MORE GENERAL ECOLOGICAL COMPETITION AMONG THREE SPECIES

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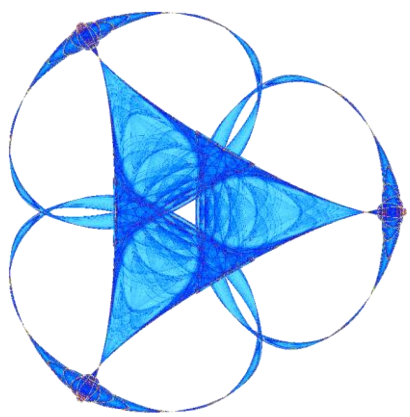

INSTITUTE FOR MATHEMATICS AND ITS APPLICATIONS
UNIVERSITY OF MINNESOTA
400 Lind Hall
207 Church Street S.E.
Minneapolis, Minnesota 55455-0436
Phone: 612-624-6066 Fax: 612-626-7370
URL: http://www.ima.umn.edu

MORE GENERAL ECOLOGICAL COMPETITION AMONG THREE SPECIES

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Ezio Marchi *

*Profesor Emérito Universidad Nacional de San Luis, Argentina.

Consejo Nacional de Investigaciones Científicas y Técnicas, Universidad Nacional de San Luis.

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INTRODUCTION

One of the most important subject in theoretical ecology is the description of competition among any number of species in an habitat

Many simple theories are available. Among them the volterra equations for n-species is a relevant subject, particulary in reference to the mathematical aspect.

The problem of two species has been already analyzed by the early studies of Volterra, (1). However for more species, even though in the case of three and four species, no much studies have been done, particulary from the point of view of the cyclic behavior.

The same Volterra examined different systems, however he did not find cycles in the general case.

In a previous study, (2), we examined a particular case for three and four species and we found the existence of cycles under suitable condition. Nevertheless the cycle layed in a special kind of surface, and two of the especies had the same phase.

In the present paper we introduce and study a more general case for three species competing in an habitat by means of the Volterra equations. The technique is as in the previous paper but with a different approach, the elimination of one of the variable through one integral of the system. This is performed using linear partial differential equations. The result is that the third variable under consideration is given as a function of the other primitive two.

It remains a systems of two ordinary differential equation much more complex than those studied by Volterra in his initial analysis. We integrate such equation following the procedure of Goel, Maitra and Montroll, (3). In thasway we obtain an integral without variable separation in the general case, and after some analysis we obtain the cycle.

Different cases are considered and the period is also evaluated in a new approximated form.

THE MODEL FOR THE THREE SPECIES SYSTEM

Consider the Volterra system of differential equations governing the interaction between three species:

$$\frac{dx}{dt} = x\,(\epsilon_1 - a_{1\,2}\,y - a_{1\,3}\,z) \quad (1)$$

$$\frac{dy}{dt} = Y\,(-\epsilon_2 + a_{2\,1}x - a_{2\,3}\mathrm{z})$$

$$\frac{dz}{dt} = z\,(-\epsilon_3 + a_{3\,1}x + a_{3\,2}y + a_{3\,3}\,\mathrm{z})$$

Where x is the number of individuals of the first species which is prey for the second and third species; y is the number of individual of the second sepecies which in turns is prey for the third species.

All the constants in the system (1), which phenomenological express the competing laws, are non-negative. The $\epsilon_1'\,s$ are the corresponding growth rates for each species. On the other hand the $a_{i\,j}'s$ represents interrelation among them.

Our first task is obtain an integral which may be related with the fact that a variable can be expressed in terms of the other two. Therefore we let:

$$z = f\,(x, y) \quad (2)$$

We need to determine such a function$f$. Derivation of equation (2) with respect to time, yields:

$$\frac{dz}{dt} = \frac{\partial f}{ax}\frac{dx}{dt} + \frac{af}{ay}\frac{dy}{dt}$$

(3)

Replacing on the left and right side the derivates with respect to time by the corresponding expressions given in systems (1), we obtain the following first order partial differential equation for the function$f$:

$$z\,(-\epsilon_3 + a_{3\,1}\,x + \ a_{3\,2}\,y - \ a_{3\,3}\,z) = \ \frac{\partial f}{\partial x}\,x\,(\epsilon_1 - \ a_{1\,2}y + \ a_{1\,3}\,z)$$

$$+\frac{\partial f}{\partial y}\,y(-e_2^{+}\,a_{2\,1}\,x -$$

$$a_{2\,3}\,z)$$

(4)

We try to solve such a equation by proposing the following system:

$$a_{3\,3}\,z \ = \ \frac{\partial f}{\partial x} a_{1\,3}\,x + \frac{\partial f}{\partial y} a_{2\,3}\,y \qquad (5)$$

And

$$z\,(\,-\epsilon_3 + \ a_{3\,1}\,\mathrm{x} + a_{3\,2}\,y) = \ \frac{\partial f}{\partial x}\,x\,(\epsilon_1 - \ a_{2\,3}\,y)$$

$$+\frac{\partial f}{\partial y}\,y\,(-\epsilon_2 \ + \ a_{2\,1}\,x) \qquad (6)$$

It is clear that if f is a solution of (5) and (6), then it is also a solution of (4). Thus we are going to solve the system (5) and (6).

By the Lagrange method, the solution of (5) is an arbitrary function:

$$f\,(k_1\ ,k_2) = 0$$

Where k_1 *and* k_2 are integral constants of the system?

$$\frac{dx}{a_{13}\,x} = \frac{dy}{a_{23}\,y} = \frac{dz}{a_{33}\,z} \qquad (7)$$

From the first two equalities, we have that:

Log $y^{1/a}\,23 = \log x^{1/a}\ 13 + k_1$

And from the last two, it turns out that

$$log \quad z^{\,1/a}33 = log \ \ y^{1/a}\,23 + k_2$$

Thus:

$$z = y\, a_{33} a_{23}\, F\, (\frac{y^{1\, a_{23}}}{x^{1 a_{13}}})$$

(8)

Where the function f is arbitrary and to be determined by equation (6)

Using the expression of z given by equation (8) in the partial differential equation (6) we have that:

$$f(\Omega)(-\epsilon_3 + a_{3\,1} x + a_{3\,2} y) = -\frac{1}{a_{13}} f'(\Omega)\Omega\ (\epsilon_1 - a_{12}\, y)$$

$$+ \frac{a_{33}}{a_{23}} f\, (\Omega)\big(- e_2 + a_{21} x\big) + \frac{1}{a_{23}} f'(\Omega)\Omega(-\epsilon_2 + a_{2\,1}\, x)(9)$$

Where introducing the new variable:

$$\Omega = \frac{y1/a_{23}}{x1/a_{13}}$$

The function f satisfies the following first order differential equation:

$$f\, (\Omega)\, (-\epsilon_3 + \epsilon_2\, a_{33} / a_{23}) + a_{31} - a_{21}\, a_{33} / a_{23})\, x + a_{32} y =$$
$$f'\, (\Omega)\, \Omega\, \{\, (-\epsilon_2 / a_{23} - \epsilon_1 / a_{13}) + a_{21} / a_{23}\, x + a_{12} / a_{13}\, y\}$$

Calling:

$$\delta_1 = -\epsilon_3 + \epsilon_2 a_{33} / a_{23}\ , \qquad \rho_1 = -\epsilon_2 / a_{23} - \epsilon_1 / a_{13}\ ,$$
$$\rho_3 = a_{12} / a_{13}$$

$$\delta_2 = a_{31} - a_{21} a_{33} / a_{23}\ , \qquad \rho_2 = a_{21} / a_{23}$$

The previous equation becomes

$$\frac{f'(\Omega)}{f\, (\Omega)} = 1/\Omega \left\{\frac{\delta_1 + \delta_2 x + a_{32} y}{\rho_1 + \rho_2\, x + \rho_3 y}\right\}$$

$$= 1/\Omega\{\frac{(\delta_1 + a_{32}y)\ \Omega^{a_{13}} + \rho_2 y^{a_{13}/\ a_{23}}}{(\rho_1 + \rho_3 y)\ \Omega^{a_{13}} + \rho_2 y^{\alpha_{13}/\ a_{23}}}\}$$

(10)

Imposing the constraints:

$$\delta_2 = \rho_2\ , \qquad \delta_1 = \rho_1\ \ and\ \ a_{32} = \rho_3$$

(11)

Then the previous equation becomes:

$$\frac{f'(\Omega)}{f\ (\Omega)} = \frac{1}{\Omega}$$

(12)

Whose integral is:

$$f\ (\Omega) = c\Omega$$

Where C is an arbitrary constant

Replacing Ω , we obtain:

$$C_o = \frac{y^{(a_{33}+1)/a_{23}}}{x^{1/a_{13}}}$$

(13)

Where now:

$$C_o = \frac{z_o x_o^{1/a_{13}}}{y_o^{(a_{33}+1)/a_{23}}}$$

For a problem starting from a point (x_o , y_o , z_o)

On the other hand, the relation (11) yields

$a_{31} = a_{21} / a_{23}$ (1+a_{33}) ,$-\epsilon_3$ + $\epsilon_2 a_{33}/ a_{23} = -\epsilon_2/ a_{23} - \epsilon_1/ a_{13}$

And

$$a_{32} = a_{12}/ a_{13}$$

(14)

Thus, replacing the value of z give by (13) in the first two equations of (1), it remains to solve the systems:

$$\frac{dx}{dt} = x(e_1 - a_{12}y - D \frac{y^a}{x^\beta})$$

$$\frac{dy}{dt} = y(-\epsilon_2 + a_{21}x - E \frac{y^a}{x^\beta})$$

(15)

Where:

D = $a_{13}C_o$, $E = a_{23}C_o$

$$\alpha = (a_{33} + 1)/a_{23} , \beta = 1/a_{13}$$

We are going to integrate (15) by using the relevant and important method of Goel, Maitra and Montroll developed in reference (3). Writing the equations (15) as:

$$\frac{dx}{dt} = \epsilon_1 x + a/\,\beta_1\, xy - D\,\frac{y^a}{x^{\beta-1}}$$

$$\frac{dy}{dt} = -\epsilon_2 y + a\,/\beta_2\, xy - E\,\frac{y^{a+1}}{x^{\beta}}$$

(16)

Where:

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

and calling:

$$q_1 = \epsilon_2/a_{21} and \;\; q_2 = \epsilon_1\,/a_{12}$$

On the other hand we define:

$$v_1 = \log\frac{x}{q_1} \;\; and\; v_2 = \log\frac{y}{q_2}$$

Which, replaced into the first of equations (16) yields:

$q_1 \exp(v_{1)}\, \frac{dv}{dt} = \epsilon_1 q_1 \exp(v_1) + a/\beta_1 q_1 \exp(v_1)\; q_2\; \exp(v_2)$

-D $q_2^{\alpha}/q_1^{\beta-1} \exp(\alpha v_2 - (\beta_1 - 1)\, v_1)$

$Eliminating\ the\ factors\ q_1\ \ /\beta_1\, exp(v_1),\ we\ obta$in:

$$\frac{dv}{dt} 1 = a q_2(\exp(v_2) - 1 - \frac{\beta_1\ D q_2^{a-1}}{a q_1^{\beta}} \exp(\alpha v_2 - \ \beta v_1\,)\,)$$

(17)

Performing a similar operation in the second of equations (16), we obtain

$$\beta_2 \frac{dv_1}{dt} = aq_1 \left(\exp(v_1) - 1 - \frac{\beta_2 E q_2^a}{a\ q^{b+1}} \exp(\alpha v_2 - \beta v_1)\right)$$
(18)

$$H = \frac{-\beta_1 D a_2^{a-1}}{a q_1^{\beta}} \qquad J = \frac{-\beta_2 E q_2^{\alpha}}{a q_1^{\beta+1}}$$

The equations (17) and (18) become:

$$\beta_1 \frac{dv_1}{dt} = aq_2(\exp(v_2) - 1 + H \exp(av_2 - \beta v_1))$$

$$\beta_2 \frac{dv_2}{dt} = aq_1(\exp(v_1) - 1 + J \exp(\alpha v_2 - \beta v_1)) \qquad (19)$$

Now multiplying the left hand side of the first equation of (19) by the right hand side of the second equation and viceversa, we get:

$$\beta_1 \frac{dv_1}{dt} \{q_1(\exp(v_1) - 1 + J \exp(\alpha v_2 - \beta v_1))\} =$$

$$\beta_2 \frac{dv_2}{dt} \{q_2(\exp(v_2) - 1 + H \exp(\alpha v_2 - \beta v_1))\}$$

But:

$$\frac{d}{dt}(\exp(\alpha v_2 - \beta v_1) = \alpha \exp(\alpha v_2 - \beta v_1) \frac{dv_2}{dt} - \beta \exp(\alpha v_2 - \beta v_1) \frac{dv_1}{dt}$$

Then:

$$\frac{d}{dt} \{\beta_1 q_1(\exp(v_1) - v_1)\} + \beta_1 q_1 J \exp(\alpha v_2 - \beta v_1) \frac{dv_1}{dt} =$$

$$\frac{d}{dt}\{\beta_2 q_2(\exp(v_2) - v_2) + \frac{H}{\alpha}\exp(\alpha v_2 - \beta v_1))\} + \beta\beta_2 q_2 \frac{H}{\alpha}\exp(\alpha v_2 - \beta v_1) \frac{dv_1}{dt} \text{(20)(20)}$$

We now call $\Psi_1$to the left hand side and Ψ_2 to the right hand side of equality (25). The function Ψ_1 has been already obtained by Volterra in his original writing and is shown in Figure 1 of reference (2). For the sake of completeness, it is also shown in figure 1a. Analogously, $\Psi_2$depens on the variable x, which is more general than in the original Volterra's treatment. The function Ψ_2 depending parametrically on x, and is shown in part b of Figure 1.

From the geometrical representation of functions Ψ_1 and $\Psi_2$ub figure 1, it is clear that a suitable interval limited by the points $x_0$and x_1 , there are exactly two values of y such that:

$$\Psi_1 (x) = \Psi_2 (x, y) \tag{26}$$

The end points x_0, x_1 , are to be determined and have the particulary property that there is only one value of y for which the equality (26) holds true. Thus, the existence of the cycle is guarantee.

Now we wish to prove the previous assertion about the existence of both points x_0 , x_1. In order to do so, let us compute the point y_0 where the function Ψ_2 reaches a minimum for a given value of x. This point is obtained from the condition:

$$\frac{\partial \Psi_2}{\partial y} = 0$$

Which yields

$$-\frac{1}{c_2 y_0} + c_2 + M\alpha \; \frac{y_0^{a-1}}{x^\beta} = 0$$

or equivalently

$$y_0^\alpha + \frac{c_2 \; x^\beta}{M\alpha} y_0 = \frac{x^\beta}{c_2 \, M \, \alpha}$$

We now wish to show that there is only a primitive value of y satisfying (27). Thus, there exist only one minimum value of $\Psi_2 \; (x,.)$. Consider as in the figure 2, the value $x^\beta c_2 \; M\alpha$, in the ordinate, them the first two terms in thr the real and positive values of y.

The function $y_0 \; (x)$ is a strictly monotonically increasing function of x, and it is shown in figure 3.

On the other hand, at the minimum we have from equation (27)

$$M \frac{y_0^\alpha}{x^\beta} = -\frac{c_2}{\alpha} y_0 + 1/ \; c_2 \; a$$

and the function Ψ_2 takes the value:

-1/

ϵ_2

$$\Psi_3(y_0) = \Psi_2(x, y_0) = P \; \frac{c_2 y_0}{\exp(c_2 y_0 + 1/c_2 \alpha - c_2/\alpha \; y_0)}$$

The variation of Ψ_3 as a function of y_0 is given in figure 4. Thus the composition: $\Psi_2 \; (x, y_0(x))$, as a function of x takes the form shown in the figures 5.

Now comparing the functions $\Psi_2 \; (x, y_0$ (x)) in figure 5 and in figure 1a, we have that under appropriate conditions of

4. Period Computation

Continuig with the particular case of the previous paragraph, in this section we wish to study an approximation for obtaining of the period of the cycle shown by this model of the competition between three species.

From the relation (25), with $\alpha = 1$ and $\beta = 1/2$, and taking natural logarithm we have:

$$1/\,\epsilon_1 \log(c_1\, x) - 1/\,\epsilon_1 c_1\, x = \log(P) - 1/\epsilon_2 \log(c_2 y) + 1\,/\epsilon_2 \left(c_2 + \frac{c_3}{x^{1/2}}\right) y \qquad (29)$$

Where the constants are:

$$c_1 = a_{21}\epsilon_2\,, c_2 = a_{12}\,/\epsilon_1\,,\ c_3 = H\,\epsilon_2 a_{12}\,/(\epsilon_1 a_{21})$$

Now taking the linear approximation:

Log y = a + by (30)

Where the parameters a and b are adjusted for each of the four parts shown in figure 7, where the cycle in the plane (x,y) is graphically shown, (this is the proyeccion of the actual cycle solution in the phase space (x,y,z).

Using the approximation, equation (30), in equation (29), one obtain for the variable y:

$$y = \frac{A + 1\,\epsilon_1\, logx - \ c_1\epsilon_1 x - B}{C + \ c_3/\,\epsilon_2 x^{1/2}} \qquad (31)$$

Where the constants are:

$$A = 1\,/\epsilon_1 \log c_1$$

$$B \log P - a/\,\epsilon_2 - 1\,/\epsilon_2 \log c_2$$

$$C = -b/\epsilon_2 + c_2/\epsilon_2$$

With the approximated value of y in the respective regions we replace it in the first basic differential equation of system (15) obtaining:

$$dt = \frac{dt}{\epsilon_1 x - (a_{12}x + Dx^{1/2})\frac{(1/\epsilon_1 \log(x) - c_1/\epsilon_1 x + A - B)}{(c_3/\epsilon_2 x^{1/2} + C)}}$$

(32)

In order to integrate (32), we again approximate the logarithm:

Log x= g + fx

Where the parameters are adjusted accordingly. Thus, one obtains:

$$dt = \frac{\left(M/x^{1/2} + C\right) dx}{\epsilon_1 x\,(M/x^{1/2} + C) - (a_{12}x - Dx^{1/2})(N + Qx)}$$

(33)

With:

$$M = c_3/\epsilon_2, Q = f/\epsilon_1 - c_1/\epsilon_2 \text{ and } N = g/\epsilon_1 + A - B$$

Now, calling:

$$H_1 = \epsilon_1 M - DN \quad , \quad H_2 = \epsilon_1 C - a_{12}N$$

$$H_3 = -DQ \qquad \text{and} \quad H_4 = -a_{12}Q$$

The previous equation (33), becomes:

$$dt = \frac{\left(M\,x^{1/2} + C\right)dx}{H_1 x^{1/2} + H_2 x + H_3\, x^{3/2} + H_4 x^2}$$

(34)

Whith the change of variable:

$$u = x^{1/2}$$

We derive the following integral, which is cosier to be evaluated:

$$dt = \frac{2\,M\,du}{u(H_1 + H_2 u + H_3 u^2 + H_4 u^3)} + \frac{2\,C\,du}{(H_1 + H_2 u + H_3 u^2 + H_4 u^3)}$$

(35)

4- An Example

Here we consider an example of the entire interaction system trated from different points of view in the previous sections. In the present example, we require the following values of the parameters of interaction equations (1):

$$\epsilon_1 = 3 \qquad a_{12} = 2 \qquad a_{13} = 2 \qquad x(0) = 2$$

$$\epsilon_2 = .5 \qquad a_{21} = 1 \qquad a_{23} = 1 \qquad y(0) = 1.5$$

$$\epsilon_3 = 2 \qquad a_{31} = 1 \qquad a_{32} = 1 \qquad z(0) = 1$$

(36)

And we recall that $a_{33} = 0$

This set of parameters satisfy the conditions imposed on them by the theory, namely equations (11), (14) and (21). We note that for these values of the parameters we have:

$$\alpha = 1/2 \quad and \quad \beta = 1$$

In order to obtain a graphic description of the variables x(t), y(t) and z(t), we use a general method namely, we consider them as analytic functions in the variable t:

$$x(t) = \ddot{\sum} x_k\, t^k$$

$$k = 0$$

$$y(t) = \ddot{\sum} y_k\, t^k$$

$$k = 0$$

$$z(t) = \ddot{\sum} z_k t^k$$

$$k = 0$$

Replacing these expressions in the system (1), we obtain after identifying coefficient that the recurrence relations are given by:

$$x_{k+1} = \frac{1}{k+1}\left(\epsilon_1 x_k - a_{12} \sum_{\ell=0}^{k} x_\ell y_{k-\ell}\right)$$

$$y_{k+1} = \frac{1}{k+1}\left(-\epsilon_2 y_k + a_{21} \sum_{\ell=0}^{k} y_\ell z_{k-\ell}\right)$$

$$z_{k+1} = \frac{1}{k+1}\left(a_{31}/a_{13}\epsilon_1 x_k - a_{32}/\, a_{23}\epsilon_2 y_k - \epsilon_3 z_k\right) +$$

$$\frac{1}{k+1}\left((a_{32}a_{21}/a_{23} - a_{31}a_{12}/a_{13}) \sum_{\ell=0}^{k} x_\ell y_{k-\ell} - a_{33} \sum_{\ell=0}^{k} z_\ell z_{k-\ell}\right) -$$

$$a_{31/}a_{13}x_{k+1} - a_{32}\,/a_{23}y_{k+1}$$

If one is interested, it is possible to solve analytically and exactly such recursive relations, but applied as in reference (5) for non-linear system.

However, we are not interested at this point in these analytic aspect of the numerical analysis. We are only interested in obtaining the graphic solution of the problem.

Using (37) with the parameters already established using standard computacional methods, the graphic of the function is obtained and drawn in figure 8.

From here, using the corresponding values of the variables the cycle is obtained and shown in figure 5.

The computation of the approximated period is done explained in the previous paragraph, resulting in the set of parameters:

$$c_1 = 2 \quad c_2 = .667 c_3 = .628$$

$$A = .231 \qquad P = .015 H = 1.332$$

$$M = 1.258 \qquad D = 1.884$$

For the interval A, shown in figure 5, the interval of variation of x is:

$$(1.606, \qquad .378)$$

While y varies in the interval:

$$(1.535\,, \qquad .615)$$

Therefore the adjusting parameters we have chosen were:

$$g = -1.23 f = 1.14$$

$$a = -1.008 b = .615$$

From here it results:

$$H_1 = 1.52, \qquad H_2 = -4.202, \quad H_3 = .541, \qquad H_4 = .574$$

The roots of the denominator o (35) are

$$u_0 = .389, \qquad u_1 = 2.025 \;\; and \;\; u_2 = -3.357$$

The limit of integration is:

$$u' = 1.267 \;\; and \; u'' = .615$$

Integrating by rational functions the expression (35), one obtains for the time of the first region:

$$T_A = \quad .682$$

In a similar form one proceeds in the parts B, C and D one my obtain:

$$T_B \;\; = \;\; .403$$

$$T_{C\,=}\;.794$$

$$T_D \;\; = \;\; 2.693$$

Resulting the period

T = 2.693

The real period is T = 2.748

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