

Predator-Prey Patterns

(Volterra-Lotka equations)

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Communicated by Robert Zwanzig, May 9, 1973

ABSTRACT A graph-theoretic condition is given for the existence of stable solutions to the Volterra-Lotka equations.

§1. INTRODUCTION

Volterra (1, 2) and others proposed the system of equations

$$\dot{x}_i = \epsilon_i x_i + \sum_j a_{ij} x_i x_j \quad i = 1, \dots, n \quad [1]$$

to describe biological competition between n species. In these equations x_i is the population of the i th species—thus, we consider only solutions with $x_i(t) > 0$ for all i ; ϵ_i is a growth coefficient, positive or negative; and $A = (a_{ij})$ is the matrix of interaction coefficients. Because of the reciprocal nature of predator-prey relations, A will usually be assumed antisymmetric, that is $a_{ij} = -a_{ji}$.

We will say system 1 is *stable* if all species $x_i(t)$ remain bounded for all time and remain bounded away from 0, and we require this to be true for all ϵ close to the original choice. Volterra showed that if

$$Ax^0 + \epsilon = 0 \quad [2]$$

has no solution, then the system cannot be stable; note that the solution of Eq. 2 is a constant solution for system 1. For each solution $x(t)$, there will be a component x_i which is either unbounded on some sequence $t_n \rightarrow \infty$ or $x_i(t) \rightarrow 0$ as $t \rightarrow \infty$. [Kerner (3-5) and Resigno (6-8) have studied specific situations in which a species dies out.] Volterra showed that system 1 is stable if A is nonsingular and ϵ is chosen so that the constant solution has positive coordinates. Of course such an ϵ can be chosen, such as $\epsilon = A(1, \dots, 1)^T$.

There is a network associated with system 1. Each node represents a species and the i th node or species is connected to the j th when i feeds on j or vice versa, that is when $a_{ij} \neq 0$. Not all networks "are stable"; that is, there are some networks for which no choice of ϵ and A , chosen so as to give the network, is stable. Volterra mentioned that the antisymmetry of A implied that the number of species must be even. The Volterra-Lotka exclusion principle is a more general restriction. Using a simplified method for calculating determinants of antisymmetric matrices, Goel, Maitra, and Montroll (9) were able to give a network of 12 species that is stable and another that is not. The main result of this paper gives a simple characterization of stable networks. We show the network is stable if and only if the set of species can be separated into nonoverlapping pairs, such that in each pair one of the species eats the other.

§2. PREDATOR-PREY NETWORKS

In conjunction with the matrix A we consider the network G , called the *predator-prey network*. The nodes of G are the species and two species are joined by an edge if and only if the corresponding $a_{ij} \neq 0$. If $a_{ij} > 0$ we call the species i the *predator* and species j the *prey* of the pair (i, j) . In this case the interaction of the species tends to promote the immediate growth of the i th species at the expense of the j th.

A set M of edges of the network G is called a *predator-prey pairing* if no species is a node of more than one edge of M ; necessarily an even number of species is represented in M . A *complete predator-prey pairing* is a predator-prey pairing in which all species are represented. Thus if n is odd, there can be no complete predator-prey pairing.

THEOREM 1. *Let A be an antisymmetric matrix and G the network associated with A . Then if A is nonsingular, the network G has a complete predator-prey pairing. Conversely, if G has a complete predator-prey pairing, then there exists an antisymmetric nonsingular matrix B for which G is also the network; moreover, B may be chosen arbitrarily close to A .*

The proof will be given in section 4.

If n is odd, then, as noted above, no complete predator-prey pairing can exist. Thus, the Volterra-Lotka exclusion principle is a special case of our theorem.

In networks describing predator-prey relations, arrows are commonly drawn from the predator to the prey; we will not do this since the directions do not appear in the statement of our theorem.

In Fig. 1a, one of the classical patterns, there is no complete predator-prey pairing since the number of species is odd. It has been frequently mentioned [for a survey see Hardin (10)] that if two predators feed on one prey species, the situation—

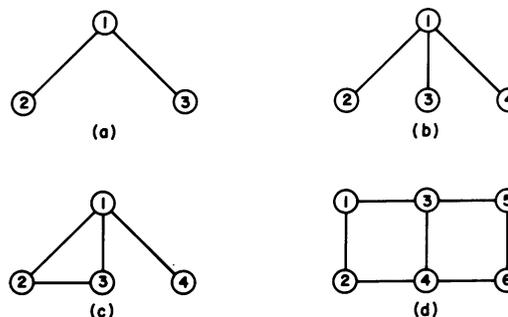


FIG. 1. Predator-prey networks.

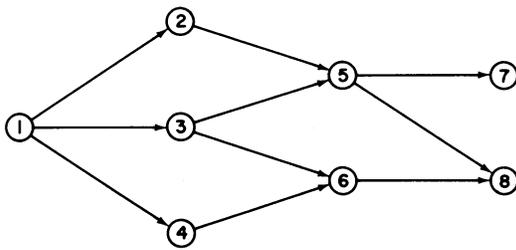


FIG. 2. A network with trophic levels.

to the extent that it is correctly described by system 1—is not stable. Our theorem shows that the two other ways of drawing the arrows (two preys and one predator, and a species 2 preys on species 1 preys on species 3 chain) are also **unstable**.

In Fig. 1b, even though n is even, there is still no complete pairing. Fig. 1c is 1b with one edge added, and now there is a complete pairing. In Fig. 1d there are in fact three choices for a complete pairing.

In Fig. 1c and d, possible choices for a nonsingular matrix A are, respectively:

$$\begin{bmatrix} 0 & .1 & .1 & 1 \\ -.1 & 0 & 1 & 0 \\ -.1 & -.1 & 0 & 0 \\ -1 & 0 & 0 & 0 \end{bmatrix} \quad \begin{bmatrix} 0 & 1 & .1 & 0 & 0 & 0 \\ -1 & 0 & 0 & .1 & 0 & 0 \\ -.1 & 0 & 0 & 1 & .1 & 0 \\ 0 & -.1 & -1 & 0 & 0 & .1 \\ 0 & 0 & -.1 & 0 & 0 & 1 \\ 0 & 0 & 0 & -.1 & -1 & 0 \end{bmatrix}$$

§3. TROPHIC PATTERNS

We will call a predator-prey network *trophic* if there is a subset S of species such that no species in S feeds on any species of S , and species not in S feed only on species in S . The biological networks studied by system 1 are often assumed to have distinct trophic levels in which each species in one trophic level feeds only on species in the next lower trophic level; the species in the lowest trophic level do not feed on any of the species of the network. That a network with trophic levels is in fact trophic may be seen by letting S be the union of the trophic levels at an odd “distance” from the bottom level. The network of Fig. 1d is trophic; the existence of trophic levels depends on the direction of the arrows.

The assumption that G is antisymmetric is biologically rather restrictive. For a general predator-prey system we would expect only a_{ij} and a_{ji} to have opposite signs. In fact if species i and j were mutually antagonistic, we might have both signs negative.

THEOREM 2. *Let A be a nonsingular matrix. Assume that the corresponding network G is trophic. Then G has a complete predator-prey pairing.*

This result is proved in the next section.

Let G be a network with trophic levels corresponding to a nonsingular A . Let λ_i be the number of species in trophic level i , $i = 1, \dots, T$. It follows immediately from *Theorem 2* that the following results must be true.

If $T = 2$, then $\lambda_1 = \lambda_2$. [3a]

If $T = 3$, then $\lambda_1 + \lambda_3 = \lambda_2$. [3b]

If $T > 3$, we may write $\lambda_i = \alpha_i + \beta_i$ for $i = 1, \dots, T$, [3c]

where α_i and β_i are nonnegative integers such that $\alpha_i = \beta_T = 0$ and $\beta_i = \alpha_{i+1}$.

These necessary conditions often simplify the hunt for a complete predator-prey pairing. In Fig. 2a below, the conditions are not met; thus, no complete pairing exists.

§4. PROOF OF THE THEOREMS

Let A be an $n \times n$ antisymmetric matrix and G the associated network.

Suppose that G has a complete predator-prey pairing M . Define the matrix $B(z)$ by $b_{ij} = a_{ij}$ if the edge joining node i to node j is in M , and $b_{ij} = za_{ij}$ otherwise, where z is a variable. Then the determinant $|B(z)|$ of $B(z)$ is given by

$$|B(z)| = \pm \prod a_{ij} a_{jt} + p(z) \tag{4}$$

where the product is taken over the edges of M and $p(z)$ is a polynomial with constant term 0. Then for $z = 0$, $|B(z)|$ is nonzero, and thus is nonzero for all but finitely many values of z . We can then choose z_0 arbitrarily close to 1 (but perhaps not equal), and let $B = B(z_0)$. Half of *Theorem 1* is thus proved.

To prove the existence of the complete pairings claimed by *Theorems 1 and 2*, assume $|A| \neq 0$ and consider the terms in the expansion of the determinant of A

$$|A| = \sum_{\pi} \pm a_{1\pi(1)} \dots a_{n\pi(n)} \tag{5}$$

where the sum is over all $n!$ permutations π of n . First form from G the network G' having directed edges: G' has a directed edge from i to j if and only if $a_{ij} \neq 0$. If a_{ij} and a_{ji} are both nonzero, there will be two edges between i and j . If t is one of the nonzero products summed in Eq. 5, then t is associated with a subgraph G_t'' of G' in which each node of G_t'' is the head of exactly one edge and the tail of exactly one edge. By Euler's theorem (11), chap. 17, G_t'' is then a disjoint union of directed cycles. If all these cycles have even lengths, then we can construct a complete predator-prey pairing for G by taking alternate edges in each cycle and erasing the arrows. If G is trophic, then clearly all cycles must have even length, and so we have now proved *Theorem 2*.

We now continue, assuming A is antisymmetric and for each summand t in Eq. 5, there is a cycle of odd length in G_t'' . The nonzero terms in Eq. 5 may be grouped together into classes according to whether they yield the same G_t'' , allowing either orientation of each cycle. Each class C is the determinant of the anti-symmetric matrix A^C , where $a^c_{ij} = a_{ij}$ if (i,j) is an edge of G_t'' and $=0$ otherwise. Reordering the species if necessary, A^C becomes a block diagonal matrix, each block corresponding to a nonoriented cycle of G_t'' , and so $|A^C|$ is the product of the determinants of the block submatrices, times ± 1 . But the antisymmetric block matrix corresponding to the odd order cycle must have determinant 0. Hence $|A| = 0$, contradicting our assumption. Hence, there must be a t in Eq. 5 all of whose cycles have even order, which thus yields a complete pairing.

If there is a large number of species, it might seem a considerable task to determine if there is a complete predator-prey pairing. Fortunately, an algorithm is available, due to Edmonds (12). This algorithm actually finds a pairing of maximum cardinality, and thus a complete pairing if one exists. In graph-theory literature, a predator-prey pairing is called a *matching*, and a trophic network is called *bipartite*.

We thank C. Tickamyer for his helpful comments. This research was partially supported under National Science Foundation Grant GP-31386X1.

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