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NOTE ON THE LOTKA-VOLTERRA MODEL AND DENSITY DEPENDENT EVOLUTIONARY GAME DYNAMICS

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Abstract: This paper is concerned with a predator-prey system, with autocompetition in both populations, supposing that there are two phenotypes in each population, all the individuals have only one phenotype, and the populations are asexual. Such populations may be modelled either by the Lotka-Volterra model or by density dependent evolutionary game dynamics. The present paper shows that in terms of asymptotic stability of dissipative systems these approaches are equivalent, given the above conditions.

Introduction

Cressman & Dash (1987) were the first who investigated the density dependent game conflict in a population in which all individuals have only one phenotype. They have superimposed a frequency dependent fitness component and a density dependent one. The density dependent part was the same for all individuals of the populations. Furthermore, they proposed a density-dependent game dynamics. The derivations of the density dependent game dynamics are analogous to those of the frequency dependent game dynamics developed by Taylor & Jonker (1978).

Cressman (1987) also studied the case when every individual has all phenotypes present in the population. Cressman gave the definition of the density dependent evolutionary stable strategy (DDESS) for this case, and derived a new, modified game dynamics. The rest point of this dynamics is asymptotically stable if and only if it is DDESS. Moreover, the author gave an example of a Lotka-Volterra system which has an asymptotically stable rest point but it is not DDESS.

Equivalence of two models

Let us consider a predator-prey system, with autocompetition in both populations. Suppose that there are two phenotypes in each population, all the individuals have only one phenotype, and the populations are asexual. For modelling such populations we have two possibilities: the Lotka-Volterra model and density dependent evolutionary game dynamics.

Consider first the following Lotka-Volterra dynamics:

$$\begin{aligned}\dot{x}_1 &= x_1(\varepsilon_1 - a_{11}x_1 - a_{12}x_2 - b_{11}y_1 - b_{12}y_2)\\ \dot{x}_2 &= x_2(\varepsilon_1 - a_{21}x_1 - a_{22}x_2 - b_{21}y_1 - b_{22}y_2)\\ \dot{y}_1 &= y_1(-\varepsilon_2 + c_{11}x_1 + c_{12}x_2 - d_{11}y_1 - d_{12}y_2)\\ \dot{y}_2 &= y_2(-\varepsilon_2 + c_{21}x_1 + c_{22}x_2 - d_{21}y_1 - d_{22}y_2)\end{aligned} \quad (1a)$$

where the x_i-s are the densities of the i-th phenotype of the asexual prey and y_i-s are that of the i-th phenotype of the asexual predator. Suppose that matrix **A** contains the parameters of the prey population which correspond to the intraspecific conflicts (competition) whereas matrix **B** contains the parameters corresponding to the interspecific conflicts (predation). Let matrices **C** and **D** contain the respective parameters of the predator population. Then, we have the community matrix of the Lotka-Volterra model in the following partitioned form

$$\Gamma = \begin{pmatrix} \mathbf{AB} \\ \mathbf{CD} \end{pmatrix}.$$

Now we introduce the following quantities: $N = x_1 + x_2$, $\mathbf{p} = \left(\frac{x_1}{N}, \frac{x_2}{N}\right)$, $M = y_1 + y_2$, $\mathbf{q} = \left(\frac{y_1}{M}, \frac{y_2}{M}\right)$, $\mathbf{e_1} = (1,0)$, and $\mathbf{e_2} = (0,1)$. With these notations, the Lotka-Volterra system can be written as

$$\begin{aligned}\dot{x}_1 &= x_1(\varepsilon_1 + \mathbf{e}_1(N\mathbf{Ap} + M\mathbf{Bq}))\\ \dot{x}_2 &= x_2(\varepsilon_1 + \mathbf{e}_2(N\mathbf{Ap} + M\mathbf{Bq}))\\ \dot{y}_1 &= y_1(-\varepsilon_2 + \mathbf{e}_1(N\mathbf{Cp} + M\mathbf{Dq}))\\ \dot{y}_2 &= y_2(-\varepsilon_2 + \mathbf{e}_2(N\mathbf{Cp} + M\mathbf{Dq}))\end{aligned} \quad (1b)$$

Let us follow Cressman's and Dash's (1987) derivation of density dependent game dynamics. The only difference between the Lotka-Volterra model and the Cressman-Dash model for density dependent game dynamics is that the latter applied other forms of density dependence. In the Lotka-Volterra model the number of interactions depends on the density, whereas in the Cressman-Dash model the additive fitness component is the same for all individuals. In the first step we give a differential equation for the time variation of the total density of prey.

$$\dot{N} = \dot{x}_1 + \dot{x}_2 =$$

$$= x_1(\varepsilon_1 + \mathbf{e}_1(N\mathbf{Ap} + M\mathbf{Bq})) + x_2(\varepsilon_1 + \mathbf{e}_2(N\mathbf{Ap} + M\mathbf{Bq})) =$$

$= N\,[\,\varepsilon_1\frac{x_1}{N} + \frac{x_1}{N}\,\mathbf{e}_1(N\mathbf{Ap} + M\mathbf{Bq}))$

$+ \varepsilon_1\frac{x_2}{N} + \frac{x_2}{N}\,\mathbf{e}_2(N\mathbf{Ap} + M\mathbf{Bq})\,] =$

$= N(\varepsilon_1 + N\mathbf{pAp} + M\mathbf{pBq}).$

In the same way we get

$\dot{M} = M(-\varepsilon_2 + N\mathbf{qCp} + M\mathbf{qDq})$

for predator density.

The differential equation for the relative frequency of the prey population is given by

$$\dot{\left(\frac{x_1}{N}\right)} = \frac{\dot{x}_1 N - x_1\dot{N}}{N^2} =$$

$$= \frac{x_1}{N}\{\varepsilon_1 + \mathbf{e}_1(N\mathbf{Ap} + M\mathbf{Bq}) - \varepsilon_1 - N\mathbf{pAp} - M\mathbf{pBq}\}$$

Note that using a simplified notation the above equation can be written in the following form:

$$\dot{p} = pW_1 - (pW_1 + (1-p)W_2\} = p\{W_1 - W\}$$

where $W_i = \frac{\dot{x}_i}{x_1}$ is the fitness of the i-th phenotype of the Lotka-Volterra model as in (1b). Formally:

$W_i(M,N,\mathbf{p},\mathbf{q}) := \varepsilon_1 + \mathbf{e}_i(N\mathbf{Ap} + M\mathbf{Bq})$

Thus, in this way the Lotka-Volterra system (1a) corresponds to the following density dependent game dynamics:

$$\begin{aligned} \dot{p} &= p(1-p)(W_1 - W_2) \\ \dot{N} &= N[p(W_1 - W_2) + W_2] \\ \dot{q} &= q(1-q)(V_1 - V_2) \\ \dot{M} &= M[q(V_1 - V_2) + V_2] \end{aligned} \qquad (2)$$

where

$V_i = \frac{\dot{y}_i}{y_i}$ (formally $V_i(M,N,\mathbf{p},\mathbf{q}) := -\varepsilon_2 + \mathbf{e}_i(N\mathbf{Cp} + M\mathbf{Dq})$)

is called the *fitness* of the i-th phenotype of the predator in the literature.

It easy to see that if the Lotka-Volterra system has a non-trivial equilibrium point, then it is also true for the density dependent game dynamics and, conversely, if there is a non-trivial equilibrium point of density dependent game dynamics, then, upto substitution, it coincides with that of the Lotka-Volterra dynamics. *So if we start with the Lotka-Volterra equation, and follow the derivation of Cressman and Dash we get a density dependent game dynamics.*

Now the question arises: does the canonical substitution $x_1 = Np,\ x_2 = N(1-p)$ and $y_1 = Mq,\ y_2 = M(1-q)$ give the same result for the stability of the corresponding equilibria?

For brevity we give the detailed mathematical analysis only for the prey population. If we perform the substitution we have

$$\dot{(Np)} = \dot{N}p + N\dot{p} = NpW_1 \qquad (3)$$

$$\dot{(N(1-p))} = \dot{N}(1-p) - N\dot{p} = N(1-p)W_2 \qquad (4)$$

Superposing (3) and (4) we get

$$\dot{N} = N[pW_1 + (1-p)W_2] \qquad (5)$$

Now multiplying (5) by x and subtracting it from (3) we have

$$\dot{p} = p(1-p)(W_1 - W_2) \qquad (6)$$

Notice that equations (5) and (6) are the same as the second and first equations of system (2) , respectively. If we apply the above procedure to the predator population then we get the whole system (2).

Hence by using the method of substitution of variables, we can again assign the Lotka-Volterra and the density dependent game dynamics to each other. The aforementioned substitution is important because by using it we can show that the Lyapunov function of the Lotka-Volterra dynamics is mapped to the Lyapunov function of the corresponding density dependent game dynamics.

The dissipativity property is very important in the theory of Lotka-Volterra systems. We say that the Lotka-Volterra system is dissipative if there exist $a_i>0$ such that, for all z different from zero, the following inequality holds:

$$A(z) = \sum_{ij} \alpha_i\,\gamma_{ij}\,z_i\,z_j < 0$$

where γ_{ij} are the elements of the community matrix for the Lotka-Volterra system.

If the Lotka-Volterra system is dissipative and $\bar{z}$ is a positive equilibrium of (1a) then the function

$$L(z) = \sum_i \alpha_i\,(\bar{z}_i \log z_i - z_i)$$

is a Lyapunov function for the system. In the literature, a dissipative Lotka-Volterra system is also called Lyapunov-Volterra stable (Hofbauer & Sigmund 1988).

Now we suppose that system (1) is dissipative with the following constants: $\alpha_1 = \alpha_2(=\alpha)$ and $\alpha_3=\alpha_4(=\beta)$, thus

$$\begin{aligned} &\alpha x_1(-a_{11}x_1 - a_{12}x_2 - b_{11}y_1 - b_{12}y_2) + \\ &+ \alpha x_2(-a_{21}x_1 - a_{22}x_2 - b_{21}y_1 - b_{22}y_2) + \\ &+ \beta y_1(c_{11}x_1 + c_{12}x_2 - d_{11}y_1 - d_{12}y_2) + \\ &+ \beta y_2(c_{21}x_1 + c_{22}x_2 - d_{21}y_1 - d_{22}y_2) < 0 \end{aligned} \qquad (7)$$

Note that the above condition is *stronger* than the condition of dissipativity because the constants α and β belong to the prey and the predator population, respectively, rather than to the phenotypes. So the function

$$L(x_1,x_2,y_1,y_2) =$$
$$=\alpha(\bar{x}_1 \log x_1 - x_1 + \bar{x}_2 \log x_2 - x_2) + \beta(\bar{y}_1 \log y_1 - y_1 + \bar{y}_2 \log y_2 - y_2)$$

is the Lyapunov function for system (1) in which $\bar{x}_i$, $\bar{y}_i$ are the coordinates of the rest point of system (1).

Now we show that when we compose our change of variables with the Lyapunov function of the Lotka-Volterra system, then the function obtained will be a Lyapunov function of the density dependent game dynamics. Indeed, if we carry out the substitution we get the function

$$L(p,N,q,M) = \alpha(\bar{x}_1 \log Np + \bar{x}_2 \log N(1-p) - N) +$$
$$+ \beta(\bar{y}_1 \log Mq + \bar{y}_2 \log M(1-q) - M) =$$

$$= \alpha(\overline{x}_1 \log p + \overline{x}_2 \log (1 - p) + (\overline{x}_1 + \overline{x}_2) \log N - N) +$$
$$+ \beta(\overline{y}_1 \log q + \overline{y}_2 \log (1 - q) + (\overline{y}_1 + \overline{y}_2) \log M - M)$$

Thus the derivative of the function L with respect to game dynamics (2) is:

$$DL = \alpha\left[\frac{(\overline{x}_1(1-p) + \overline{x}_2 p}{p(1-p))}\dot{p} + \frac{\overline{x}_1 + \overline{x}_2 - N}{N}\dot{N}\right]$$
$$+ \beta\left[\frac{\overline{y}_1(1-q) + \overline{y}_2 q}{q(1-q)}\dot{q} + \frac{\overline{y}_1 + \overline{y}_2 - M}{M}\dot{M}\right] =$$
$$= \alpha[(\overline{x}_1(1-p) + \overline{x}_2 p)(W_1 - W_2) - (\overline{x}_1 + \overline{x}_2 - N)W]$$
$$+ \beta[(\overline{y}_1(1-q) + \overline{y}_2 q)(V_1 - V_2) - (\overline{y}_1 + \overline{y}_2 - M)V].$$

Since $W = pW_1 + (1-p)W_2$ and $V = qV_1 + (1-q)V_2$, so

$$DL = \alpha(\overline{x}_1 W_1 + \overline{x}_2 W_2 - NW) + \beta(\overline{y}_1 V_1 + \overline{y}_2 V_2 - MV)$$

Hence, by $NW = x_1 W_1 + x_2 W_2$ and $MV = y_1 V_1 + y_2 V_2$, we have

$$DL = \alpha((\overline{x}_1 - x_1)W_1 + (\overline{x}_2 - x_2)W_2) +$$
$$\beta((\overline{y}_1 - y_1)V_1 + (\overline{y}_2 - y_2)V_2)$$

Function DL must be positive definite. As a consequence, the Lotka-Volterra system (1) is dissipative. (We give the calculation only for the first phenotype of the prey.)

$$\alpha(\overline{x}_1 - x_1)W_1 =$$
$$= \alpha(\overline{x}_1 - x_1)[\varepsilon_1 - a_{11}(x_1 - \overline{x}_1) - a_{12}(x_2 - \overline{x}_2) - b_{11}(y_1 - \overline{y}_1)$$
$$- b_{12}(y_2 - \overline{y}_2) - a_{11}\overline{x}_1 - a_{12}\overline{x}_2 - b_{11}\overline{y}_2 - b_{12}\overline{y}_2] =$$
$$= + \alpha(\overline{x}_1 - x_2)[-a_{11}(x_1 - \overline{x}_1) - a_{12}(x_2 - \overline{x}_2)$$
$$- b_{11}(y_1 - \overline{y}_1) - b_{12}(y_2 - \overline{y}_2)] .$$

If we carry through this simple transformation for the other individual fitness function too, we obtain the inequality

$$-\sum_i \alpha_i \gamma_{ij}(z_i - \overline{z}_i)(z_j - \overline{z}_j) < 0$$

This inequality follows from the special dissipativity (7) of the Lotka-Volterra system. So, the Lyapunov function of the *Lotka-Volterra system also provides a Lyapunov function of the density dependent game dynamics.*

In conclusion, we have shown that in case of (strong) dissipativity *the Lotka-Volterra dynamics and the density dependent game dynamics display the same stability property, and they have essentially the same Lyapunov function.*

Discussion

One of the basic models of ecology is the Lotka-Volterra model. Within the framework of this model we can merely include those asexual "clones" which possess only one phenotype. In the theory of frequency dependent evolutionary matrix games it is obvious that the following two cases result in the same distribution of phenotypes:

– each individual possesses only one of the possible behavioural phenotypes of the population;

– all individuals mix all possible behavioural phenotypes of the population.

In this paper the first case is considered because the second one is not appropriate for the Lotka-Volterra model.

Cressman (1990) examined a density dependent game dynamics where – within a particular population – all individuals can display each possible behavioural phenotypes. Cressman also gave an example for such a Lotka-Volterra model, the asymptotically stable equilibrium point of which is not evolutionarily stable. His example was a two dimensional system involving a predator and a prey phenotype of the same species. The individuals in this model are capable of invading the equilibrium system, provided it mixes the "predator" and "prey" strategies with an equal rate of 0.5. Notice that in this case of Cressman's example all individuals must possess both phenotypes. An individual, however, in most cases is either a prey or a predator.

A common conclusion of Cressman's result and that of the present paper may be that any ecologically meaningful model has to incorporate the distribution of the phenotypes of the individual.

Hence, the result of this paper poses the following problem: If in a predator-prey system within both species we have two phenotypes and all individuals possess merely one phenotype, then how can we find a definition for "evolutionary stability" which gives a result equivalent to the Lotka-Volterra model? The equivalence of these models can be based on the fact that "evolutionary" stability cannot be imagined without ecological stability. Moreover, the basic conditions of the two model families are the same. The clarification of such issues could be an important development for the application of evolutionary game theory.

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