STUDY OF ECOLOGICAL COMPETITION AMONG FOUR SPECIES

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STUDY OF ECOLOGICAL COMPETITION AMONG FOUR SPECIES

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1- INTRODUCTION

Following a previous paper (1), on the Lotka- Volterra equations for the interactive competition of three species in an habitat, we wish to analyze in the competition between four species, specially in relation with the important feature of the existence of cycles.

In the literature, there are important studies, which attack different problems related to the Lotka- Volterra equations. For example Bojadziev and Chan (2), consider oscillations governed by the generalized Volterra- Gause- Witt equation for two species to include retardation effect in population dynamics. They use the Krylov- Bogolinbov- Mitropelskii perturbation method with an extension for differential equations with retarded argument. They also discuss models with small time delay. On the other hand in an interesting paper, De Angelis (3) applies perturbation methods to the differential equation of the predator- prey model, to find approximate amplitudes and periods of limit cycles solutions.

Other important discussion of oscillatory models for two interacting species is found in Van de Vaart (4), where a complete enumeration is given of the condition that the parameters of these models must satisfy in order that a part of the phase space be filled with a family of closed curves.

Recently there have been studies about the structural perturbations of the Lotka- Volterra equations. Let us mention the work by Ikeda and Siljak. Finally we note the paper by Bell (5) on predator prey type equations for simulating an immune response between antigen and antibody production.

However there is not a detailed analysis for more than three species. In this paper we wish to develop a general- method for four species, which will give rise to an important step in the general study of the existence of cycles for an arbitrary number of species, a problem to be study a next paper.

2- FOUR SPECIES MODEL

We now consider the Lotka- Volterra systems for four species, whose equations take the form:

$$\frac{dx}{dt} = x\,(\varepsilon_1 - a_{1\,2}\,y + a_{1\,3}\,z + a_{1\,4}\,u) \tag{1}$$

$$\frac{dy}{dt} = y\,(-\varepsilon_2 + a_{2\,1}\,x + a_{2\,3}\,z + a_{2\,4}\,u)$$

$$\frac{dz}{dt} = z\,(\varepsilon_3 + a_{3\,1}\,x + a_{3\,2}\,y + a_{3\,3}z + a_{3\,4}\,u)$$

$$\frac{du}{dt} = u\,(\varepsilon_4 + a_{4\,1}\,x + a_{4\,2}\,y + a_{4\,3}\,z + a_{4\,4}\,u)$$

where x, y, z and u represent the population densities of the four species under consideration. The parameters have the standard meaning in this type of problem. We consider that $\varepsilon_1, \varepsilon_2, a_{12}$ and $a_{2\,1}$ are positive, while the other parameters can take real value.

Our task in this paper is to find the general condition for the existence of cyclic variation of the population densities.

Therefore, we assume that the variable u, is related to the variables x, y and z through a function f_1:

$$u = f_1(x, y, z) \tag{2}$$

Derivation with respect to time yields:

$$\frac{du}{dt} = \frac{\partial f_1}{\partial x}\,\frac{dx}{dt} + \frac{\partial f_1}{\partial y}\,\frac{dy}{dt} + \frac{\partial f_1}{\partial z}\,\frac{dz}{dt} \tag{3}$$

Now, using system (1) in equation (3), we obtain:

$$\begin{aligned} u\,(\varepsilon_4 + a_{4\,1}\,x + a_{4\,2}\,y + a_{4\,3}\,z + a_{4\,4}\,u) &= \frac{\partial f_1}{\partial x}\,x\,(\varepsilon_1 - a_{1\,2}\,y + a_{1\,3}\,z + a_{1\,4}\,u) \\ &+ \frac{\partial f_1}{\partial y}\,y\,(-\varepsilon_2 + a_{2\,1}\,x + a_{2\,3}\,z + a_{2\,4}\,u) \\ &+ \frac{\partial f_1}{\partial z}\,z\,(\varepsilon_3 + a_{3\,1}\,x + a_{3\,2}\,y + a_{3\,3}z + a_{3\,4}\,u) \end{aligned} \tag{4}$$

To solve this order partial differential equation, we first try to solve the following separate parts:

(5)

$$a_{4\,4}\,u = \frac{\partial f_1}{\partial x} a_{1\,4}\,x + \frac{\partial f_1}{\partial y} a_{2\,4}\,y + \frac{\partial f_1}{\partial z} a_{3\,4}\,z$$

$$u\,(\varepsilon_4 + a_{4\,1}\,x + a_{4\,2}\,y + a_{4\,3}\,z) = \frac{\partial f_1}{\partial x}\,x(\varepsilon_1 - a_{1\,2}\,y + a_{1\,3}\,z)$$

$$+\frac{\partial f_1}{\partial y}\,y(-\varepsilon_2 + a_{2\,1}\,x + a_{2\,3}\,z) + \frac{\partial f_1}{\partial z}\,z\,(\varepsilon_3 + a_{3\,1}\,x + a_{3\,2}\,y + a_{3\,3}z) \qquad (6)$$

We remark that if we solve equation (5) in such a way that the arbitrary function which appears in the solution of equation (4).

By standard methods, as it was obtained in the previous paper (1), the solution of equation (5) is:

$$u = z^{a_{44}/a_{34}}\,F\left(\frac{y^{1/a_{24}}}{x^{1/a_{14}}}, \frac{z^{1/a_{34}}}{y^{1/a_{24}}}\right) \qquad (7)$$

where F is an arbitrary function. Now, calling:

$$\omega_1 = \frac{y^{1/a_{24}}}{x^{1/a_{14}}} \qquad , \qquad \omega_2 = \frac{z^{1/a_{34}}}{y^{1/a_{24}}}$$

and replacing the expression (7) for u in equation (6), we obtain the first order partial differential equation:

(8)

$$F(\varepsilon_4 + a_{4\,1}\,x + a_{4\,2}\,y + a_{4\,3}\,z)$$

$$= -\frac{\omega_1}{a_{14}}\frac{\partial F}{\partial \omega_1}(\varepsilon_1 - a_{1\,2}\,y + a_{1\,3}\,z)$$

$$+\left(\frac{\omega_1}{a_{24}}\frac{\partial F}{\partial \omega_1} - \frac{\omega_2}{a_{24}}\frac{\partial F}{\partial \omega_2}\right)(-\varepsilon_2 + a_{2\,1}\,x + a_{2\,3}\,z)$$

$$+\left(\frac{a_{44}}{a_{34}}\,F + \frac{\omega_2}{a_{34}}\frac{\partial F}{\partial \omega_2}\right)(\varepsilon_3 + a_{3\,1}\,x + a_{3\,2}\,y + a_{3\,3}z)$$

In order to solve this last partial differential equation, we try the following system of first order partial differential equations:

$$F = \alpha_1 \omega_1 \frac{\partial F}{\partial \omega_1} + \alpha_2 \omega_2 \frac{\partial F}{\partial \omega_2} \tag{9}$$

where the constant are:

$$\alpha_1 = \left(-\frac{\varepsilon_1}{a_{14}} - \frac{\varepsilon_2}{a_{24}}\right) \Big/ \left(\varepsilon_4 - \varepsilon_3 \frac{a_{44}}{a_{34}}\right) \quad ; \quad \alpha_2 = \left(\frac{\varepsilon_3}{a_{34}} + \frac{\varepsilon_2}{a_{24}}\right) \Big/ \left(\varepsilon_4 - \frac{a_{44}}{a_{34}}\right)$$

and

$$\begin{aligned} F(a_{41}x + a_{42}y + a_{43}z) \\ &= -\frac{\omega_1}{a_{14}} \frac{\partial F}{\partial \omega_1} (- a_{1\,2}\, y \, + \, a_{1\,3}\, z\,) \\ &+ \left(\frac{\omega_1}{a_{24}} \frac{\partial F}{\partial \omega_1} - \frac{\omega_2}{a_{24}} \frac{\partial F}{\partial \omega_2}\right) (a_{2\,1}\, x \, + \, a_{2\,3}\, z) \\ &+ \left(\frac{a_{44}}{a_{34}}\, F + \frac{\omega_2}{a_{34}} \frac{\partial F}{\partial \omega_2}\right) (a_{3\,1}\, x \, + \, a_{3\,2}\, y \, + \, a_{3\,3} z) \end{aligned} \tag{10}$$

The general solution of equation (9) is given by:

$$F = {\omega_1}^{(1/\alpha_1)}\, K\left({\omega_1}^{(1/\alpha_1)} / {\omega_2}^{(1/\alpha_2)}\right) \tag{11}$$

where K is an arbitrary function.

Calling:

$$\xi = {\omega_1}^{(1/\alpha_1)} / {\omega_2}^{(1/\alpha_2)}$$

and replacing the expression (11) in the partial differential equation (10), it turns out that:

(12)

$$K(\xi)(a_{4\,1}\,x + \ a_{4\,2}\,y \ + \ a_{4\,3}\,z)$$

$$= \left(\frac{a_{12}}{\alpha_1 a_{14}} y - \frac{a_{13}}{\alpha_1 a_{14}}\ z\right)\left(K(\xi) + \xi \frac{d}{d\xi} K(\xi)\right)$$

$$+ \left(\frac{a_{21}}{\alpha_1 a_{24}} x + \frac{a_{23}}{\alpha_1 a_{24}}\ z\right)\left(K(\xi) + \xi \frac{d}{d\xi} K(\xi)\right)$$

$$+ \left(\frac{a_{21}}{\alpha_1 a_{24}} x + \frac{a_{23}}{\alpha_1 a_{24}}\ z\right)\left(\xi \frac{d}{d\xi} K(\xi)\right)$$

$$+ \left(\frac{a_{31} a_{44}}{a_{34}}\ x + \frac{a_{32} a_{44}}{a_{34}}\ y + \frac{a_{33} a_{44}}{a_{34}}\ z\right)\ K(\xi)$$

$$+ \left(-\frac{a_{31}}{\alpha_2 a_{34}}\ x + \frac{a_{32}}{\alpha_2 a_{34}}\ y + \frac{a_{33}}{\alpha_2 a_{34}}\ z\right) \xi \frac{d}{d\xi} K(\xi)$$

or, equivalently:

$$\frac{K'}{K} = \frac{1}{\xi}\left(\frac{\lambda_1\ x + \lambda_2\ y + \lambda_3\ z}{\delta_1\ x + \delta_2\ y + \delta_3\ z}\right) \tag{12'}$$

where the constant appearing in the last equation take the form:

$$\lambda_1 = a_{41} - \frac{a_{21}}{\alpha_1 a_{24}} - \frac{a_{31} a_{44}}{a_{34}} \quad ; \quad \lambda_2 = a_{42} - \frac{a_{12}}{\alpha_1 a_{14}} - \frac{a_{32} a_{44}}{a_{34}}$$

$$\lambda_3 = a_{43} + \frac{a_{13}}{\alpha_1 a_{14}} - \frac{a_{23}}{\alpha_1 a_{24}} - \frac{a_{33} a_{44}}{a_{34}} \quad ; \quad \delta_1 = \frac{a_{21}}{\alpha_1 a_{24}} + \frac{a_{21}}{\alpha_2 a_{24}} - \frac{a_{31}}{\alpha_2 a_{34}}$$

$$\delta_2 = \frac{a_{12}}{\alpha_1 a_{14}} - \frac{a_{32}}{\alpha_2 a_{34}} \quad ; \quad \delta_3 = -\frac{a_{13}}{\alpha_1 a_{14}} + \frac{a_{23}}{\alpha_1 a_{24}} + \frac{a_{23}}{\alpha_2 a_{24}} - \frac{a_{33}}{\alpha_2 a_{34}}$$

To continue in our analysis, we impose the following restriction:

$$\frac{\lambda_1}{\lambda_3} = \frac{\delta_1}{\delta_3} \quad \text{and} \quad \frac{\lambda_2}{\lambda_3} = \frac{\delta_2}{\delta_3}$$

Under these condition we have that equation (12') becomes:

$$K' = \frac{\lambda_3}{\delta_3}\frac{1}{\xi}K$$

The solution of this last equation is:

$$K(\xi) = C_1 \xi^{(\lambda_3/\delta_3)} \tag{13}$$

where C_1 is a constant to be determined.

From here we obtain the following functional for u:

$$u(x, y, z) = C_1\, x^{r_1}\, y^{r_2}\, z^{r_3} \tag{14}$$

with:

$$r_1 = -\left(\frac{1}{\alpha_1 a_{14}} + \frac{\lambda_3}{\alpha_1 \delta_3 a_{14}}\right)$$

$$r_2 = \frac{1}{\alpha_1 a_{24}} + \frac{\lambda_3}{\delta_3 a_{24}}\left(\frac{1}{\alpha_1} + \frac{1}{\alpha_2}\right)$$

$$r_3 = \frac{a_{44}}{a_{34}} - \frac{\lambda_3}{\alpha_2 \delta_3 a_{34}}$$

We note that the value of C_1 is determined with the initial conditions of the problem.

In this way, we have reduced the number of initial equations from four to three, namely:

$$\frac{dx}{dt} = x\,(\varepsilon_1 - a_{12}\,y + a_{13}\,z + a_{14}\,C_1\,x^{r_1}\,y^{r_2}\,z^{r_3})$$

$$\frac{dy}{dt} = y\,(-\varepsilon_2 + a_{21}x + a_{23}\,y + a_{24}C_1\,x^{r_1}\,y^{r_2}\,z^{r_3}) \tag{15}$$

$$\frac{dz}{dt} = z\,(\varepsilon_3 + a_{31}x + a_{32}\,y + a_{33}\,z + a_{34}C_1\,x^{r_1}\,y^{r_2}\,z^{r_3})$$

Next we are going to relate the variable z to the first two variables. The procedure is correct when a cyclic solution exists.

Letting:

$$z = f_2(x, y) \tag{16}$$

Again, to determine the function f_2, derivate z with respect to time:

$$\frac{dz}{dt} = \frac{\partial f_2}{\partial x}\frac{dx}{dt} + \frac{\partial f_2}{\partial y}\frac{dy}{dt} \tag{17}$$

and replace the values of the derivatives by what we have in system (15), obtaining the partial differential equation:

$$\begin{aligned} z(\varepsilon_3 + a_{31}\, x + a_{32}\, y + a_{33}\, z + a_{34} C_1\, x^{r_1}\, y^{r_2}\, z^{r_3}) \\ = \frac{\partial f_2}{\partial x}\, x(\varepsilon_1 - a_{12} y + a_{13} z + a_{14} C_1\, x^{r_1}\, y^{r_2}\, z^{r_3}) \\ + \frac{\partial f_2}{\partial y}\, y(-\varepsilon_2 + a_{21} x + a_{23} z + a_{24} C_1\, x^{r_1}\, y^{r_2}\, z^{r_3}) \end{aligned} \tag{17'}$$

We solve this equation in steps. The first step is to consider the equation:

$$a_{34} z = a_{14}\, x \frac{\partial f_2}{\partial x} + a_{24}\, y \frac{\partial f_2}{\partial y} \tag{18}$$

whose solution is given by:

$$z = y^{(a_{34}/a_{24})}\, Q(\emptyset) \tag{19}$$

where Q is an arbitrary function and:

$$\emptyset = \frac{y^{(1/a_{24})}}{x^{(1/a_{14})}}$$

Replacing z by the expression (19), equation (17') turns out to be:

$$\begin{aligned} \left(\varepsilon_3 + a_{31}\, x + a_{32}\, y + a_{33}\, y^{(a_{34}/a_{24})} Q\right) Q \\ = (-1/a_{14}) Q'(\emptyset)\left(\varepsilon_1 - a_{12} y + a_{13} y^{(a_{34}/a_{24})}\, Q\right) + (a_{34}/a_{24}) \\ + 1/a_{24} Q'(\emptyset)\left(-\varepsilon_2 + a_{21} x + a_{23} y^{(a_{34}/a_{24})}\, Q\right) \end{aligned} \tag{20}$$

or equivalently:

$$\frac{Q'}{Q} = b(1/\emptyset) \tag{21}$$

With

$$b = \frac{a_{14}(a_{23} a_{34} - a_{33} a_{24})}{(a_{13} a_{24} - a_{23} a_{14})}$$

Under the conditions:

$$\varepsilon_3 = -\frac{\varepsilon_1}{a_{14}} - \frac{\varepsilon_2}{a_{24}}\,(1 + a_{34})$$

$$a_{31} = \frac{a_{21}}{a_{24}}(1 + a_{34}) \quad and \quad a_{32} = \frac{a_{12}}{a_{14}}$$

The solution of (21) is:

$$Q(\emptyset) = C_2 \emptyset^b$$

Where the arbitrary constant C_2 is determined by the initial condition of the problem.

Thus the variable z becomes:

$$z(x,y) = C_2 x^{S_1} y^{S_2} \tag{22}$$

where: $s_1 = -b/a_{14}$ and $s_2 = 1/a_{24}\,(b + a_{34})$

Replacing the value of z in the system of differential equations (15), it yields the reduced system: (23)

$$\frac{dx}{dt} = x\big(\varepsilon_1 - a_{12}\,y + \bar{a}_{13}\,x^{s_1}\,y^{s_2} + \,\bar{a}_{14}\,x^{(r_1+s_1r_3)}y^{(r_2+s_2r_3)}\big)$$

$$\frac{dy}{dt} = y\big(-\varepsilon_2 + a_{21}x + \bar{a}_{23}\,x^{s_1}\,y^{s_2} + \,\bar{a}_{24}\,x^{(r_1+s_1r_3)}y^{(r_2+s_2r_3)}\big)$$

where:

$$\bar{a}_{13} = C_2 a_{13} \quad ; \quad \bar{a}_{23} = C_2 a_{23}$$

$$\bar{a}_{14} = C_1 C_2^{r_3} a_{14} \quad ; \quad \bar{a}_{24} = C_1 C_2^{r_3} a_{24}$$

3- SOLUTION OF THE REDUCED EQUATIONS

Our task in the paragraph is to solve the systems (23), which is the reduced form of the system of four equation (1).

We perform a substitution of variables similar to that used by Goel et al. in (6).

Calling:

$$a_{12} = -a/\beta_1 \quad ; \quad a_{21} = a/\beta_2$$

$$q_1 = \varepsilon_2\beta_2/a \quad ; \quad q_2 = -\varepsilon_1\beta_1/a$$

with the change of variables:

$$v_1 = \log(x/q_1) \quad ; \quad v_2 = \log(y/q_2)$$

the system (23) becomes:

$$\frac{dv_1}{dt} = \varepsilon_1 + \frac{a}{\beta_1} q_2 \exp(v_2) + \bar{a}_{13} q_1^{s_1} q_2^{s_2}\, exp(s_1 v_1 + s_2 v_2)$$

$$+ \left(\bar{a}_{14} q_1^{(r_1+s_1 r_3)} q_2^{(r_2+s_2 r_3)}\right) exp\big((r_1 + s_1 r_3) v_1 + (r_2 + s_2 r_3) v_2\big)$$

which with the constants:

$$H_1 = \frac{\beta_1 \bar{a}_{13} q_2^{(s_2-1)}}{a\, q_1^{s_1}}$$

$$H_2 = (\beta_1/a)\, \bar{a}_{14} q_1^{(r_1+s_1 r_3)} q_2^{(r_2+s_2 r_3-1)}$$

becomes:

$$\frac{dv_1}{dt} = a\, q_2 \big\{\exp(v_2) - 1 + H_1 exp(s_1 v_1 + s_2 v_2) + H_2\, exp\big((r_1 + s_1 r_3) v_1 + (r_2 + s_2 r_3) v_2\big)\big\} \tag{24}$$

similarly, for the second equation:

$$\frac{dv_2}{dt} = a q_1 \big\{\exp(v_1) - 1 + H_3 exp(s_1 v_1 + s_2 v_2) + H_4 exp\big((r_1 + s_1 r_3) v_1 + (r_2 + s_2 r_3) v_2\big)\big\} \tag{25}$$

where the coefficient are now:

$$H_3 = \frac{\beta_1 \bar{a}_{13} q_2^{(s_2)}}{a\, q_1^{(-s_1+1)}} \quad ; \quad H_4 = (\beta_2/a)\, \bar{a}_{24} q_1^{(r_1+s_1 r_3-1)} q_2^{(r_2+s_2 r_3)}$$

Cross- multiplication equation (24) and (25) yields after some manipulations: (26)

$$\frac{d}{dt}\{\beta_1 q_1(\exp(v_1) - v_1)\}$$

$$= \frac{d}{dt}\{\beta_2 q_2(\exp(v_2) - v_2)\}$$

$$+\ exp(s_1 v_1 + s_2 v_2)\left(\beta_2 q_2 H_1 \frac{dv_2}{dt} - \beta_1 q_1 H_3 \frac{dv_1}{dt}\right)$$

$$+ exp\big((r_1 + s_1 r_3) v_1 + (r_2 + s_2 r_3) v_2\big)\left(\beta_2 q_2 H_2 \frac{dv_2}{dt} - \beta_1 q_1 H_4 \frac{dv_1}{dt}\right)$$

With the new constants:

$$\beta_2 q_2 H_1 = A_1 s_2 \quad ; \quad \beta_1 q_1 H_3 = -A_2 s_1$$

$$\beta_2 q_2 H_2 = A_3 (r_2 + s_2 r_3) \quad ; \quad \beta_1 q_1 H_4 = -A_4 (r_1 + s_1 r_3)$$

And if:

$$A = A_1 = A_2 \qquad ; \qquad B = A_3 = A_4$$

equation (26) becomes:

(27)

$$\frac{d}{dt}\{\beta_1 q_1(\exp(v_1) - v_1)\} = \frac{d}{dt}\{\beta_2 q_2(\exp(v_2) - v_2)\}$$

$$+ A\,exp(s_1 v_1 + s_2 v_2)\left(s_1 \frac{dv_1}{dt} + s_2 \frac{dv_2}{dt}\right)$$

$$+ \ Bexp\big((r_1 + s_1 r_3)v_1 + (r_2 + s_2 r_3)v_2\big)\left((r_2 + s_2 r_3)\frac{dv_2}{dt} + (r_2 + s_2 r_3)\frac{dv_1}{dt}\right)$$

Now using the equality:

$$\frac{d}{dt}\{exp(\lambda v_1 \pm n v_2)\} = exp(\lambda v_1 \pm n v_2)\left(\left(\lambda \frac{dv_1}{dt} \pm n \frac{dv_2}{dt}\right)\right)$$

equation (27) turns out to be:

(28)

$$\frac{d}{dt}\{\beta_1 q_1(\exp(v_1) - v_1)\}$$

$$= \frac{d}{dt}\{\beta_2 q_2(\exp(v_2) - v_2)\} + \ \frac{d}{dt}\{A\,exp(s_1 v_1 + s_2 v_2)\}$$

$$+ \frac{d}{dt}\big\{B\,exp\big((r_1 + s_1 r_3)v_1 + (r_2 + s_2 r_3)v_2\big)\big\}$$

Integrating, we obtain:

(29)

$$\beta_1 q_1(\exp(v_1) - v_1) - A\,exp(s_1 v_1 + s_2 v_2)$$

$$= \ C_3 + \beta_2 q_2(\exp(v_2) - v_2) + B\,exp\big((r_1 + s_1 r_3)v_1 + (r_2 + s_2 r_3)v_2\big)$$

where C_3 is an arbitrary constant to be determined with the initial values of the problem.

Now going back to the old variables, we obtain for the solution the functional relation:

$$-\frac{1}{\varepsilon_1}\left(\frac{x}{q_1} - \log\frac{x}{q_1}\right) + P_1\big(y^{a_1}/x^{b_1}\big) = C'_3 + \frac{1}{\varepsilon_2}\left(\frac{y}{q_2} - \log\frac{y}{q_2}\right) - P_2\big(y^{a_2}/x^{b_2}\big) \qquad (30)$$

where:

$$a_1 = s_2 \quad ; \quad b_1 = -s_1 \quad ; \quad a_2 = r_2 + s_2 r_3 \quad ; \quad b_2 = -s_1 r_3 - r_1$$

$$C'_3 = \frac{C_3}{a\,q_1 q_2} \qquad ; \qquad P_1 = \frac{-A}{a\,q_2^{(s_2+1)} q_1^{(s_1+1)}}$$

and

$$P_2 = -B/\left(aq_1^{(r_1+s_1r_3+1)}q_2^{(r_2+s_2r_3+1)}\right)$$

This equation can take the form:

$$\left\{\frac{(x/q_1)}{exp(x/q_1)}\right\}^{1/\varepsilon_1} = K\left\{\frac{(y/q_2)}{exp(y/q_2)}\right\}^{-1/\varepsilon_2} exp\left(-P_1\, y^{a_1}/x^{b_1} - P_2\, y^{a_2}/x^{b_2}\right) \tag{31}$$

with the constant:

$$K = exp(C'_3)$$

It is worth comparing equation (31) with the integral obtained by Volterra in these prey- predator systems, we note that equation (31) has an additional term, the last one of the right side. This term takes into consideration the competition of the third and fourth species between them and among with the first two species.

4- CYCLE EXISTENCE

Having the integral or relationship given by equation (31) between the two primitive variables of the problem x and y, in this paragraph we are going to show the existence of a cyclic behavior in the population densities x and y.

We study only a general situation, other cases might also be worked out, but for simplicity in the presentation, we do not include them here.

As before, let us call ζ_1 the function described in the left side of the equation (31), we call ζ_2 the right side of the same equation.

When:

$$a_1 = 1 \quad and \quad a_2 = 1$$

with:

$$\bar{P}_1 = -P_1 < 0 \quad and \quad \bar{P}_2 = -P_2 < 0$$

the last function becomes:

$$\zeta_2(x,y) = K(1/q_2)^{(-1/\varepsilon_2)}\, y^{(-1/\varepsilon_2)} \exp(F(x)\, y) \tag{32}$$

where:

$$F(x) = (1/q_2\varepsilon_2) + \bar{P}_1\left(1/x^{b_1}\right) + \bar{P}_2\left(1/x^{b_2}\right)$$

Now we follow the procedure out lined in reference (1), that is, we look for the dependence of the minimum of the function ζ_2 with respect to y, parametrically in x. Hence we partially derive ζ_2 and impose the minimum condition:

$$\frac{\partial \zeta_2}{\partial y} = K(1/q_2)^{(-1/\varepsilon_2)} \left\{ -\frac{1}{\varepsilon_2}\, y^{\,-1/\varepsilon_2 - 1} \exp(F(x)y) + y^{\,-1/\varepsilon_2}\, F(x) \exp(F(x)y) \right\} = 0$$

The ordinate y_r of such a minimum is related with the variable x by:

$$-(1/\varepsilon_2)(1/y_r) + F(x) = 0$$

or equivalently:

$$y_r = (1/\varepsilon_2\, F(x)) \tag{33}$$

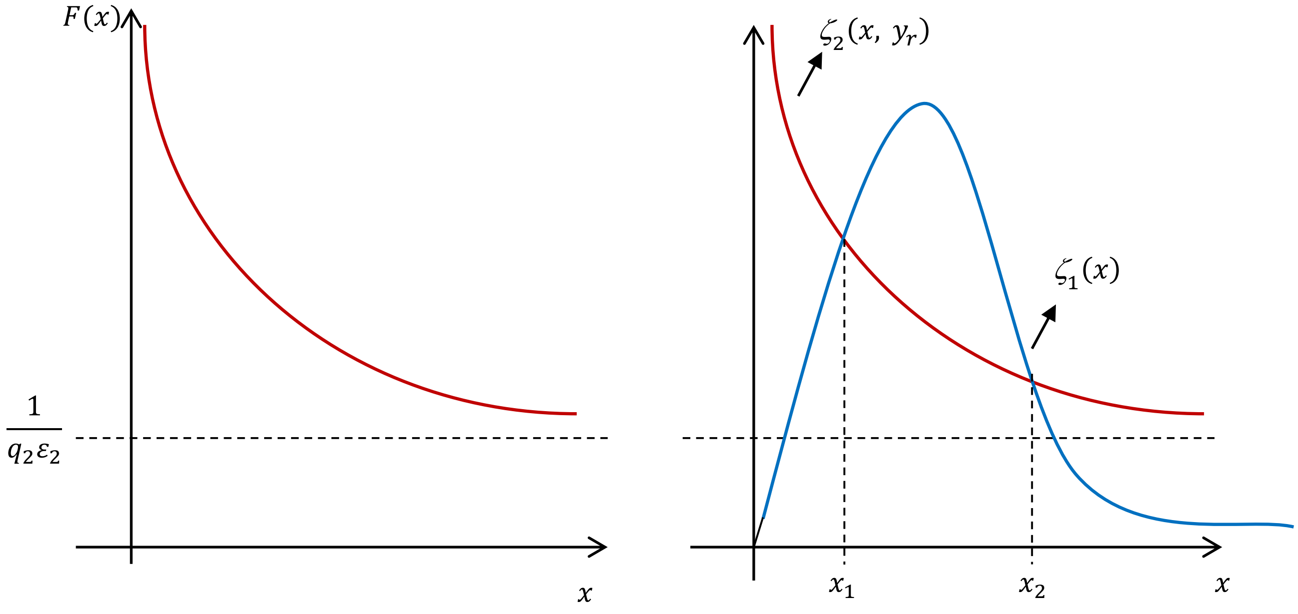
In order to obtain the parametric curves of the minima in terms of x, we replace equation (33) into equation (32), obtaining:

$$\zeta_2(x,\, y_r) = \bar{K}(F(x))^{1/\varepsilon_2} \tag{34}$$

where:

$$\bar{K} = K(q_2\varepsilon_2)^{1/\varepsilon_2} \exp\,(1/\varepsilon_2)$$

Hence we now have the following qualitative curves for $b_1, b_2 > 0$: ζ_1



$Figure\ 1$

At this point, by a analysis similar to the previous paper (1) we obtain the existence of the cycle under very general condition. (See the behavior of the functions $\zeta_1(x), \zeta_2(x,\, y_r)$).

5- COMPUTATION OF THE PERIOD

In the previous paragraphs we have proven the existence and computed the cycle for the competition among the four species under consideration. Here we are going to calculate the period of the general cycle.

Let us consider equation (31), from which we have for a new variable:

$$\Psi = \left\{\frac{(x/q_1)}{exp\,(x/q_1)}\right\}^{1/\varepsilon_1} = K\left\{\frac{(1/q_2)}{exp(1/q_2)}\right\}^{-1/\varepsilon_2} exp\left(-P_1\, y^{a_1}/x^{b_1} - P_2\, y^{a_2}/x^{b_2}\right) \tag{35}$$

Now taking logarithm and derivating we get:

$$\frac{1}{\Psi}\frac{d\Psi}{dt} = (1/\varepsilon_1)\left(\frac{\varepsilon_2^2 - a_{21}^2 x}{\varepsilon_2 a_{21} x}\right)\frac{dx}{dt} \tag{36}$$

Now, replacing the derivate of x with respect to time in equation (23), we obtain:

$$\frac{1}{\Psi}\frac{d\Psi}{dt} = \frac{1}{\Psi}\left(\frac{\varepsilon_2^2 - a_{21}^2 x}{\varepsilon_2 a_{21} x}\right)\left(\varepsilon_1 - a_{12}y + \bar{a}_{13}y^{a_1}x^{-b_1} + \bar{a}_{14}y^{a_2}x^{-b_2}\right) \tag{37}$$

and therefore:

$$P = \int_{T_1}^{T_2} dt = \int_{\Psi_1}^{\bar{\Psi}_1} \varepsilon_1\left\{\left(\frac{\varepsilon_2^2 - a_{21}^2 x}{a_{21}\varepsilon_2}\right)\left(\varepsilon_1 - a_{12}y + \bar{a}_{13}y^{a_1}x^{-b_1} + \bar{a}_{14}y^{a_2}x^{-b_2}\right)\right\}^{-1}\frac{d\Psi}{\Psi} \tag{39}$$

where T_1 is the time corresponding to Ψ_1, for the point with the minimum y, while T_2 is the time when the solution passes next through such a point $\Psi_1 = \bar{\Psi}_1$. Thus the exact computation of the period P can be obtained.

We now wish to estimate the period P. For this find a suitable relationship between Ψ an x, in order to replace it in the integral. From the first part of equation (35) we have:

$$\Psi^{\varepsilon_1} = (a_{21}/\varepsilon_2)x\; exp(-\,a_{21}/\varepsilon_2\, x) \tag{40}$$

Now taking:

$$x = x_0 + w_1 \tag{41}$$

where x_0 is the equilibrium value of the number of individuals of the first species, an w_1 is the perturbation from this average value of the population.

Replacing (41) in (40) it yields:

$$\begin{aligned} \varepsilon_2/a_{21}\,\Psi^{\varepsilon_1}\, exp(a_{21}/\varepsilon_2\, x) &= (x_0 + w_1)exp(-\,a_{21}/\varepsilon_2\, w_1) \\ &= (x_0 + w_1)\left(1 - (a_{21}/\varepsilon_2)\, w_1 + \frac{1}{2}(a_{21}/\varepsilon_2)^2\, w_1 - \ldots\right) \\ &\cong x_0 + w_1 - (a_{21}/\varepsilon_2)x_0 w_1 \end{aligned} \tag{42}$$

where in the last part we have neglected terms of higher order in $w_1$since it is considered that the perturbation is small.

From equation (42) we get:

$$w_1 = \frac{H_1 \Psi^{\varepsilon_1} - x_0}{H_2} \tag{43}$$

where:

$$H_1 = (\varepsilon_2/a_{21}) exp(a_{21}/\varepsilon_2\, x_0) \quad and \quad H_2 = (1 - \ (a_{21}/\varepsilon_2\ )x_0) \tag{44}$$

consider:

$$y = y_0 + w_2 \tag{45}$$

where y_0 is the equilibrium value of the number of individual in the second species. The value w_2 is a small perturbation. Now taking the right side of equation (35), we arrive to:

$$(\varepsilon_1/a_{12})(\Psi/K)^{-\varepsilon_2} = (y_0 + w_2)$$

$$exp\{-\, \varepsilon_2 a_{12}/\varepsilon_1 (y_0 + w_2) + \varepsilon_2 P_1 (y_0 + v_2)^{a_1} (x_0 + w_1)^{-b_1} + \varepsilon_2 P_2 (y_0 + w_2)^{a_2} (x_0 + w_1)^{-b_2}\} \tag{46}$$

Expanding the binomial and exponential functions we arrive at:

$$\Psi^{-\varepsilon_2} H_3 \exp(H_4 w_1) - y_0 = (H_5 - 1) w_2 \tag{47}$$

where:

$$\begin{gathered} H_3 = K^{\varepsilon_2}\ \varepsilon_1/a_{12} exp\left((\varepsilon_2 a_{12}/\varepsilon_1) y_0\right) - \varepsilon_2 P_1 {y_0}^{a_1} {x_0}^{-b_1} - \varepsilon_2 P_2 {y_0}^{a_2} {x_0}^{-b_2} \\ H_4 = \varepsilon_2 P_1 b_1 {y_0}^{a_1} {x_0}^{-(b_1+1)} + \varepsilon_2 P_2 b_2 {y_0}^{a_2} {x_0}^{-(b_2+1)} \\ H_5 = \varepsilon_2 P_1 a_1 {y_0}^{a_1} x^{-b_1} + \varepsilon_2 P_2 a_2 {y_0}^{a_2} x^{-b_2} - (\varepsilon_2 a_{12}/\varepsilon_1) y_0 \end{gathered} \tag{48}$$

From equation (47) we get:

$$w_2 = \frac{H_7 ex\, p(-H_6 \Psi^{\varepsilon_1})\, \Psi^{-\varepsilon_2} - y_0}{H_5 - 1} \tag{49}$$

with:

$$H_6 = H_4 H_1 / H_2 \quad and \quad H_7 = H_3 exp(H_4 x_0 / H_2) \tag{50}$$

Now replacing the equation (41), (43), (45), and (49) in the integral (39) we arrive at the following expression:

$$P = \int_{\Psi_1}^{\overline{\Psi}_1} \varepsilon_1 \varepsilon_2 a_{21} \left\{ \left({\varepsilon_2}^2 - a_{21}^2 (x_0 + w_1) \right) \left(\varepsilon_1 - a_{12} (y_0 + w_2) + \bar{a}_{13} (y_0 + w_2)^{a_1} (x_0 + w_1)^{-b_1} \right) + \bar{a}_{14} (y_0 + w_2)^{a_2} (x_0 + w_1)^{-b_2} \right\}^{-1} \frac{d\Psi}{\Psi} \tag{51}$$

Expanding the binomials and keeping only first order terms in the perturbations, we get: (52)

$$P = \int_{\Psi_1}^{\bar{\Psi}_1} \frac{\varepsilon_1 \varepsilon_2 a_{21} d\Psi}{\Psi(\varepsilon_2{}^2 - a_{21}{}^2 x_0 - a_{12}{}^2 w_1)(H_8 + H_9 w_1 + H_{10} w_2)}$$

where:

(53)

$$H_8 = \varepsilon_1 - a_{12} y + \bar{a}_{13} y_0{}^{a_1} x_0{}^{-b_1} + \bar{a}_{14} y_0{}^{a_2} x_0{}^{-b_2}$$

$$H_9 = -\bar{a}_{13} b_1 y_0{}^{a_1} x_0{}^{-b_1 - 1} - \bar{a}_{14} b_2 y_0{}^{a_2} x_0{}^{-b_2 - 1}$$

$$H_{10} = -a_{12} + \bar{a}_{13} a_1 y_0{}^{a_1 - 1} x_0{}^{-b_1} + \bar{a}_{14} a_2 y_0{}^{a_2 - 1} x_0{}^{-b_2}$$

After some manipulation, we obtain the following integral:

(54)

$$P = \int_{\Psi_1}^{\bar{\Psi}_1} \frac{H_{11} d\Psi}{(H_{16} + H_{17} \Psi^{\varepsilon_1} + H_{18} \Psi^{-\varepsilon_2}\, exp(-H_6 \Psi^{\varepsilon_1}))}$$

with:

(55)

$$H_{11} = \varepsilon_1 \varepsilon_2 a_{21} \quad ; \quad H_{12} = a_2{}^2 - a_{21}{}^2 x_0$$

$$H_{13} = H_{12} H_8 \quad ; \quad H_{14} = H_{12} H_9 - a_{21}{}^2 H_8$$

$$H_{15} = H_{12} H_{1o} \quad ; \quad H_{16} = H_{13} + H_{14}\, x_0 / H_2 - H_{15}\, y_0 / (H_5 - 1)$$

$$H_{17} = H_{14}\, H_1 / H_2 \;;\; H_{18} = H_{15} H_7 / (H_5 - 1)$$

6- A PARTICULAR CASE

In this paragraph we present a particular case with all the important features related with the cycle. We choose the particular set of parameters:

$\varepsilon_1 = 0{,}1$	$a_{12} = 0{,}4$	$a_{13} = -0{,}06$	$a_{14} = -0{,}3$
$\varepsilon_2 = 0{,}4$	$a_{21} = 0{,}3$	$a_{23} = 0{,}2$	$a_{24} = 0{,}4$
$\varepsilon_3 = -0{,}466$	$a_{31} = 0{,}6$	$a_{32} = -1{,}333$	$a_{33} = 0{,}08$
$\varepsilon_4 = -0{,}3$	$a_{41} = 0{,}337$	$a_{42} = -0{,}6$	$a_{43} = 0{,}12$
	$a_{34} = -0{,}2$	$a_{44} = 0$	

From the general equations we obtain the curve show in $Fig.1$ which with initial values:

$$x(0) = 0{,}48 \;\; ; \;\; y(0) = 0{,}064 \;\; ; \;\; z(0) = 0{,}044 \;\; ; \;\; u(0) = 0{,}027$$

takes the shape shown in $Fig.2$.

In order to get the cycle, we perform the proyection on three planes of the phase space. In this way $Figures\ 3, 4, 5$ are obtained.

Or the other hand, in order to obtain a sequence of the variables x, y, z and u it is convenient to study first the curve of the velocity $\frac{dx}{dt}$ as a function of x in the cycle. This can be done employing systems (23) together with the proyection of the cycle in the face (x, y). Thus we get the $Figure\ 6$. From here it is possible to derive the real function of the time as indicated in $Figure\ 7$.

The period can be obtained as:

$$P = 1{,}161$$

hare we have used the approximate formula (54) which have been evaluated by Simpson formula. The equilibrium values are:

$$x_e = 1{,}066 \qquad y_e = 0{,}099$$

and it was integrated in four parts: (Ψ_1, Ψ_2); (Ψ_2, Ψ_3); (Ψ_3, Ψ_4) and (Ψ_4, Ψ_1) where:

$$\Psi_1 = 0{,}011 \quad \Psi_2 = 0{,}403 \quad \Psi_3 = 0{,}977 \quad \Psi_4 = 2{,}27$$

which correspond to the vertex points of the cycle in the phase space.

Figure 2

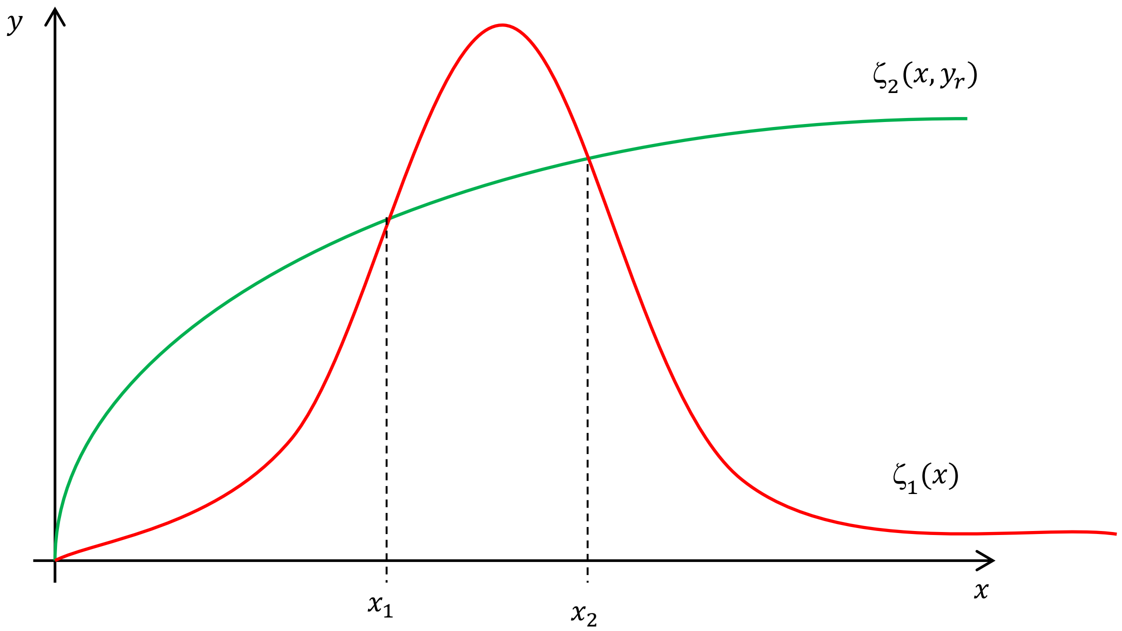


Figure 3

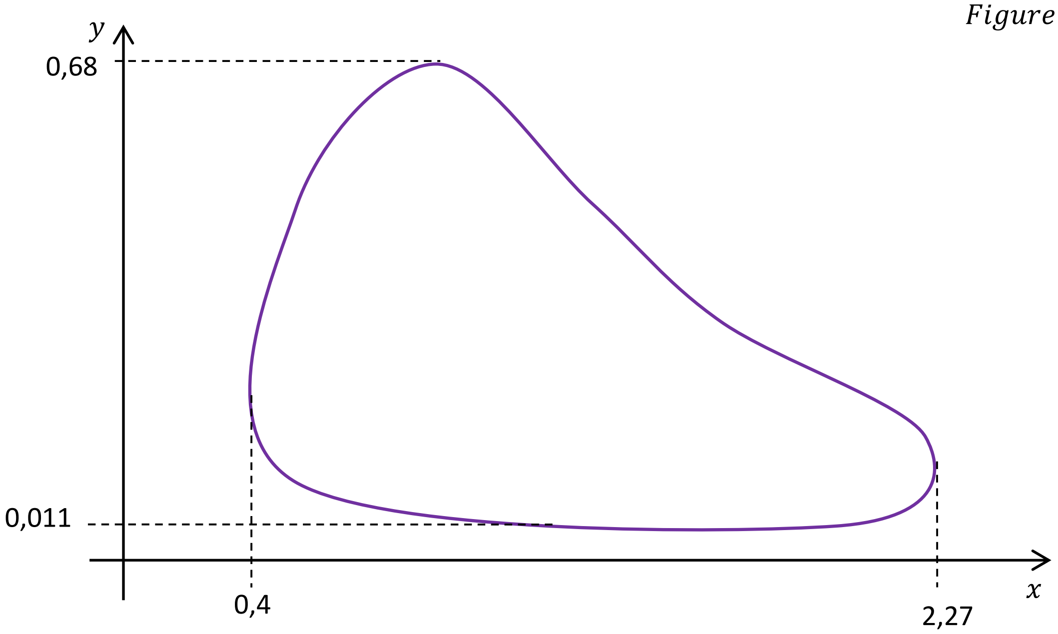
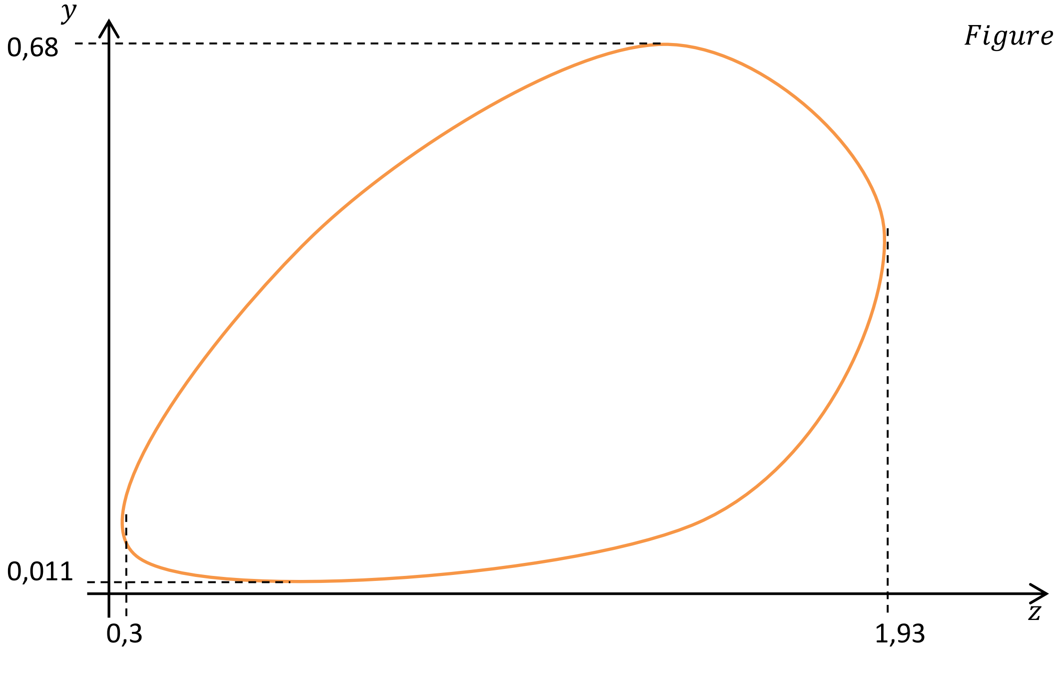


Figure 4



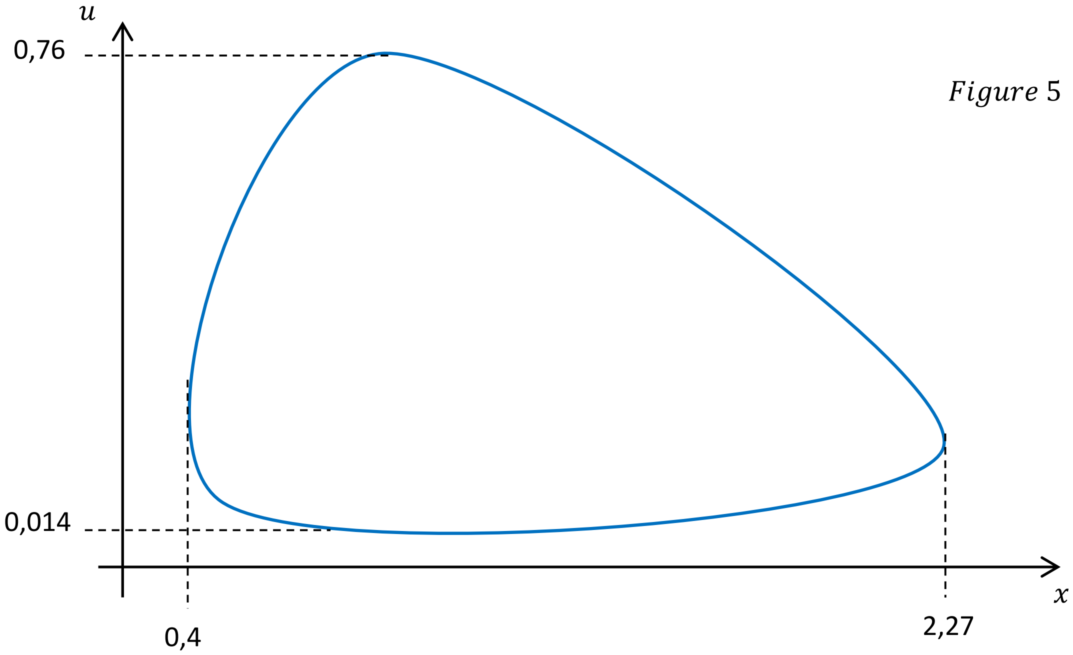


Figure 5

Figure 6

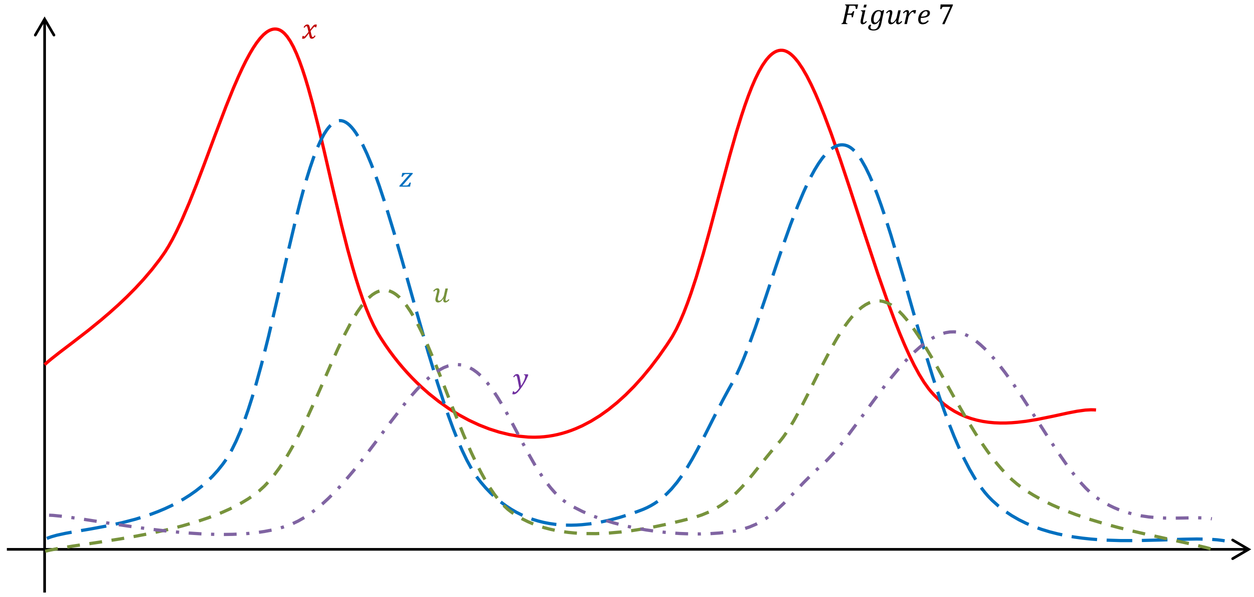


Figure 7

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