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STABILITY IN MODELS OF MUTUALISM

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In theoretical population biology mutualism has received very little attention compared to that given to prey-predator interactions or competition among species. May (1974) noted that this lack of interest in mutualism appears to have its roots in history, not biology. Well-known monographs on population dynamics by May (1974), Maynard Smith (1974), Pianka (1974), and Williamson (1972) define this type of interaction. However, these books give only very brief verbal discussions of mutualism as defined by Odum (1971). This unsatisfactory state of the theory of mutualism is surprising in view of the fact that mutualism, also called symbiosis, among animals and plants has been documented by Odum (1971), Henry (1966, 1967), Gilbert (1975) and Alexander (1971). In the literature there are very few mathematical models of mutualism. It appears that the first mathematical analysis of a mutualism between two species is given in the survey paper by Rescigno and Richardson (1973). Similar analyses were carried out by Albrecht et al. (1974) and Hirsch and Smale (1974). Recently May (1976) proposed and studied a new model of a mutualism between two species. A discussion of May's model is given in the book by Whittaker (1975). The mathematical theorems of Siljak (1975) for complex systems can be used to determine finite regions of stability for an equilibrium in a model of mutualism.

Here I shall describe some very general nonlinear models of mutualism and some simple tests to determine if a nonlinear model of a mutualism is globally stable or stable in a finite region. Compared with models of competition and prey-predator interactions, mutualistic models are more amenable to mathematical analysis. In the proposed tests for global stability in a nonlinear model of mutualism, it is helpful to understand the conditions for global stability in a Lotka-Volterra model of a mutualism. I shall establish that in Lotka-Volterra models of mutualism among any finite number of species, local stability implies global stability. Thus, ironically, this subset of Lotka-Volterra models which has been ignored by population theorists turns out to be the class of Lotka-Volterra models which is most tractable with respect to mathematical analysis.

Some ecologists (e.g., Watt 1968, p. 340) are quite skeptical about the relevance of Lotka-Volterra models in ecology. It is premature to write off this class of models. If direct and precise biological interpretations are not ascribed to the parameters in a Lotka-Volterra model, but the model is used in a phenomenological way as described by Swartz and Bremermann (1975), then a Lotka-Volterra model can

provide a robust description of the qualitative behavior of population interactions. The common criticism that the rate of increase per individual in the logistic model of a single species population is only a linear function is not as serious as some ecologists have believed. Consider the standard logistic model,

$$\dot{N} = (r/K)N(K - N). \quad (1)$$

Qualitatively this logistic model has the same stability behavior as a very general nonlinear model of a single species population,

$$\dot{N} = N\phi(N), \quad (2)$$

where (i) $\phi(N)$ is an autonomous and continuous function of N , (ii) $\phi(K) = 0$, and (iii) $\phi(N) > 0$ if $K > N > 0$ and $\phi(N) < 0$ if $N > K$. Both of the above models have a feasible equilibrium at $N = K$, and both are globally stable. In the same way it will be shown that members of a large class of nonlinear models of mutualism have the same qualitative behavior as members of a subset of Lotka-Volterra models of mutualism.

NONLINEAR MODELS OF MUTUALISM

By definition, in a mutualism (Odum 1971) between two species the interaction is beneficial for the growth of both species. In a commensalism between two species, one species benefits from the interaction while the other species is not affected. Some ecologists believe that commensal interactions occur more frequently in nature than mutualistic interactions. In a general mathematical analysis it is inconvenient to distinguish between these two types of interactions, and I shall use the word mutualism to refer to both interactions. It is only worthwhile to make the distinction between the two types when specific classes of models are considered.

Let $N_i(t)$ be the density of the i th species. Consider a mutualism among m species. Let a model of this interaction be

$$\dot{N}_i = N_i F_i(N_1, N_2, \dots, N_m), \quad \text{for } i = 1, 2, \dots, m. \quad (3)$$

Suppose this model has a feasible equilibrium at $(\bar{N}_1, \bar{N}_2, \dots, \bar{N}_m)$. This means $\bar{N}_i > 0$ for $i = 1, 2, \dots, m$ and

$$F_i(\bar{N}_1, \bar{N}_2, \dots, \bar{N}_m) = 0, \quad \text{for } i = 1, 2, \dots, m. \quad (4)$$

In mutualism, we have

$$\partial F_i(N_1, N_2, \dots, N_m) / \partial N_j \geq 0 \quad (5)$$

whenever $i \neq j$, and this inequality applies at every feasible point (N_1, N_2, \dots, N_m) . It can be shown that a necessary condition for the equilibrium to be stable is

$$\partial F_i(\bar{N}_1, \bar{N}_2, \dots, \bar{N}_m) / \partial N_i < 0 \quad (6)$$

for all $i = 1, 2, \dots, m$.

For convenience, let $N = (N_1, N_2, \dots, N_m)$ and $\bar{N} = (\bar{N}_1, \bar{N}_2, \dots, \bar{N}_m)$. Applying Taylor's theorem to each of the functions F_1, F_2, \dots, F_m in model (3), we get

$$\dot{N}_i = N_i \sum_{j=1}^m \frac{\partial F_i}{\partial N_j} (N_j - \bar{N}_j), \quad i = 1, 2, \dots, m. \quad (7)$$

For a given value of i the vector $(\partial F_i / \partial N_j)$ is computed at the point $\bar{N} + \theta_i(N - \bar{N})$ where $0 < \theta_i < 1$. In other words, the vector $(\partial F_i / \partial N_j)$ is computed at a point between \bar{N} and N . For a given value of i the vector $(\partial F_i / \partial N_j)$ is normal to the isocline $\{N | F_i(N) = \text{constant}\}$ which passes through the point $\bar{N} + \theta_i(N - \bar{N})$. Therefore if all the nonlinear isoclines of model (3) are not too different from hyperplanes the solutions of (3) would be qualitatively the same as the solutions of a Lotka-Volterra model.

For any nonlinear set of functions $F_i(N)$, where $i = 1, 2, \dots, m$, if the derivatives $\partial F_i / \partial N_j$ are continuous functions in a neighborhood of \bar{N} , model (3) can be approximated in a neighborhood of \bar{N} by the Lotka-Volterra equations,

$$\begin{aligned}\dot{N}_i &= N_i \sum_{j=1}^m \frac{\partial F_i(\bar{N})}{\partial N_j} (N_j - \bar{N}_j) \\ &= N_i \sum_{j=1}^m a_{ij}(N_j - \bar{N}_j),\end{aligned}\quad (8)$$

where $a_{ij} = \partial F_i(\bar{N}) / \partial N_j$. Note a_{ij} is independent of N . From (8) the linearized dynamics of model (3) in a neighborhood of \bar{N} is

$$\dot{N}_i = \bar{N}_i \sum_{j=1}^m a_{ij}(N_j - \bar{N}_j), \quad \text{for } i = 1, 2, \dots, m. \quad (9)$$

Let $x_i = N_i - \bar{N}_i$; these equations become

$$\dot{x}_i = \sum_{j=1}^m \bar{N}_i a_{ij} x_j, \quad \text{for } i = 1, 2, \dots, m. \quad (10)$$

The Lotka-Volterra model (8) can give more information on the behavior of model (3) than the linearized dynamics (10) could provide. This is because (8) is a quadratic model and is valid in a larger neighborhood than the linearized model.

For convenience the results established in this paper are summarized in theorems.

THEOREM 1. Model (3) is globally stable in the feasible region $\{N | N_i > 0, i = 1, 2, \dots, m\}$ if there exists positive constants c_1, c_2, \dots, c_m such that

$$\sum_{i=1}^m c_i (N_i - \bar{N}_i) F_i(N_1, N_2, \dots, N_m) \quad (11)$$

is negative in the region $\{N | N_i > 0, i = 1, 2, \dots, m; N \neq \bar{N}\}$.

The theorem is proved by means of the Lyapunov function (Goh 1977)

$$V(N) = \sum_{i=1}^m c_i \left[N_i - \bar{N}_i - \bar{N}_i \ln \left(\frac{N_i}{\bar{N}_i} \right) \right]. \quad (12)$$

The time derivative of $V(N)$ computed along solutions of model (3) is

$$\dot{V} = \sum_{i=1}^m c_i (N_i - \bar{N}_i) F_i(N_1, N_2, \dots, N_m). \quad (13)$$

When the conditions of the theorem are satisfied, $\dot{V}(N)$ is negative in the feasible region, less the equilibrium. Hence model (3) is globally stable in the feasible region.

COROLLARY 1. Let $V(N)$ be the function displayed in (12). If μ is a positive constant and $\dot{V}(N)$ is negative in the set

$$W = \{N \mid V(N) \leq \mu, N \neq \bar{N}\}, \quad (14)$$

then W is a finite region of attraction of the equilibrium \bar{N} .

There is a problem in the use of theorem 1. It may be difficult to verify that there is a suitable set of positive constants c_1, c_2, \dots, c_m so that the function $\dot{V}(N)$ is negative in the region $\{N \mid N_i > 0, i = 1, 2, \dots, m; N \neq \bar{N}\}$. One way to choose the positive constants c_1, c_2, \dots, c_m is to choose them so that the Lotka-Volterra model (8) which approximates (3) in a neighborhood of \bar{N} is globally stable. If this has been achieved $\dot{V}(N)$ given in (13) is examined, and tested to see if it is negative in the feasible region, less the equilibrium. If this condition is satisfied model (3) is globally stable. If not the corollary of theorem 1 is employed to establish stability in a finite region. Thus a good understanding of the global stability properties of Lotka-Volterra models is necessary. Another way to test whether $\dot{V}(N)$ is negative in the feasible region less the equilibrium \bar{N} is to maximize $\dot{V}(N)$ and establish it as a unique global maximum at \bar{N} .

The following theorem provides a convenient way to establish that $\dot{V}(N)$ is negative in the feasible region, less the equilibrium \bar{N} . It is possible for a model to satisfy theorem 1 but not theorem 2. In other words, theorem 1 is more general than theorem 2.

THEOREM 2. Model (3) is globally stable in the feasible region if the equilibrium \bar{N} is feasible and there exists positive constants c_1, c_2, \dots, c_m such that the matrix

$$(c_i \partial F_i / \partial N_j + c_j \partial F_j / \partial N_i) \quad (15)$$

is negative definite at every point in the feasible region $\{N \mid N_i > 0, i = 1, 2, \dots, m\}$.

Proof. Applying Taylor's theorem to (13) we get

$$\dot{V} = \sum_{i=1}^m c_i (N_i - \bar{N}_i) \frac{\partial F_i}{\partial N_j} (N_j - \bar{N}_j). \quad (16)$$

For a given value of i the vector $(\partial F_i / \partial N_j)$ is computed at $\bar{N} + \theta_i(N - \bar{N})$ and $0 < \theta_i < 1$. $\bar{N} + \theta_i(N - \bar{N})$ is a point on the line segment joining the points N and \bar{N} . In matrix notation, equation (16) is

$$\dot{V} = \left(\frac{1}{2}\right)(N - \bar{N})^T \left(\frac{c_i \partial F_i}{\partial N_j} + \frac{c_j \partial F_j}{\partial N_i} \right) (N - \bar{N}). \quad (17)$$

If the matrix

$$(c_i \partial F_i / \partial N_j + c_j \partial F_j / \partial N_i) \quad (18)$$

is negative definite at every feasible point, a fortiori the expression in (17) is negative definite. This completes the proof of the theorem.

COROLLARY 2. Let $c_1 = c_2 = \dots = c_m = 1$. It follows that model (3) is globally stable if the equilibrium \bar{N} is feasible and $(\partial F_i / \partial N_j + \partial F_j / \partial N_i)$ is negative definite at every feasible point.

THEOREM 3. Suppose there exists a constant matrix E such that at every feasible point model (3) satisfies the inequalities,

$$\partial F_i / \partial N_i \leq E_{ii} < 0 \quad \text{for } i = 1, 2, \dots, m, \quad (19)$$

and

$$E_{ij} \geq \partial F_i / \partial N_j \geq 0 \quad \text{for } i \neq j. \quad (20)$$

If the model has a feasible equilibrium and all the leading principal minors of $-E$ are positive then it is globally stable in the feasible region.

The proof of this theorem is given in the Appendix. The essence of theorem 3 is that if model (3) satisfies the conditions of the theorem, it has the same global stability property as the Lotka-Volterra model,

$$\dot{N}_i = N_i \sum_{j=1}^m E_{ij}(N_j - \bar{N}_j), \quad \text{for } i = 1, 2, \dots, m. \quad (21)$$

This again underlines the importance of Lotka-Volterra models for understanding the stability of complex nonlinear population models. Note that theorem 3 is less general than theorem 1.

COROLLARY 3. Let model (3) satisfy conditions (19) and (20) in the region

$$W' = \{N \mid V(N) \leq \mu'\}, \quad (22)$$

where μ' is a positive number. For each value of μ' we get a matrix E from conditions (19) and (20). Let the equilibrium \bar{N} be feasible. Model (3) is stable in the region W' if all the leading principal minors of $-E$ are positive.

Suppose we have a pure commensalism among m species. In the interaction between the i th and the j th species, one species profits from the interaction while the other species is unaffected. In the interaction between the i th species and the j th species, let the i th species profit from the interaction while the j th species is unaffected. If this is the case, we have

$$\partial F_i / \partial N_j > 0 \quad \text{and} \quad \partial F_j / \partial N_i = 0 \quad (23)$$

at every feasible point N . Without loss of generality, we can assume the matrix $(\partial F_i / \partial N_j)$ is an upper-triangle matrix. This can always be achieved in a pure commensalism by assigning the appropriate index to each species.

Suppose model (3) satisfies (19), (20), and (23). It follows that theorem 3 is automatically satisfied as matrix E is an upper-triangle matrix with negative diagonal elements, and hence all the leading principal minors of $-E$ are trivially positive. Hence in pure commensalism we have global stability if each species sustains density dependent mortalities due to intraspecific competition. The strength of the interactions between any pair of species in a pure commensalism do not play any role in the stability or instability of a commensal system.

TWO-SPECIES INTERACTIONS

In this section we shall examine in some detail a Lotka-Volterra model of a two-species mutualism. From the discussions in the previous section this detailed analysis would enable us to understand the global stability of a large class of nonlinear models of a two-species mutualism. It is convenient in the general analysis

not to make a distinction between mutualism and commensalism. With this abuse of terminology a Lotka-Volterra model of a mutualism is

$$\begin{aligned}\dot{N}_1 &= N_1[k_1 + a_{11}N_1 + a_{12}N_2] \\ \dot{N}_2 &= N_2[k_2 + a_{21}N_1 + a_{22}N_2]\end{aligned}\quad (24)$$

where $a_{12} \geq 0$ and $a_{21} \geq 0$.

The nontrivial equilibrium is the solution of the system of equations,

$$\begin{aligned}k_1 + a_{11}N_1 + a_{12}N_2 &= 0 \\ k_2 + a_{21}N_1 + a_{22}N_2 &= 0.\end{aligned}\quad (25)$$

Denote the nontrivial equilibrium by (\bar{N}_1, \bar{N}_2) . If \bar{N}_1 or \bar{N}_2 is negative the system (24) is unstable in the feasible region, $\{(N_1, N_2) | N_1 > 0, N_2 > 0\}$. Assume the equilibrium (\bar{N}_1, \bar{N}_2) belongs to the feasible region. The linearized dynamics of model (24) in a neighborhood of (\bar{N}_1, \bar{N}_2) is

$$\begin{aligned}\dot{x}_1 &= \bar{N}_1 a_{11}x_1 + \bar{N}_1 a_{12}x_2 \\ \dot{x}_2 &= \bar{N}_2 a_{21}x_1 + \bar{N}_2 a_{22}x_2,\end{aligned}\quad (26)$$

where $x_1 = N_1 - \bar{N}_1$, $x_2 = N_2 - \bar{N}_2$. The Routh-Hurwitz necessary and sufficient conditions for stability (see May 1974) are

$$\bar{N}_1 a_{11} + \bar{N}_2 a_{22} < 0 \quad (27)$$

and

$$\det(\bar{N}_i a_{ij}) > 0. \quad (28)$$

We have

$$\det(\bar{N}_i a_{ij}) = \bar{N}_1 \bar{N}_2 (a_{11}a_{22} - a_{12}a_{21}). \quad (29)$$

As $\bar{N}_1 > 0$, $\bar{N}_2 > 0$, $a_{12} \geq 0$, $a_{21} \geq 0$, condition (28) can only be satisfied if a_{11} and a_{22} are both nonzero and both have the same sign. By (27) it follows that

$$a_{11} < 0 \quad \text{and} \quad a_{22} < 0. \quad (30)$$

Conditions (28) and (29) imply that

$$\det A = a_{11}a_{22} - a_{12}a_{21} > 0. \quad (31)$$

In biological terms, condition (30) states that each species must sustain density dependent mortalities due to intraspecific competition. Otherwise, the system is unstable. This is similar to a two-species competition.

We now show that in model (24) local stability implies global stability. This model is globally stable in the feasible region if there exist positive constants c_1 and c_2 such that $CA + A^T C$ is negative definite. This is satisfied if

$$2c_1 a_{11} < 0 \quad (32)$$

and

$$\begin{aligned}\det(CA + A^T C) &= 4c_1 c_2 a_{11} a_{22} - (c_1 a_{12} + c_2 a_{21})^2 > 0, \\ 4c_1 c_2 (a_{11} a_{22} - a_{12} a_{21}) - (c_1 a_{12} - c_2 a_{21})^2 &> 0.\end{aligned}\quad (33)$$

If $a_{12} \neq 0$ and $a_{21} \neq 0$, let $c_2 = 1$ and choose c_1 so that

$$c_1 a_{12} - c_2 a_{21} = 0. \quad (34)$$

Condition (33) is satisfied as $\det A$ is positive. If $a_{12} = 0$, let $c_2 = 1$ and c_1 be a large positive number. Then condition (33) is satisfied as a_{11} and a_{22} are negative. If $a_{21} = 0$, we make a similar choice of the parameters, c_1 and c_2 . In brief, when model (24) is locally stable it is possible to choose positive constants, c_1 and c_2 , such that $CA + A^T C$ is negative definite. Hence in a Lotka-Volterra model of a two-species mutualism, local stability implies global stability. This result applies also in a Lotka-Volterra model of a mutualism among any number of species.

The conditions $a_{11} < 0$, $a_{22} < 0$, $a_{12} \geq 0$, and $a_{21} \geq 0$ imply that the isoclines

$$\begin{aligned} F_1(N_1, N_2) &= k_1 + a_{11}N_1 + a_{12}N_2 = 0 \\ F_2(N_1, N_2) &= k_2 + a_{21}N_1 + a_{22}N_2 = 0 \end{aligned} \quad (35)$$

have nonnegative slopes in the (N_1, N_2) space. If the nontrivial equilibrium is feasible, there are two cases depending on whether $\det A$ is positive or negative. In each case at least one of the parameters k_1 and k_2 must be positive. Let $u = (a_{11}, a_{12}, 0)$ and $v = (a_{21}, a_{22}, 0)$. These are the gradients (normals) of the isoclines $F_1(N_1, N_2) = 0$ and $F_2(N_1, N_2) = 0$, respectively. The vector product

$$u \times v = (0, 0, a_{11}a_{22} - a_{12}a_{21}) = (0, 0, \det A). \quad (36)$$

For stability, $\det A$ must be positive. Hence the vector $u \times v$ points in the direction outward and perpendicular to the (N_1, N_2) plane. If $\det A$ is negative, the equilibrium is unstable and $u \times v$ points in the other direction. In other words, for the equilibrium to be stable the angle between the u and v vectors in the anticlockwise direction from u to v must be positive and less than 180° . Examples of the first and second cases are given in figures 1 and 2, respectively. The main feature of this graphical analysis is that it directly utilizes the analytical condition which determines whether or not the equilibrium is stable.

In a two-species mutualism the inverse of the interaction matrix A can be computed explicitly. We have

$$A^{-1} = \frac{1}{\det A} \begin{pmatrix} a_{22} & -a_{12} \\ -a_{21} & a_{11} \end{pmatrix}. \quad (37)$$

When the equilibrium is stable we have $\det A > 0$, $a_{11} < 0$ and $a_{22} < 0$. Hence all the elements of A^{-1} are nonpositive. Clearly A^{-1} is associated with a Lotka-Volterra model of a competition or an amensalism between two species. Let $B = (b_{ij}) = A^{-1}$. If model (24) is stable there is associated with it a unique and stable Lotka-Volterra model of a two-species competition. It is

$$\dot{N}_i = N_i \sum_{j=1}^2 b_{ij}(N_j - \bar{N}_j), \text{ for } i = 1, 2. \quad (38)$$

Conversely, if we start with a stable Lotka-Volterra model of a two-species competition, the inverse of its interaction matrix is the interaction matrix of a stable Lotka-Volterra model of a mutualism. We deduce that in terms of the interaction

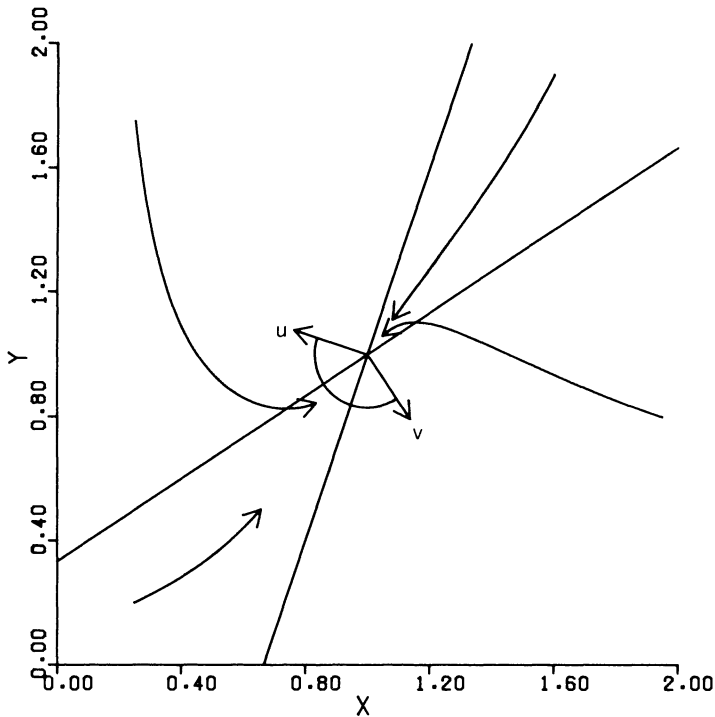


FIG. 1.—Computer solutions of a globally stable Lotka-Volterra model of a two-species mutualism. The equations are $\dot{N}_1 = N_1[2 - 3N_1 + N_2]$ and $\dot{N}_2 = N_2[1 + 2N_1 - 3N_2]$. For convenience we let $N_1 = X$ and $N_2 = Y$.

matrix the number of stable Lotka-Volterra models of mutualism between two species is exactly equal to the number of stable Lotka-Volterra models of competition between two species. Hence in terms of Lotka-Volterra models the statement that stable models of two-species mutualism are rarer than stable models of two-species competition is false. In the next section we shall find that this result is not true in interactions among three or more species.

LOTKA-VOLTERRA MODELS OF MUTUALISM

Let the Lotka-Volterra model,

$$\dot{N}_i = N_i[k_i + \sum_{j=1}^m a_{ij}N_j], \quad \text{for } i = 1, 2, \dots, m, \quad (39)$$

describe a mutualism among m species. Here by mutualism we mean each species promotes the growth of every other species or is unaffected by the interaction; hence $a_{ij} \geq 0$ whenever $i \neq j$. In this class of models, local stability implies global stability. Moreover, there is a very simple test for global stability. These results are summarized in theorem 4.

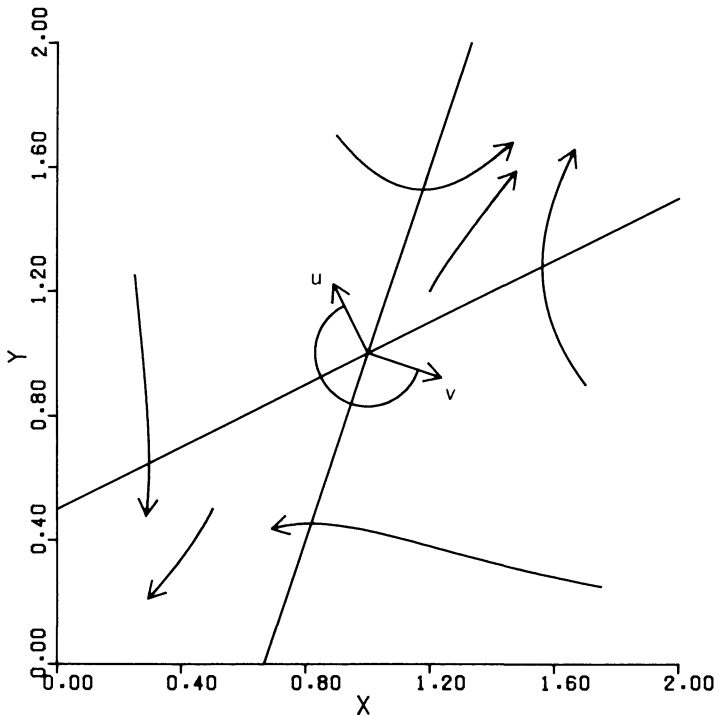


FIG. 2.—Computer solutions of an unstable Lotka-Volterra model of a two-species mutualism. The equations are $\dot{N}_1 = N_1[-1 - N_1 + 2N_2]$ and $\dot{N}_2 = N_2[-2 + 3N_1 - N_2]$. For convenience we let $N_1 = X$ and $N_2 = Y$.

THEOREM 4. If the nontrivial equilibrium of (39) is feasible, a necessary and sufficient condition for local and global stability is that all the leading principal minors of $-A$ are positive.

Proof. Let $x_i = N_i - \bar{N}_i$. The linearized dynamics of model (39) is

$$\dot{x}_i = \bar{N}_i \sum_{j=1}^m a_{ij} x_j, \quad \text{for } i = 1, 2, \dots, m. \quad (40)$$

As $\bar{N}_i > 0$ for $i = 1, 2, \dots, m$, the matrix $(\bar{N}_i a_{ij}) = \text{diag}(\bar{N}_1, \bar{N}_2, \dots, \bar{N}_m)A$, has the same sign pattern as A . A matrix whose off diagonal terms are all nonnegative is known as an M -matrix or a Metzler matrix. By a theorem due to Kotelyanskii (see Gantmacher 1959, p. 74), a necessary and sufficient condition for $(\bar{N}_i a_{ij})$ to be a stable matrix is that all the leading principal minors of $-(\bar{N}_i a_{ij})$ are positive. As $(\bar{N}_i a_{ij}) = \text{diag}(\bar{N}_1, \dots, \bar{N}_m)A$ and $\bar{N}_i > 0$ for $i = 1, 2, \dots, m$, all the leading principal minors of $-(\bar{N}_i a_{ij})$ are positive if and only if all the leading principal minors of $-A$ are positive. It follows that the condition on matrix A in the theorem is a necessary and sufficient condition for (39) to have a locally stable equilibrium.

By means of the Lyapunov function (12) we deduce that a sufficient condition for (39) to be globally stable is that there exists a positive diagonal matrix C such that $CA + A^T C$ is negative definite. Johnson (1974) has established that if an M -matrix is

stable then there exists a positive diagonal matrix, $C = \text{diag}(c_1, c_2, \dots, c_m)$, such that $CA + A^T C$ is negative definite. Hence model (39) is globally stable when A is a stable matrix. This is the case when all the leading principal minors of $-A$ are positive.

Theorem 4 can be considered as a special case of theorem 3. The latter applies to a general class of nonlinear models of mutualism while theorem 4 applies only to Lotka-Volterra models. An interesting biological consequence of theorem 4 is that for stability each species must sustain density dependent mortalities due to intraspecific competition. This is as expected.

If $(\bar{N}_1, \bar{N}_2, \dots, \bar{N}_m)$ is the feasible equilibrium, model (39) can be rewritten in the form,

$$\dot{N}_i = N_i \sum_{j=1}^m a_{ij}(N_j - \bar{N}_j) \text{ for } i = 1, 2, \dots, m. \quad (41)$$

Let $B = (b_{ij}) = A^{-1}$. We can associate with model (41) the model

$$\dot{N}_i = N_i \sum_{j=1}^m b_{ij}(N_j - \bar{N}_j) \text{ for } i = 1, 2, \dots, m. \quad (42)$$

Theorem 5 describes a very interesting relationship between models (41) and (42).

THEOREM 5. If model (41) is a globally stable model of mutualism, model (42) is a globally stable model of competition.

Proof. If model (41) describes a mutualism, the off-diagonal elements of the matrix A are nonnegative. Such a matrix is called an M -matrix. A well known property of a stable M -matrix is that the elements of its inverse are nonpositive (Fiedler and Ptak 1962). Hence we have

$$B_{ij} \leq 0 \text{ for } i, j = 1, 2, \dots, m. \quad (43)$$

It follows that model (42) is a model of a competition or an amensalism.

In the proof of theorem 4 we noted that if model (41) is globally stable there exists a positive diagonal matrix C such that $CA + A^T C$ is negative definite. Let

$$\begin{aligned} CA + A^T C &= G \\ \Rightarrow (A^{-1})^T C + CA^{-1} &= (A^{-1})^T G A^{-1} \\ B^T C + CB &= (A^{-1})^T G A^{-1} \end{aligned} \quad (44)$$

As A^{-1} is nonsingular, the matrix $(A^{-1})^T G A^{-1}$ is negative definite if G is negative definite. Employ Lyapunov function (12); it follows that (42) is globally stable. This completes the proof of the theorem.

Example 1.—Consider the following model of a mutualism among three species:

$$\begin{aligned} \dot{N}_1 &= N_1[0.5 - 2N_1 + N_2 + 0.5N_2] \\ \dot{N}_2 &= N_2[-3 + 5N_1 - 4N_2 + 2N_3] \\ \dot{N}_3 &= N_3[4 + N_1 + 2N_2 - 7N_3]. \end{aligned} \quad (45)$$

The nontrivial equilibrium is at (1, 1, 1). If A denotes the interaction matrix, all the leading principal minors of $-A$ are positive. By theorem 4, model (45) is globally stable. If $C = \text{diag}(5, 1, 1)$,

$$CA + A^T C = \begin{bmatrix} -20 & 10 & 3.5 \\ 10 & -8 & 4 \\ 3.5 & 4 & -14 \end{bmatrix}. \quad (46)$$

This matrix is negative definite. This confirms that model (45) is globally stable.

The inverse of the interaction matrix of (45) is given by

$$-B = -A^{-1} = \begin{bmatrix} 6 & 2 & 1 \\ 9.25 & 3.375 & 1.625 \\ 3.5 & 1.25 & 0.75 \end{bmatrix}. \quad (47)$$

Thus associated with model (45) is a globally stable Lotka-Volterra model of a three-species competition. It is

$$\begin{aligned} \dot{N}_1 &= N_1[9 - 6N_1 - 2N_2 - N_3] \\ \dot{N}_2 &= N_2[14.25 - 9.25N_1 - 3.375N_2 - 1.625N_3] \\ \dot{N}_3 &= N_3[5.5 - 3.5N_1 - 1.25N_2 - 0.75N_3]. \end{aligned} \quad (48)$$

Again the equilibrium is at (1, 1, 1). If $C = \text{diag}(5, 1, 1)$, we have

$$-(CB + B^T C) = \begin{bmatrix} 60.0 & 19.25 & 8.5 \\ 19.25 & 6.75 & 2.875 \\ 8.5 & 2.875 & 1.5 \end{bmatrix}. \quad (49)$$

The matrix $CB + B^T C$ is negative definite. This confirms (48) is globally stable.

Example 2.—The following competition matrix is given in the monograph by Levins (1968):

$$\alpha = \begin{bmatrix} 1 & .30 & .42 & .61 & .16 \\ .72 & 1 & .92 & .72 & .6 \\ .88 & .81 & 1 & .96 & .47 \\ .90 & .44 & .67 & 1 & .38 \\ .18 & .28 & .25 & .29 & 1 \end{bmatrix}. \quad (50)$$

Let $(\bar{N}_1, \bar{N}_2, \dots, \bar{N}_5)$ be the feasible equilibrium. Consider the abstract competition model

$$\dot{N}_i = N_i \sum_{j=1}^5 (-\alpha_{ij})(N_j - \bar{N}_j) \quad \text{for } i = 1, 2, \dots, 5. \quad (51)$$

This model is an abstract model, as the α matrix is not usually used in this manner. We can show that $\alpha + \alpha^T$ is positive definite. Hence (51) is globally stable.

However we have approximately

$$\alpha^{-1} = \begin{bmatrix} 2.31 & -0.34 & 0.30 & -1.53 & 0.27 \\ -0.88 & 5.47 & -6.48 & 3.20 & -1.31 \\ 0.76 & -5.75 & 9.67 & -5.90 & 1.03 \\ -2.32 & 1.98 & -4.10 & 5.17 & -0.83 \\ 0.31 & -0.61 & 0.53 & -0.64 & 1.31 \end{bmatrix}. \quad (52)$$

Note that some of the off diagonal terms of $-\alpha^{-1}$ are negative. Hence the inverse of the interaction matrix of a globally stable Lotka-Volterra model of a competition may not be an interaction matrix for a Lotka-Volterra model of mutualism. It is also possible to construct a three-species example that has the same property.

From theorem 5 and example 2 it is concluded that the continuum of globally stable Lotka-Volterra models of mutualism among three or more species is smaller than the continuum of globally stable Lotka-Volterra models of competition among the same number of species. It can be shown that the continuum of globally stable Lotka-Volterra models of a single-prey and a single-predator interaction is larger than the continuum of globally stable Lotka-Volterra models of competition between two species. These results support the hypothesis of some ecologists that in nature mutualism and commensalism are relatively rare in comparison with competition and prey-predator interactions.

An interesting consequence of theorem 5 is that an effective way to establish global stability of some Lotka-Volterra models of competition is to examine the inverse of the interaction matrix.

DISCUSSION

An interesting result in this analysis is that the continuum of globally stable Lotka-Volterra models of mutualism among three or more species is smaller than the continuum of globally stable Lotka-Volterra models of competition among the same number of species. It can also be shown that the continuum of globally stable Lotka-Volterra models of competition is smaller than the continuum of globally stable Lotka-Volterra models of prey-predator interactions involving the same number of species. This lends support to the expectation among some theoretical population biologists that in nature mutualism and commensalism are relatively less common compared with competition and prey-predator interactions. However, as pointed out by a reviewer of this paper, there is a serious gap between this mathematical result and what actually happens in nature. One immediate problem is that experimental ecologists have not measured the relative frequency of mutualism vis-à-vis competition or prey-predator interactions in nature. Incidentally, May's (1974) major contribution to ecology that in the mathematical universe stability decreases with diversity suffers from a similar difficulty in that there is a gap between the mathematical result and what actually happens in the real world. Similarly, the results established by Goh (1975), that diversity per se does not make a model ecosystem less vulnerable to an unpredictable and continual disturbance, suffers from the same difficulty. Nevertheless, each of these results provides some insight into the factors that affect the stability of a complex ecosystem.

Theorem 3 requires that the leading principal minors of a certain matrix must be positive. Biologically this means that if each species in a mutualism sustains density dependent mortalities due to intraspecific interaction, and if the combined strength of the interspecific interactions for each species, measured in a certain way, is weaker than the strength of its intraspecific interactions, then the mutualism is globally stable. In this way a complex mutualism has the stability property of a collection of isolated single species populations, each of which has a positive carrying capacity. This is the

robust strategy which real populations can use, irrespective of the type of interactions they are engaged in, in order to enhance the stability of their overall ecosystems.

Global stability is established in a large class of nonlinear differential equation models of mutualism. This result implies that the corresponding interactions in the real world have properties which help them to persist. However, we must remember that a differential equation model is usually unable to adequately represent an interaction when one or more of its populations are at very low levels. Also, global stability does not necessarily ensure that a model ecosystem can persist if it is continually disturbed (Goh 1976).

If a model of a two-species mutualism has an unstable equilibrium, both species may increase indefinitely from certain initial states (see fig. 2). This unrealistic behavior occurs in Lotka-Volterra models, May's (1976) model of mutualism, and other nonlinear models of mutualism. Hence such models with an unstable equilibrium cannot be valid globally. However, this type of failure in a population model at points far away from an equilibrium is not peculiar to mutualistic interactions. In the prey-predator model,

$$\dot{N}_1 = N_1(5.6 - 0.5N_1 - 0.6N_2) \quad (53a)$$

$$\dot{N}_2 = N_2(-11 + N_1 + N_2), \quad (53b)$$

the solution from the initial state (11, 3) tends rapidly towards the point (0, ∞). Clearly this model is invalid when the prey density N_1 is small and the predator density is large. When this type of breakdown occurs in a model, the overall behavior of the system in the real world can be described by the behavior of several models, each of which is valid in a portion of the state space.

SUMMARY

A simple test for global stability in a large class of nonlinear models of mutualism is derived. In Lotka-Volterra models of mutualism, local stability implies global stability. In the space of the interaction parameters, the continuum of stable Lotka-Volterra models of two-species mutualism is equal to the continuum of stable Lotka-Volterra models of competition, but it is smaller than the continuum of stable Lotka-Volterra models of a single-prey and a single-predator interaction. For three or more species the continuum of globally stable Lotka-Volterra models of mutualism is smaller than the continuum of globally stable Lotka-Volterra models of competition or prey-predator interactions. This mathematical result suggests that in nature mutualism is less common than competition and predation.

APPENDIX

Proof of theorem 3. At every feasible point N , we have

$$\dot{N}_i = N_i F_i(N_1, N_2, \dots, N_m), \quad i = 1, 2, \dots, m \quad (A1)$$

where

$$\partial F_i(N)/\partial N_i \leq E_{ii} < 0, \quad i = 1, 2, \dots, m \quad (A2)$$

and

$$E_{ij} \geq \partial F_i(N)/\partial N_j \geq 0 \quad \text{if } i \neq j. \quad (\text{A3})$$

The matrix $E = (E_{ij})$ is a constant matrix.

Let c_1, c_2, \dots, c_m be positive constants which will be specified later. A Lyapunov function for model (A1) is

$$V(N) = \sum_{i=1}^m c_i \left[N_i - \bar{N}_i - \bar{N}_i \ln \left(\frac{N_i}{\bar{N}_i} \right) \right], \quad (\text{A4})$$

where $\bar{N} = (\bar{N}_1, \bar{N}_2, \dots, \bar{N}_m)$ is a feasible equilibrium of model (A1).

Computing $\dot{V}(N)$ along solutions of model (A1) we get

$$\begin{aligned} \dot{V}(N) &= \sum_{i=1}^m c_i (N_i - \bar{N}_i) F_i(N) \\ &= \sum_{i=1}^m \frac{c_i (N_i - \bar{N}_i) \partial F_i[\bar{N} + \theta_i(N - \bar{N})]}{\partial N_j}, \end{aligned} \quad (\text{A5})$$

where $0 < \theta_i < 1$. This condition is obtained by an application of Taylor's theorem. Conditions (A2), (A3), and (A5) imply

$$\dot{V}(N) \leq \sum_{i=1}^m c_i E_{ii} (N_i - \bar{N}_i)^2 + \sum_{j \neq i} c_i E_{ij} |N_i - \bar{N}_i| |N_j - \bar{N}_j|. \quad (\text{A6})$$

Let $p_i = |N_i - \bar{N}_i|$ for $i = 1, 2, \dots, m$, $p = (p_i)$ and $C = \text{diag}(c_1, c_2, \dots, c_m)$. Condition (A6) implies

$$\dot{V}(N) \leq \frac{1}{2} p^T (CE + E^T C) p. \quad (\text{A7})$$

A matrix whose diagonal elements are negative and whose off-diagonal elements are positive is an M -matrix. From (A2) and (A3) the matrix E is an M -matrix. If the leading principal minors of $-E$ are positive, then there exists a positive diagonal matrix C such that $CE + E^T C$ is negative definite (see Johnson 1974). From (A7) this implies that $\dot{V}(N)$ is negative for all N such that $N_i > 0$, $i = 1, 2, \dots, m$ and $N \neq \bar{N}$. Hence model (A1) is globally stable.

If we replace condition (A3) by the condition

$$E_{ij} \geq |\partial F_i(N)/\partial N_j| \geq 0 \quad (\text{A8})$$

whenever $i \neq j$, theorem 3 is applicable to a large class of nonlinear population models which can contain any kind of population interactions in the same system. These could be competitive, prey-predator, and mutualistic interactions.

LITERATURE CITED

- Albrecht, F., H. Gatzke, A. Haddad, and N. Wax. 1974. The dynamics of two interacting populations. *J. Math. Anal. Appl.* 46: 658-670.
- Alexander, M. 1971. *Microbial ecology*. Wiley, New York.
- Fiedler, M., and V. Ptak. 1962. On matrices with non-positive off diagonal elements and positive principal minors. *Czech. Math. J.* 12: 382-400.
- Gantmacher, F. R. 1959. *The theory of matrices*. Vol. 2. Chelsea, New York.
- Gilbert, L. E. 1975. Ecological consequences of a coevolved mutualism between butterflies and plants. Pages 210-239 in L. E. Gilbert and P. H. Raven, eds. *Coevolution of animals and plants*. University of Texas Press, Austin.
- Goh, B. S. 1975. Stability, nonvulnerability and persistence of complex ecosystems. *Ecol. Model.* 1:105-116.

- . 1976. Nonvulnerability of ecosystems in unpredictable environments. *Theor. Pop. Biol.* 10:83–95.
- . 1977. Global stability in many-species systems. *Am. Nat.* 111:135–143.
- Henry, S. M. 1966. *Symbiosis*. Vol. 1. Academic Press, New York.
- . 1967. *Symbiosis*. Vol. 2. Academic Press, New York.
- Hirsch, M. W., and S. Smale. 1974. *Differential equations, dynamical systems, and linear algebra*. Academic Press, New York.
- Johnson, C. D. 1974. Sufficient conditions for *D*-stability. *J. Econ. Theory* 9:53–62.
- Levins, R. 1968. *Evolution in changing environments*. Princeton University Press, Princeton, N.J.
- May, R. M. 1974. *Stability and complexity in model ecosystems*. 2d ed. Princeton University Press, Princeton, N.J.
- . 1976. Models for two interacting populations. Pages 49–70 in R. M. May, ed. *Theoretical ecology: principles and applications*. Blackwell, Oxford.
- Maynard Smith, J. 1974. *Models in ecology*. Cambridge University Press, Cambridge.
- Odum, E. P. 1971. *Fundamentals of ecology*. 3d ed. Saunders, Philadelphia.
- Pianka, E. R. 1974. *Evolutionary ecology*. Harper & Row, New York.
- Rescigno, A., and E. W. Richardson. 1973. The deterministic theory of population dynamics. Pages 283–360 in R. Rosen, ed. *Foundations of mathematical biology*. Vol. 3. Academic Press, New York.
- Siljak, D. D. 1975. Connective stability of competitive equilibrium. *Automatica* 11:389–400.
- Swartz, J., and H. J. Bremermann. 1975. Discussion of parameter estimation in biological modelling: algorithms for estimation and evaluation of the estimates. *J. Math. Biol.* 1:241–257.
- Watt, K. E. F. 1968. *Ecology and resource management*. McGraw-Hill, New York.
- Whittaker, R. H. 1975. *Communities and ecosystems*. 2d ed. Macmillan, New York.
- Williamson, M. 1972. *The analysis of biological populations*. Arnold, London.