BIOLOGICAL CONTINOUS MODELS. THE OPTIMALITY OF THE LOTKA-VOLTERRA MODEL

NINA DRAGOESCU (CAZACU)[1, 2]

[1] *Industrial Scholar Group "Constructii Cai Ferate", 12206, Bucharest, Romania*

[2]*Ovidius University of Constanta, Mathematics Doctoral School, 900527, Constanta, Romania*

Abstract. *This paper contains a particular point of view about the evolution of the Lotka-Volterra models when a disturbing external factor is present.*

Keywords: *optimal, Lotka-Volterra, solution.*

1. INTRODUCTION

The mathematical model Volterra for the existence of prey-predator species explains the variable levels of the fish chaches in the Adriatic. If N(t) is the prey population, and P(t) is the predators, at the moment t, then the Volterra' s model is:

$$\frac{dN}{dt} = N(a - bP)$$
$$\frac{dP}{dt} = P(cN - d)$$

where a, b, c and d are positive constants [1]. The assumptions are:

a) In the absence of any predation, the prey grows unboundedly, aspect revealed by the aN term.

b) The effect of the predation is to reduce the prey's growth rate, a component proportional to both populations: -bNP term.

c) In the absence of any prey, the predator's death rate of the predators results in exponential decay: -dP term.

d) The prey's contribution to the predators' growth rate is revealed by the cNP term, which means, it is proportional to both populations.

The NP terms can be understood as representing the conversion of energy from one source to another: bN P is taken from the prey and cN P is given to the predators.

This model, even if it has drawbacks and was some discussions about in the literature, it is used as main motivation in the present study.

2. THE COMPETITIVE EXCLUSION MODEL

Among the others, Hsu, having the Volterra example, also proposed an interesting model when two species compete for the same limited resources of existence, food, territory, etc., one of the species becoming extinct: (the species are named with N_1, N_2 and have a logistic growth in the absence of the other [1]

Here we have one of the Murray's simple models:

$$\frac{dN_1}{d\tau} = r_1 N_1 [1 - \frac{N_1}{K_1} - b_{12} \frac{N_2}{K_1}]$$
$$\frac{dN_2}{d\tau} = r_2 N_2 [1 - \frac{N_2}{K_2} - b_{21} \frac{N_1}{K_2}]$$

where r_1, K_1, r_2, K_2, b_{12}, b_{21} are positive constants, $r_{1,2}$ are the linear birth rates and $K_{1,2}$ are the carrying capacities, b_{12}, respective b_{21} measure the competitive effect of N_2 on N_1, and of N_1 on N_2, respectively.

In order to nondimensionalise this model, the author writes:

$$u_1 = \frac{N_1}{K_1}, u_2 = \frac{N_2}{K_2}, \quad t = r_1 \cdot \tau$$

$$\varepsilon = \frac{r_2}{r_1}, a_{12} = b_{12}\frac{K_2}{K_1}, \quad a_{21} = b_{21}\frac{K_1}{K_2}$$

The dynamical system will have the following form:

$$(S) \quad \begin{aligned} \frac{du_1}{dt} &= u_1(1 - u_1 - a_{12}u_2) = f_1(u_1, u_2) \\ \frac{du_2}{dt} &= \varepsilon \cdot u_2(1 - u_2 - a_{21}u_1) = f_2(u_1, u_2) \end{aligned}$$

The steady states, and phase plane singularities, u_1^*, u_2^* are solutions of the equations: $f_1(u_1,u_2)=f_2(u_1,u_2)=0$.

The four possibilities have been studied and represented by the author, in order to determine the stability of the steady states. The conclusions are similar with those presented in the "Lotka-Volterra" system example, so that the singularity point $(u_1, u_2)=(0,0)$ leads to instability, and in the others cases the result depending of the sign of the Eigen values λ of its community matrix . The singularities are:

$$u_1^* = u_2^* = 0; u_1^* = 1, u_2^* = 0; \quad u_1^* = 0, u_2^* = 1; u_1^* = \frac{1 - a_{12}}{1 - a_{12} \cdot a_{21}}; \quad u_2^* = \frac{1 - a_{21}}{1 - a_{12} \cdot a_{21}};$$

the last having sense only if: $a_{12} \cdot a_{21} \neq 1$. The community matrix is formed with the partial derivatives of the two functions f_1, f_2:

$$\begin{pmatrix} \frac{\partial f_1}{\partial u_1} & \frac{\partial f_1}{\partial u_2} \\ \frac{\partial f_2}{\partial u_1} & \frac{\partial f_2}{\partial u_2} \end{pmatrix}_{u_1^*, u_2^*} = \begin{pmatrix} 1 - 2 \cdot u_1 - a_{12} \cdot u_2 & a_{12} \cdot u_1 \\ -\varepsilon \cdot a_{12} \cdot u_2 & \varepsilon \cdot (1 - 2 \cdot u_2 - a_{21} \cdot u_1) \end{pmatrix}_{u_1^*, u_2^*}$$

The Eigen values, $\lambda_{1,2}$, calculated in each case as solutions of the characteristic equation $|A-\lambda I_2|=0$, determine the stability according to the values of a_{12}, a_{21} terms [1].

1) Our contribution is a new point of view about the proposed model and the study of the new properties. Supposing that we are in the general case, with: $u_1, u_2 \neq 0$. It is noted:

$$p(t) = \begin{pmatrix} u_1(t) & 0 \\ 0 & u_2(t) \end{pmatrix}, R = \begin{pmatrix} -1 & 0 \\ 0 & -\varepsilon \end{pmatrix}, \quad S = \begin{pmatrix} 1 & 0 \\ 0 & \varepsilon \end{pmatrix}, T = \begin{pmatrix} -a_{12} & 0 \\ 0 & -\varepsilon \cdot a_{21} \end{pmatrix}$$

Replacing in the linearised Volterra's equations we obtain the next relation, with $M_2(R)$ coefficients:

$$\dot{p}(t) + R \cdot p(t) + S \cdot p^2(t) = T \cdot u_1 u_2$$

Ignoring the free term, we obtain a Bernoulli equation in p(t) variable:

$$\dot{p}(t) + R \cdot p(t) + S \cdot p^2(t) = 0_2$$

with: p(t), $p: R \to L(R)$ self adjoint continuous differentiable operator on $(t_0,t_1) \subset [T_1, T_2] \subset R_+$.

Using the notation $\dot{v}(t) = p(t) \cdot [p(t)]^{-2}$ [2], can be lead to the differential equation: $\dot{v}(t) - R \cdot v(t) = -S$, with the solution:

$$v(t) = e^{\int_0^t R dv}[C_1 - \int_0^t S \cdot e^{\int_0^s -R dv} ds] = e^{Rt}(C_1 + I_2) - I_2, \text{ as } S=-R.$$

where: $C_1 = e^{-2A}-e^{-3A}-I_2$, which has been calculated from the condition: v(1)=-[p(1)]$^{-1}$, p(1)=e^A.

Concequently: p(t)=-[v(t)]$^{-1}$=$[I_2 - e^{2At}(e^{-2A} - e^{-3A})]^{-1} = [I_2 - e^{2A(t-1)} + e^{A(2t-3)}]^{-1}$

If R=A+A*, then: $A = \begin{pmatrix} -\frac{1}{2} & 0 \\ 0 & -\frac{\varepsilon}{2} \end{pmatrix}$; also if S=BB*, we obtain: $B = \begin{pmatrix} 1 & 0 \\ 0 & \sqrt{\varepsilon} \end{pmatrix}$.

Let us consider the equation: $\dot{x} = A \cdot x + B \cdot \omega = \begin{pmatrix} -\frac{1}{2} & 0 \\ 0 & -\frac{\varepsilon}{2} \end{pmatrix} \cdot x + \begin{pmatrix} 1 & 0 \\ 0 & \sqrt{\varepsilon} \end{pmatrix} \cdot \omega$ which can be written:

$$(S^*) \quad \begin{cases} \begin{pmatrix} \dot{x}_1 \\ \dot{x}_2 \end{pmatrix} = \begin{pmatrix} -\frac{1}{2} & 0 \\ 0 & -\frac{\varepsilon}{2} \end{pmatrix} \cdot \begin{pmatrix} x_1 \\ x_2 \end{pmatrix} + \begin{pmatrix} 1 & 0 \\ 0 & \sqrt{\varepsilon} \end{pmatrix} \cdot \begin{pmatrix} \omega_1 \\ \omega_2 \end{pmatrix} \\ \begin{pmatrix} y_1 \\ y_2 \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ 0 & 0 \end{pmatrix} \cdot \begin{pmatrix} x_1 \\ x_2 \end{pmatrix} \end{cases}$$

or:

$$(S^{**}) \quad \begin{cases} \begin{pmatrix} \dot{x}_1 \\ \dot{x}_2 \end{pmatrix} = \begin{pmatrix} -\frac{1}{2} & 0 \\ 0 & -\frac{\varepsilon}{2} \end{pmatrix} \cdot \begin{pmatrix} x_1 \\ x_2 \end{pmatrix} + \begin{pmatrix} 1 & 0 \\ 0 & \sqrt{\varepsilon} \end{pmatrix} \cdot \begin{pmatrix} \omega_1 \\ \omega_2 \end{pmatrix} \\ \begin{pmatrix} y_1 \\ y_2 \end{pmatrix} = \begin{pmatrix} 0 & 0 \\ 0 & 1 \end{pmatrix} \cdot \begin{pmatrix} x_1 \\ x_2 \end{pmatrix} \end{cases}$$

The initial equation being transformed in a dynamical one, together with the out equation, the response of the system, with no deal over the optimal command ω, response which depends on the optimal trajectory x(t). Let's call the systems (S*) and (S**) as "dynamical systems associated with the Volterra's equations, association revealed by a duality relation:

a) According to the algorithm for the solution of an optimal problem with quadratic cost function [2], for having the optimal command of the Volterra's associated systems, it must be solved a Bernoulli equation, formed with the system coefficients:

$$\dot{p}(t) = -(A + A^*) \cdot p(t) - B \cdot B^* \cdot p^2(t) \text{ ,where: } p(t)=p^*(t) \text{ , } \sigma(t)=1, \rho(t)=0$$

It know that : A+A*=R and BB*=S(ρ(t)=0, σ(t)=1), so that the Bernoulli equation can be written: $\dot{p}(t) = -R \cdot p(t) - S \cdot p^2(t)$ or: $\dot{p}(t) + R \cdot p(t) + S \cdot p^2(t) = 0_2$, which is exactly the Volterra homogeneous equation.

b) The optimal command ω, has been found knowing the associate system coefficients, that is the Volterra's system coefficients; according to the algorithm [2] ω has the following formula: $\omega(t,x) = -\sigma^{-1}(t) \cdot B^* \cdot p(t) \cdot x(t) = -B^* \cdot p(t) \cdot x(t)$ and the optimal trajectory x(t) is the solution of the equation: $\dot{x}(t) = [A - S(t) \cdot p(t)] \cdot x(t)$ in which p(t) is the solution of the Volterra homogeneous equation.

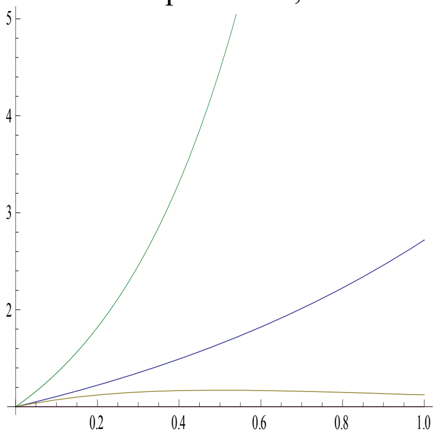
2) Supposing we are again in the previous conditions and consider the linearised Volterra equations, with the variables u_1, u_2.

It keeps the linear terms of the system only, because it is interested about the existence of an optimal external disturbing factor, which acting on the predator population leads to an optimal result on the prey population. Note: ω=(ω_1,ω_2) the external disturbing factor, the command, and let $y=(y_1,y_2)$ represent "the system response" to the external factor. The algorithm for the optimal solution [2] can be used and the optimal command can be calculated. The Volterra's system is reconstructed for this purpose, reformulated in the state variables form:

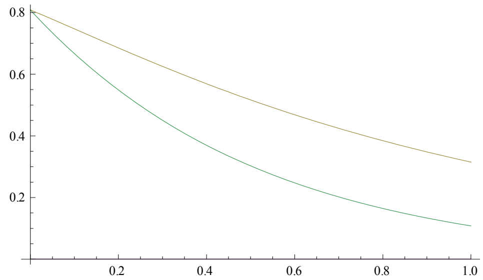
$$\begin{pmatrix}\dot{u}_1(t)\\ \dot{u}_2(t)\end{pmatrix}=\begin{pmatrix}1 & 0\\ 0 & \varepsilon\end{pmatrix}\cdot\begin{pmatrix}u_1(t)\\ u_2(t)\end{pmatrix}+\begin{pmatrix}0 & 0\\ 0 & 1\end{pmatrix}\cdot\begin{pmatrix}\omega_1(t)\\ \omega_2(t)\end{pmatrix}$$

$$\begin{pmatrix}y_1(t)\\ y_2(t)\end{pmatrix}=\begin{pmatrix}1 & 0\\ 0 & 0\end{pmatrix}\cdot\begin{pmatrix}u_1(t)\\ u_2(t)\end{pmatrix} \qquad (*)$$

Let: $\varepsilon=3>0$. With the optimal solution algorithm ([2]) it is obtained, for the considered value of the parameter, the next results ($\sigma(t)=1,\rho(t)=0$) :

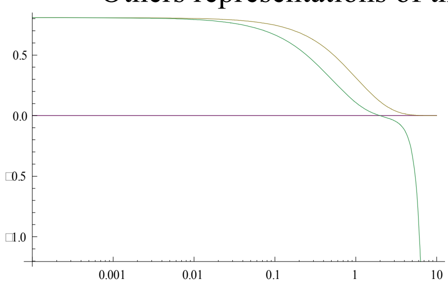


Optimal trajectory

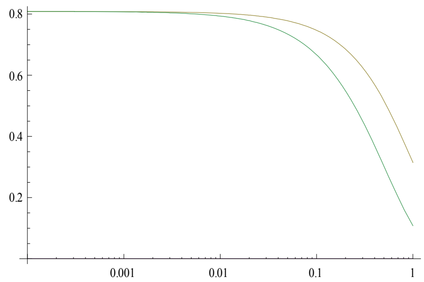


Optimal command components: green=predator, brown=prey

Others representations of the optimal command:



1 u.t time interval



10 u.t time interval

3. THE MUTUALISM OR SYMBIOSIS FOR TWO SPECIES MODEL

The simplest mutualism model equivalent to the classical Lotka–Volterra predator–prey system is:

$$\frac{dN_1}{d\tau}=r_1N_1+a_1\cdot N_1\cdot N_2$$
$$\frac{dN_2}{d\tau}=r_2N_2+a_2\cdot N_1\cdot N_2$$

where: r_1, r_2, a_1, a_2 are positive constants.

As $\frac{dN_1}{d\tau} > 0$ and $\frac{dN_2}{d\tau} > 0$, it results that N_1 and N_2 grow unboundedly. This is not a realistic model.

In Nature, there exist stability periods, as well as limit cycle oscillations, the most of the models having being described by Whittaker; a practical example is presented by May , model which is the start point in the present considerations [1]. Both species are considered, as it is realistic, with limited carrying capacities:

$$\frac{dN_1}{d\tau} = r_1 N_1 [1 - \frac{N_1}{K_1} + b_{12}\frac{N_2}{K_1}]$$
$$\frac{dN_2}{d\tau} = r_2 N_2 [1 - \frac{N_2}{K_2} + b_{21}\frac{N_1}{K_2}]$$

where: r_1, K_1, r_2, K_2, b_{12}, b_{21} are positive constants.

Using the same non-dimensionalisation as in the competition model, from the previous paragraph, the authors obtained the linearised system:

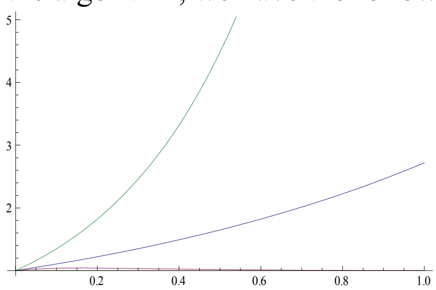
$$\frac{du_1}{dt} = u_1(1 - u_1 + a_{12}u_2) = f_1(u_1, u_2)$$
$$\frac{du_2}{dt} = \varepsilon \cdot u_2(1 - u_2 + a_{21}u_1) = f_2(u_1, u_2)$$

with respect to the same conventions.

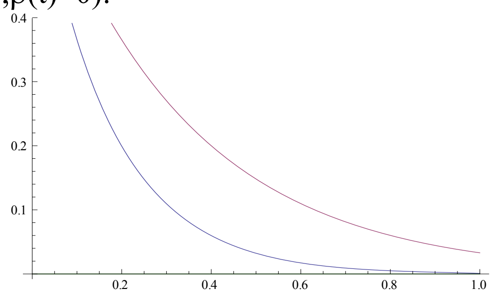
We propose once again to ignore the nonlinear terms and keep the linear ones, also to introduce the external command, represented by the vector $\omega=(\omega_1, \omega_2)$. The "impuls" will act on the "host" (prey) with effect on the "guest" (predator). The representation in the state form, with respect to the same conventions:

$$\begin{pmatrix} \dot{u}_1(t) \\ \dot{u}_2(t) \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ 0 & \varepsilon \end{pmatrix} \cdot \begin{pmatrix} u_1(t) \\ u_2(t) \end{pmatrix} + \begin{pmatrix} 1 & 0 \\ 0 & 0 \end{pmatrix} \cdot \begin{pmatrix} \omega_1(t) \\ \omega_2(t) \end{pmatrix}; \quad \begin{pmatrix} y_1(t) \\ y_2(t) \end{pmatrix} = \begin{pmatrix} 0 & 0 \\ 0 & 1 \end{pmatrix} \cdot \begin{pmatrix} u_1(t) \\ u_2(t) \end{pmatrix} \qquad (**)$$

For the $\varepsilon=3$ value of the parameter, like the previous numerical example, according to the algorithm, we have the following results ($\sigma(t)=1, \rho(t)=0$):

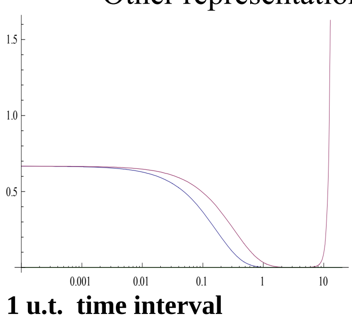


Optimal trajectory

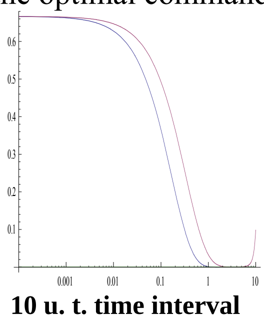


Optimal command(1 u.t)

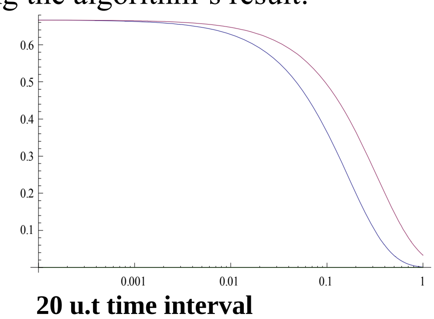
Other representations for the optimal command, using the algorithm's result:



1 u.t. time interval



10 u. t. time interval



20 u.t time interval

Red = prey, Blue = predator

The dynamical systems noted (*) and (**), which result from the homogeneous Volterra's equations are similar, with the single difference that the commanded action and the expected result are different with regard to the selected population segment. These systems can form a special set, whose properties can be evaluated no matter the action of the external command or the expected response. The equivalent relation, noted by "≅", between the set elements can be defined with aid of the command matrix operator which is present in all these systems, for the same σ(t) and ρ(t): $(S_1) \cong (S_2) \Leftrightarrow [\, B_1=B_2 \;\&\; \varepsilon_1=\varepsilon_2]$, $\varepsilon>0$, $B_i \in M_2(R)$ $_{(i=1,2)}$.

The equivalent relation is sufficiently defined only by the first equation, the dynamical one. For all these systems we shall be in the context of the algorithm for the optimal command of the dynamical systems with quadratic cost function. According to this algorithm, the difference between the results will be made only by the x(t) solution of the Riccati equation, which, in turn, could be the second equivalent relation , this time, between the "associate" Volterra equations. The fact that the defined "≅" relation is an equivalent relation, can be demonstrated taking account to the properties of the system terms:

$(S_1) \cong (S_1)$

$(S_1) \cong (S_2) \Rightarrow (S_2) \cong (S_1)$ because: $(B_1=B_2 \;\&\; \varepsilon_1 =\varepsilon_2) \Rightarrow (B_2=B_1 \;\&\; \varepsilon_2 =\varepsilon_1)$

$(S_1) \cong (S_2) \;\&\; (S_2) \cong (S_3) \Rightarrow (S_1) \cong (S_3)$ because: $(B_1=B_2 \;\&\; \varepsilon_1 =\varepsilon_2) \;\&\; (B_2=B_3 \;\&\; \varepsilon_2 =\varepsilon_3) \Rightarrow (B_1=B_3 \;\&\; \varepsilon_1 =\varepsilon_3)$

4. CONCLUSIONS

It can conclude that two systems, noted (*) and (**), are in the same equivalent class if the external command acts on the same population segment and the quadratic operator parameter in the homogeneous equation is the same, no matter of the response of the system, which can be different. The non-unicity of the matrix C, which corresponds to the same optimal control, represents an obstacle ignored by the definition of the equivalent relation on the set of the dynamical equations and the definition of some canonical forms.

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