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NOTE

GRAPH THEORETICAL CRITERIA FOR STABILITY AND BOUNDEDNESS OF PREDATOR–PREY SYSTEMS

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We introduce a graphical approach in the study of the qualitative behaviour of m species predator–prey systems. We prove that tree graphs imply global stability for Volterra models and local stability for general models; furthermore, we derive sufficient conditions so that loop graphs imply stability and boundedness of the solutions.

1. Introduction. Consider the Volterra model for m species predator–prey systems:

$$\dot{N}_i = N_i\left(b_i + \sum_{j=1}^{m} a_{ij}N_j\right), \qquad i, j = 1, \ldots, m \tag{1}$$

under the assumptions $a_{ij}a_{ji} \leqslant 0$, $a_{ii} \leqslant 0$.

It has been proven (see, e.g., May, 1974) that in a pure predator–prey system with antisymmetric community matrix $\mathbf{A} = (a_{ij})$, a positive equilibrium state, if it exists, is globally stable. Recently, some authors studied models with sign-antisymmetric matrix $\mathbf{A}$. Krikorian (1979) considered three species predator–prey systems and he proved that in the following cases, (1) food chains; (2) two predators competing for one prey; (3) one predator acting on two prey, the positive critical point, if it exists, is globally asymptotically stable in the positive sector. Moreover, he proved the boundedness of solutions for 'acyclic' loops and obtained a sufficient condition for the boundedness in the case of 'cyclic' loops.

Goh (1977, 1978) proved the following:

THEOREM. *If the nontrivial equilibrium* $(\bar{N}_1, \ldots, \bar{N}_m)$ *of the model* (1) *is feasible and there exists a constant positive diagonal matrix* $\mathbf{C}$ *such that* $\mathbf{CA} + \mathbf{A}^T\mathbf{C}$ *is negative definite, then the Lotka–Volterra model is globally stable in the feasible region.*

To prove this theorem, Goh used the scalar function

$$V = \sum_{i=1}^{m} c_i(N_i - \bar{N}_i - \bar{N}_i \ln N_i/\bar{N}_i),\ c_i > 0$$

already introduced by Volterra (1931) as constant of motion in conservative systems. In this theorem the term 'global stability' is used by Goh as synonymous with global asymptotic stability.

To avoid any ambiguity we introduce the stability's nomenclature followed in this note: by Liapunov function we intend a scalar function having the properties given by La Salle and Lefschetz (1961). When these properties hold over the entire positive orthant of R_m we say that the positive equilibrium is globally stable.

When the domain of attraction of $(\bar{N}_1, \ldots, \bar{N}_m)$ is the entire positive orthant of R_m, we say that the equilibrium is globally asymptotically stable. Within the frame of Goh's theorem, Harrison (1979) proved that if a Lotka–Volterra food chain has a positive equilibrium, then, under the assumption $a_{11} < 0$, $a_{ii} \leq 0$ for $i > 1$, the equilibrium is globally asymptotically stable. We believe that Goh's theorem leads in a natural way to a graphical approach to the qualitative behaviour of system (1) and the results of Krikorian and Harrison can be framed within such a graphical approach as particular cases.

A similar graph theory has already been applied by us, together with Vetrano and Lazzari (Beretta *et al.*, 1979), to systems of nonlinear chemical reactions.

2. Graph Theory. First suppose that $a_{rs} \neq 0$ implies $a_{sr} \neq 0$ for all r, s, and put $\underset{r}{\bullet}\!\!-\!\!-\!\!-\!\!\underset{s}{\bullet} \Longleftrightarrow a_{rs}\, a_{sr} < 0$.

According to Harary (1972), a loop will be an elementary chain which returns to the initial knot and a tree will be a connected graph without loops. We underline that a food chain, which is often met in literature, is a particular case of a tree graph.

We will suppose that there exists a unique positive equilibrium state $\bar{N}$. The following result holds:

THEOREM 1. *If the system* (1) *is represented by a tree graph, the equilibrium is globally stable; if $a_{rr} < 0$ for all $r = 1, \ldots, m$, then the equilibrium is globally asymptotically stable.*

Proof. Let $\mathbf{N} = (N_1, \ldots, N_m)^T$ and the equilibrium $\bar{\mathbf{N}} = (\bar{N}_1, \ldots, \bar{N}_m)^T$ be vectors of R_m^+. The scalar function used by Goh is C^1 over R_m^+ and has an isolated minimum for $\mathbf{N} = \bar{\mathbf{N}}$, which value is $V(\bar{\mathbf{N}}) = 0$. Since

$$\dot{V} = \frac{1}{2}(\mathbf{N} - \bar{\mathbf{N}})^T(\mathbf{CA} + \mathbf{A}^T\mathbf{C})(\mathbf{N} - \bar{\mathbf{N}}),$$

if a constant positive diagonal matrix $\mathbf{C}$ exists such that $\mathbf{CA} + \mathbf{A}^T\mathbf{C}$ is negative semidefinite, then $\dot{V} \leqslant 0$ in R_m^+. Thus, according to the above nomenclature, $V(\mathbf{N})$ is a Liapunov function and the equilibrium $\bar{\mathbf{N}}$ is globally stable. We define the elements of $\mathbf{C}$ requiring

$$c_r|a_{rs}| = c_s|a_{sr}| \quad r, s = 1, \ldots, m \tag{2}$$

so that $\mathbf{CA} + \mathbf{A}^T\mathbf{C} = \text{diag}\ (c_1 a_{11}, \ldots, c_m a_{mm})$, where $c_i > 0$ for all $i = 1, \ldots, m$ and $a_{ii} \leqslant 0$ for all $i = 1, \ldots, m$. Therefore, $\mathbf{CA} + \mathbf{A}^T\mathbf{C}$ is negative semidefinite. Hearon (1953) proved that system (2) is solvable without requiring any condition among the elements a_{rs} if $m - 1$ equations alone of (2) are not identically vanishing. Since a system with associated tree has exactly $m - 1$ non-vanishing coefficients among a_{rs}, $r < s$, system (2) is always solvable for tree graphs. Let us number by '1' a terminal knot of the tree. Every other knot 'k' of the graph is reached from '1' by one, and only one, elementary chain $\mathscr{C}_k$. Then the elements of $\mathbf{C}$ may be defined by

$$c_1 = 1,\ c_k = \Pi \left|\frac{a_{ij}}{a_{ji}}\right|, \qquad k = 2, \ldots, m, \tag{3}$$

where the 'a_{ij}' are the flows related to the branches of the elementary chain $\mathscr{C}_k$ from knot 1 to knot k. The first part of Theorem 1 is therefore proven. Suppose now that $a_{ii} < 0$ for all $i = 1, \ldots, m$. Therefore, $\mathbf{CA} + \mathbf{A}^T\mathbf{C}$ is negative definite, that is, $\dot{V}(\mathbf{N}) \leqslant 0$ and $\dot{V}(\mathbf{N}) = 0$ iff $\mathbf{N} = \bar{\mathbf{N}}$. This completes the proof.

For tree graphs, using (3), it follows that

$$\dot{V} = \sum_{i=1}^{m} c_i a_{ii} (N_i - \bar{N}_i)^2.$$

Let $\mathscr{R}$ be the set of points for which $\dot{V} = 0$. When some diagonal elements of $\mathbf{A}$ are zero, one may apply the La Salle–Lefschetz (1961) extension theorem to look for the conditions on $\mathbf{A}$ by which the largest invariant subset of $\mathscr{R}$ reduces to equilibrium. Then the following holds:

COROLLARY 1. *A tree graph with 'ρ' terminal knots is globally asymptotically stable if '$\rho - 1$' of the 'a_{rr}' concerning the terminal knots are different from zero.*

Since the proof is an easy generalization of that provided by Krikorian (1979) for three species and by Harrison (1979) for food chains, it will be omitted.

If a pair of indices (r, s), *so that* $a_{rs} = 0$ and $a_{sr} \neq 0$ occurs in **A**, the irreversible branch $\underset{r}{\bullet} \!-\!\!\!/\!\!- \underset{s}{\bullet}$ will be associated to (r, s).

The proof of Theorem 1 may be extended to the case in which one or more irreversible branches occur in a tree graph.

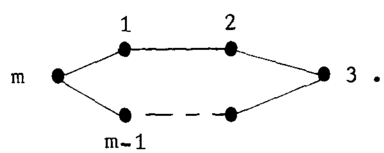
COROLLARY 2. *If the associated graph of* (1) *is a tree in which one or more irreversible branches* $\bullet \!-\!\!\!/\!\!- \bullet$ *occur, then the equilibrium is globally stable provided that* $a_{rr}a_{ss} \neq 0$ *for each irreversible branch.*

Proof. For the case of a single irreversible branch $\bullet \!-\!\!\!/\!\!- \bullet$, according to Theorem 1, we can take **C** so that **CA** is skew symmetric with reference to the reversible components of the graph. Then $\mathbf{CA} + \mathbf{A}^T\mathbf{C}$ will have a diagonal structure, with the exception of the diagonal block:

$$\begin{bmatrix} c_r a_{rr} & \dfrac{c_s a_{sr}}{2} \\ \dfrac{c_s a_{sr}}{2} & c_s a_{ss}. \end{bmatrix}$$

Since 's' is the first knot of the second reversible component of the graph, c_s is arbitrary in **C** and therefore may be chosen so that the diagonal block is negative definite. This procedure can be extended to any number of irreversible branches.

Now, suppose that the graph associated with system (1) is a loop



Then, system (2) has m equations, whose mth is $c_m|a_{m1}| = c_1|a_{1m}|$, where c_1 and c_m are defined in (3). Then

$$c_m = c_1 \prod_{i=1}^{m-1} \left|\frac{a_{i,i+1}}{a_{i+1,i}}\right| = c_1 \left|\frac{a_{1m}}{a_{m1}}\right|;$$

and, therefore, a sufficient condition for global stability is

$$|a_{12}a_{23} \cdots a_{m-1,m}| = |a_{21}a_{32} \cdots a_{m,m-1}|. \tag{4}$$

Furthermore, if there exist at least two consecutive species for which a_{rr} are different from zero, the equilibrium is globally asymptotically stable. When (4) is not satisfied, a sufficient condition for global asymptotic stability is

$$a_{11}a_{mm}c_m > \frac{(c_m a_{m1} + a_{1m})^2}{4}, \; c_m = \prod_{i=1}^{m-1} \left|\frac{a_{i,\,i+1}}{a_{i+1,\,i}}\right|. \tag{5}$$

We can observe that in case of loops the conditions (4) or (5) are to be satisfied for stability, while for tree graphs the stability of equilibrium immediately follows.

However, interesting results can be obtained regarding boundedness of the loop's solutions, by orientating the loop as follows: according to Krikorian (1979) we put $\underset{s}{\bullet}\!\longrightarrow\!\underset{r}{\bullet}$ if $a_{rs} > 0$, and suppose that in system (1)

$$b_r \neq 0, \text{ and } b_r > 0 \Rightarrow a_{rr} < 0. \tag{6}$$

The loop is called 'cyclic' if all the branches are orientated in the same direction, and called 'acyclic' in any other case.

We can prove that:

THEOREM 2. *If the graph associated with the system is an 'acyclic' loop, then the solutions are bounded; if the graph is a 'cyclic' loop, and, for example,* $a_{m1} < 0$, *then the solutions are bounded if*

$$\left|\frac{a_{21}a_{32}\cdots a_{1m}}{a_{12}a_{23}\cdots a_{m1}}\right| < 1. \tag{7}$$

Proof. Let $S = \sum_{r=1}^{m} c_r N_r$. In order that $S(t)$ be upper bounded, it is sufficient that there exists a real constant M so that $\dot{S} + \epsilon S < M$ when $\epsilon > 0$. Substituting (1) in $\dot{S}$ and applying the assumption (6), it follows that a sufficient condition for boundedness is

$$\sum_{r \neq s} c_r a_{rs} N_r N_s < 0.$$

Then, we require

$$c_i a_{i,\,i+1} + c_{i+1} a_{i+1,\,i} \leqslant 0 \quad i = 1, \ldots, m-1 \tag{8}$$

$$c_1 a_{1m} + c_m a_{m1} < 0. \tag{9}$$

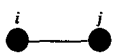
If $a_{m,m-1}$ and a_{m1} have the same sign, that is, the branches $(m-1, m)$ and $(m, 1)$ are orientated in an opposite direction, then inequalities (8), (9) are satisfied without requiring any other condition among the elements a_{rs}. Therefore the solutions are bounded. However, that is not generally true for cyclic loops because $a_{m,m-1}$ and a_{m1} have opposite signs. In such a case, applying the equality in (8) and substituting $c_m = \prod_{i=1}^{m-1} |(a_{i,i+1}/a_{i+1,i})|$ in (9), we obtain (7), which is the extension to m species of the condition obtained by Krikorian for three species.

3. *General Models.* Now, consider a very general predator–prey system described by

$$\dot{N}_i = N_i K_i(N_1, \ldots, N_m), \; i = 1, \ldots, m, \tag{10}$$

where K_i are continuous functions with their first derivatives, and $(\partial K_i/\partial N_j)(\partial K_j/\partial N_i) \leq 0$. Suppose that there exists an isolated positive equilibrium point $\bar{\mathbf{N}}$ and let $K_{ij} = (\partial K_i/\partial N_j)_{\mathbf{N}=\bar{\mathbf{N}}}$ be the elements of the community matrix $\mathbf{A}$. Then, the Jacobian matrix of (10) evaluated at equilibrium is given by

$$\mathbf{J} = \mathrm{diag}(\bar{N}_1, \ldots, \bar{N}_m)\mathbf{A} = [\bar{N}_i K_{ij}]. \tag{11}$$

For any pair of indices (i, j), $i \neq j$, of $\mathbf{J}$ we put  if either K_{ij} or K_{ji} is different from zero. Owing to (11), the graph associated with $\mathbf{J}$ and $\mathbf{A}$ is the same.

If the graph is a tree (or a balanced loop) and $K_{ii} < 0$ for all i, then a constant diagonal positive matrix $\mathbf{C}$ exists such that $\mathbf{CJ} + \mathbf{J}^T\mathbf{C}$ is a negative diagonal matrix; therefore, $\mathbf{J}$ has eigenvalues with negative real part, that is, the equilibrium is locally asymptotically stable.

The same result can be obtained by the Liapunov function $\mathbf{W} = (\mathbf{N} - \bar{\mathbf{N}})^T\mathbf{C}(\mathbf{N} - \bar{\mathbf{N}})$, of which the time derivative $\dot{\mathbf{W}}$ is approximated by $(\mathbf{N} - \bar{\mathbf{N}})^T (\mathbf{CJ} + \mathbf{J}^T\mathbf{C})(\mathbf{N} - \bar{\mathbf{N}})$ when taking the linear part of (10) around the equilibrium $\bar{\mathbf{N}}$. Because of this approximation on $\dot{\mathbf{W}}$, the La Salle–Lefschetz extension theorem does not readily apply to general models.

Thus, we can conclude that for general models Theorem 1 and Corollary 2 still hold in the local sense, while Corollary 1 does not.

Concerning systems represented by trees, the local asymptotic stability may also be derived from a result of Quirk and Ruppert (1965) about sign stability.

It is also to be quoted the Goh's (1977) criterion for global asymptotic stability, in which the Jacobian matrix of (10) is evaluated in some point $\mathbf{N}^*$ between $\mathbf{N}$ and $\bar{\mathbf{N}}$. However, since $\mathbf{N}^*$ implicitly depends on time, we believe that, unless the particular case in which $\mathbf{J}+\mathbf{J}^T$ is negative definite, it is hard to find the constant matrix $\mathbf{C}$ which assures negative definiteness of $\mathbf{CJ}+\mathbf{J}^T\mathbf{C}$.

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