 1 contribution factor, a_{11}/a_{12}, is the persistence multiplicative effect of level 1 on trophic level 2. Trophic level 2 has a multiplicative contribution factor of

$\dfrac{a_{12}a_{21}}{a_{11}a_{23}}$ on trophic level 3 while level has multiplicative contribution

factor $\dfrac{a_{11}a_{23}a_{32}}{a_{12}a_{21}a_{34}}$ for level 4. The antipodal character of certain of the

trophic level influence factors might not have been anticipated.

In general, the bifurcation value is persistence indeterminant. In the noncarrying capacity model, Freedman and Waltman (1977) have shown, for the three dimensional system, $\mu = 0$ implies persistence. On the other hand, for the four dimensional food chain (10) with $a_{11} = 0$ there is a continuum of critical points in the positive $x_1 x_2 x_3$ space when $\mu_0 = 0$. A subset of these satisfies $x_3 < a_{40}/a_{43}$. Linearization about any of these

latter equilibrium points indicates that each has an asymptotically stable manifold which intersects the positive cone in R^4 (the eigenvalue in the x_4 direction is negative). Thus, there are solutions with positive initial conditions which tend toward these equilibriums as t approaches infinity and $\mu = 0$ corresponds to nonpersistence.

Goh (1977) has recently shown, under certain conditions, that whenever systems of form (1) have an equilibrium in the positive cone in R^n, it is globally asymptotically stable. This is, of course, a persistence result when it it applicable. To contrast our conclusions with Goh's, we have found that the existence of an equilibrium in the positive cone is equivalent to persistence modulo the bifurcation value $\mu = 0$.

It is worth noting that for odd dimensional models (4) without carrying capacity, persistence $(\mu_0 > 0)$ results even though there is no positive equilibrium.

SUMMARY

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 these factors.

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LEGEND FOR FIGURE 1

Equilibrium points of (10) are listed hierarchically in terms of coordinates. "$\Longrightarrow$" represents implications for the appropriate coordinate orderings. Trophic level influence factors for each level are listed (see text for explanation).