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POPULATION DYNAMICS VIA GAMES THEORY AND MODIFIED VOLTERRA EQUATIONS

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Volterra's system of differential equations for n interacting species has been modified and it is shown that the modified system is equivalent to the system of cubic differential equations obtained earlier for animal conflicts from considerations of theory of games. The growth of the total population size has been examined and the new model has also been generalized.

INTRODUCTION

Maynard Smith and Price (1973) and Maynard Smith (1974, 1976) gave a static model for the evolution of animal conflicts by using concepts from the theory of games. Later Taylor and Jonker (1978) and Zeeman (1979a, b) introduced a dynamic into the model. Zeeman (1979b) obtained a system of cubic differential equations and discussed the existence of repellors and attractors as well as the flows on an $(n + 1)$-simplex. Earlier the same system of cubic differential equations had cropped up at the other end of the evolutionary scale in the model of Schuster *et al.* (1978, 1979) for the evolution of macromolecules.

Animal conflicts arise due to competition for territory or mates. Competition among species for resources is also discussed by using Volterra's system of non-linear differential equations (Goel *et al.* 1971). In the present paper, we attempt to reconcile the two approaches by obtaining Zeeman's system of cubic differential equations from Volterra's modified equations and vice versa.

VOLTERRA'S MODIFIED AND ZEEMAN'S SYSTEMS OF DIFFERENTIAL EQUATIONS

Let $N_i(t)$ denote the population of the ith species at time t, then Volterra's system of equations is

$$\frac{dN_i}{dt} = k_i N_i + N_i \sum_{j=1}^{n} a_{ij} N_j; \; i = 1, 2, ..., n. \qquad ...(1)$$

Considering the case when $k_i = 0$, we get

$$\frac{dN_i}{dt} = N_i \sum_{j=1}^{n} a_{ij} N_j; \; i = 1, 2, ..., n \qquad ...(2)$$

so that the growth of the populations of the n species depends only on the interactions between the species. Here the contribution of the jth species to the growth rate of the ith species is taken to be $a_{ij}N_iN_j$. This contribution can also depend on the total population size $N(t)$ of all species since this size will determine the availability of the resources to the ith species; the larger the value of N, the smaller will be the resources available to the ith species and the smaller will be its growth rate. Thus we modify Volterra's equations to get

$$\frac{dN_i}{dt} = \frac{N_i}{N} \sum_{j=1}^{n} a_{ij}N_j, \; i = 1, 2, \ldots, n \qquad \ldots(3)$$

where

$$N(t) = N_1(t) + N_2(t) + \ldots + N_n(t). \qquad \ldots(4)$$

Now let $x_i(t)$ denote the proportion of the population of the ith species so that

$$x_i(t) = \frac{N_i(t)}{N(t)}, \; i = 1, 2, \ldots, n \qquad \ldots(5)$$

then

$$\frac{\dot{x}_i}{x_i} = \frac{\dot{N}_i}{N_i} - \frac{\dot{N}}{N} = \sum_{j=1}^{n} \frac{a_{ij}N_j}{N} - \frac{\sum_{i=1}^{n} \dot{N}_i}{N}$$

$$= \frac{\sum_{j=1}^{n} a_{ij}N_j}{N} - \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} a_{ij}N_iN_j}{N^2}$$

$$= \sum_{j=1}^{n} a_{ij}x_j - \sum_{i=1}^{n} \sum_{j=1}^{n} a_{ij}x_ix_j$$

$$= (AX)_i - (X^TAX) \qquad \ldots(6)$$

where X is the column matrix $[x_1, x_2, \ldots, x_n]$, X^T is its transposed row matrix, A is the matrix (a_{ij}) and $(AX)_i$ denotes the ith element of the column matrix AX. From (6)

$$\dot{x}_i = x_i\,[(AX)_i - (X^TAX)], \; i = 1, 2, \ldots, n \qquad \ldots(7)$$

which is the system of cubic differential equations obtained by Zeeman (1979b). In his case x_i denotes the proportion of the population following the ith strategy and A is the corresponding $n \times n$ pay-off matrix. The pay-offs determine the reprodutive capacities of the groups.

Conversely from (5) and (7)

$$\frac{\dot{N}_i}{N_i} - \frac{\dot{N}}{N} = \Big(\sum_{j=1}^{n} a_{ij}N_j\Big)\Big/N - \Big(\sum_{i=1}^{n}\sum_{j=1}^{n} a_{ij}N_iN_j\Big)\Big/N^2. \qquad \ldots(8)$$

We have to solve for $\dot{N}_1(t)$, $\dot{N}_2(t)$, ..., $\dot{N}_n(t)$ from (8). The solution is obviously given by

$$\frac{\dot{N}_i}{N_i} = \left(\sum_{j=1}^{n} a_{ij} N_j \right) \Big/ N, \; i = 1, 2, \ldots, n \qquad \ldots(9)$$

since when (9) is satisfied

$$\frac{\dot{N}}{N} = \left(\sum_{i=1}^{n} \dot{N}_i \right) \Big/ N = \sum_{i=1}^{n} \sum_{j=1}^{n} a_{ij} N_i N_j \Big) \Big/ N^2. \qquad \ldots(10)$$

Growth of the Total Population Size

From (3) and (4)

$$\frac{dN}{dt} = \left(\sum_{i=1}^{n} \sum_{j=1}^{n} a_{ij} N_i N_j \right) \Big/ N \qquad \ldots(11)$$

so that the total population size will increase if $\sum_{i=1}^{n} \sum_{j=1}^{n} a_{ij} N_i N_j \geqslant 0$ when $N_i \geqslant 0$, $N_j \geqslant 0$. For Zeeman's game-theoretic example of animal conflicts

$$A = \begin{bmatrix} -2 & 6 & 6 & -2 \\ 0 & 2 & 0 & 2 \\ 0 & 6 & 3 & 0 \\ -2 & 2 & 6 & 2 \end{bmatrix} \qquad \ldots(12)$$

$$\sum_{i=1}^{4} \sum_{i=1}^{4} a_{ij} N_i N_j = -2N_1^2 + 2N_2^2 + 3N_3^2 + 2N_4^2 + 6N_1N_2 + 6N_1N_3$$
$$- 4N_1N_4 + 6N_2N_3 + 4N_2N_4 + 6N_3N_4. \qquad \ldots(13)$$

(i) If $N_1 = 0$ initially, it always remains zero. In the absence of hawks, the above expression (13) is always positive and so a population consisting of doves, bulleys and retaliators will always increase as a result of mutual interactions.

(ii) If $N_1 = 0$, $N_3 = 0$, we get

$$\frac{dN}{dt} = \frac{2(N_2 + N_4)^2}{N} = 2N \qquad \ldots(14)$$

so that a population consisting of doves and retaliators only will increase exponentially with time.

Generalization of the Model

We consider the model

$$\frac{\dot{N}_i}{N_i} = f_i\left(\frac{N_1}{N}, \frac{N_2}{N}, \ldots, \frac{N_n}{N}\right), \; i = 1, 2, \ldots, n \qquad \ldots(15)$$

so that we get

$$\frac{\dot{x}_i}{x_i} = f_i(x_1, x_2, \ldots, x_n) - \sum_{j=1}^{n} x_j f_j(x_1, x_2, \ldots, x_n). \qquad \ldots(16)$$

The equilibrium positions are obtained by solving

$$f_1(x_1, x_2, \ldots, x_n) = f_2(x_1, x_2, \ldots, x_n) = \ldots = f_n(x_1, x_2, \ldots, x_n) \qquad \ldots(17)$$

$$x_1 = 0, f_2(0, x_2, \ldots, x_n) = f_3(0, x_2, \ldots, x_n) = \ldots = f_n(0, x_2, \ldots, x_n) \qquad \ldots(18)$$

$$x_1 = x_2 = 0, f_3(0, 0, x_3, \ldots, x_n) = f_4(0, 0, x_3, \ldots, x_n) = \ldots = f_n(0, 0, x_3, \ldots, x_n) \qquad \ldots(19)$$

and similar equations, provided the solutions obtained are positive.

For Volterra's second modified model

$$\frac{\dot{N}_i}{N_i} = k_i + \sum_{j=1}^{n} a_{ij}\frac{N_j}{N}, \; i = 1, 2, \ldots, n \qquad \ldots(20)$$

we get

$$\frac{\dot{x}_i}{x_i} = k_i + \sum_{j=1}^{n} a_{ij}x_j - \sum_{i=1}^{n} k_i x_i - \sum_{i=1}^{n}\sum_{j=1}^{n} a_{ij}x_i x_j. \qquad \ldots(21)$$

Since $X^T I X = 1$, we get

$$\frac{\dot{x}_i}{x_i} = X^T k_i I - X^T A X + (AX)_i - (KX)_i \qquad \ldots(22)$$

where

$$K = \begin{vmatrix} k_1 & k_2 & \ldots & k_n \\ k_1 & k_2 & \ldots & k_n \\ \ldots & \ldots & \ldots & \ldots \\ k_1 & k_2 & \ldots & k_n \end{vmatrix} \qquad \ldots(23)$$

so that

$$\frac{\dot{x}_i}{x_i} = [(A - KI)X]_i - [x^T(A - k_i I)X] \quad (i = 1, 2, \ldots, n). \qquad \ldots(24)$$

We can also write (21) as

$$\frac{\dot{x}_i}{x_i} = \sum_{j=1}^{n} (a_{ij} + k_i - k_j) x_j - \sum_{i=1}^{n} \sum_{j=1}^{n} (a_{ij} + k_i - k_j) x_i x_j. \qquad \text{...(25)}$$

The Case of Two Species or Two Strategies

We now consider two species which grow according to Volterra's second modified law or of two groups like hawks and doves, which are not only involved in conflict but are subject to biological births and deaths. In this case, we get

$$\frac{\dot{x}_1}{x_1} = k_1 + (a_{11}x_1 + a_{12}x_2) - (k_1x_1 + k_2x_2)$$
$$- [a_{11}x_1^2 + (a_{12} + a_{21}) x_1x_2 + a_{22}x_2^2] \qquad \text{...(26)}$$

$$\frac{\dot{x}_2}{x_2} = k_2 + (a_{21}x_1 + a_{22}x_2) - (k_1x_1 + k_2x_2)$$
$$- [a_{11}x_1^2 + (a_{12} + a_{21}) x_2x_2 + a_{22}x_2^2]. \qquad \text{...(27)}$$

Remembering that $x_1 + x_2 = 1$, we get

$$\frac{\dot{x}_1}{x_1} = x_2[(k_1 - k_2) + (a_{12} - a_{22}) - x_1(a_{12} - a_{22} + a_{21} - a_{11})] \qquad \text{...(28)}$$

$$\frac{\dot{x}_2}{x_2} = x_1[(k_2 - k_1) + (a_{21} - a_{11}) - x_2(a_{21} - a_{11} + a_{12} - a_{22})]. \qquad \text{...(29)}$$

Case (*i*) — Let $k_1 = k_2$, then if $a_{12} > a_{22}, a_{21} > a_{11}$, there is a position of equilibrium

$$\bar{x}_1 = \frac{a_{12} - a_{22}}{(a_{12} - a_{22}) + (a_{21} - a_{11})}, \quad \bar{x}_2 = \frac{a_{21} - a_{11}}{(a_{21} - a_{11}) + (a_{12} - a_{22})} \qquad \text{...(30)}$$

and this is an attractor. If there are two groups of the same species with different conflict behaviour, $k_1 = k_2$ is a reasonable assumption. If there are two different species k_1 may not be equal to k_2.

Case (*ii*) — If $k_1 \neq k_2$, then if $k_1 - k_2 + a_{12} - a_{22} > 0$, $k_2 - k_1 + a_{21} - a_{11} > 0$, then

$$\bar{\bar{x}} = \frac{k_1 - k_2 + a_{12} - a_{22}}{(a_{12} - a_{22}) + (a_{21} - a_{11})}, \quad \bar{\bar{x}}_2 = \frac{(k_2 - k_1) + a_{21} - a_{11}}{(a_{12} - a_{22}) + (a_{21} - a_{11})} \qquad \text{...(31)}$$

so that $\bar{\bar{x}}_1 \gtrless \bar{x}_1$ according as $k_1 \gtrless k_2$.

Thus the equilibrium population of the first species increases if its intrinsic growth rate is greater than that of the second.

The Case of Three or More Species (Strategies)

We may note that we can simplify our discussion by taking diagonal elements of the matrix A to be zero, so that we get

$$\frac{\dot{x}_1}{x_1} = (k_1 - k_2)\, x_2 + (k_1 - k_3)\, x_3 + (a_{12}x_2 + a_{13}x_3)$$
$$- [(a_{12} + a_{21})\, x_1x_2 + (a_{13} + a_{31})\, x_1x_3 + (a_{23} + a_{32})\, x_2x_3] \quad \ldots(32)$$

$$\frac{\dot{x}_2}{x_2} = (k_2 - k_1)x_1 + (k_2 - k_3)\, x_3 + (a_{21}x_1 + a_{23}x_3)$$
$$- [(a_{12} + a_{21})x_1x_2 + (a_{13} + a_{31})\, x_1x_3 + (a_{23}+a_{32})\, x_2x_3] \quad \ldots(33)$$

$$\frac{\dot{x}_3}{x_3} = (k_3 - k_1)x_1 + (k_3 - k_2)x_2 + (a_{31}x_1 + a_{32}x_2)$$
$$- [(a_{12} + a_{21})\, x_1x_2 + (a_{13} + a_{31})\, x_1x_3 + (a_{23} + a_{32})\, x_2x_3]. \ldots(34)$$

For the matrix considered by Zeeman viz.

$$\begin{bmatrix} 0 & 4 & 3 \\ 2 & 0 & -3 \\ 2 & 4 & 0 \end{bmatrix} \quad \ldots(35)$$

if $k_1 = \frac{1}{3}$, $k_2 = 9/3$, $k_3 = 2/3$, we get the equilibrium position

$$\bar{x}_1 = \bar{x}_2 = \bar{x}_3 = \tfrac{1}{3} \quad \ldots(36)$$

which shows that for the modified model, a position of equilibrium exists inside the 2-simplex.

In the case of conflicts within animal groups of the same species, $k_1 = k_2 = k_3$ and then (32) - (34) become independent of k_1, k_2, k_3 and so flows are independent of the growth rates of the species. The result is also obviously true for n strategies. If k's are same, all the results of Zeeman (1979a, b) remain true. If these are different, we simply replace a_{ij} by $a_{ij} + k_i - k_j$.

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