

STABILITY AND BIFURCATION IN A GENERAL PREDATOR-PREY MODEL

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Abstract A mathematical model from biology describing the evolution of two species being in a predator-prey relationship is analyzed. The model is a Cauchy problem for a system consisting of two first order ordinary differential equations with quadratic nonlinearities and containing six real parameters. Two parameters are the growth rates of the involved species, other two are the carrying capacities of the species and the last two parameters represent the action of one species on the other. The phase functions are assumed to be positive and the only last two parameters are allowed to vary. Numerically it is found that the only candidates for the Lyapunov asymptotically stable or unstable sets governing the phase portrait are the equilibrium points, so that their type was investigated by means of the spectrum of the matrix defining the linearized equations around the equilibrium. In the case of nonhyperbolic equilibria the Lyapunov-Perron theorem upon the first approximation is no longer valid. This is why in this paper the normal form method is applied to get a nonhyperbolic Lyapunov asymptotically unstable nondegenerate saddle-node mainly responsible for the phase plane. The corresponding global dynamic bifurcation diagram is carried out numerically.

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1. INTRODUCTION

There are many instances in nature where one species of animal feeds on another species of animal, which in turn feeds on other things. The first

species is called the predator and the second is called the prey. In a predator-prey situation the growth rate of one population is decreased and the other increased. There are more s.o.d.e.s which represent the predator-prey model. We study here only one of them [3], i.e.

$$\begin{cases} \dot{x} = r_1x(1 - x/K_1 - p_{12}y/K_1), \\ \dot{y} = r_2y(1 - y/K_2 + p_{21}x/K_2), \end{cases} \quad (1)$$

where x, y represent the two species (x is the prey and y is the predator), $r_1 < 0$, $r_2 > 0$ - the growth rates of these species, K_1, K_2 -the carrying capacity of every species, $p_{12} > 0$ - the effect of species y on the growth of species x and $p_{21} > 0$ - the the effect of species x on the growth of species y . In this study we consider r_1, r_2, K_1 and K_2 as fixed, hence in (1) only two parameters, p_{12} and p_{21} , occur.

Due to physical reasons, the phase space must be the first quadrant (without axes of coordinates). However, for theoretical reasons we consider these half-axes too.

2. THE EQUILIBRIUM POINTS

The system (1) has the following equilibria: $O(0, 0)$, $E_1(K_1, 0)$, $E_2(0, K_2)$, $E_3\left(\frac{K_1 - K_2p_{12}}{1 + p_{12}p_{21}}, \frac{K_2 + K_1p_{21}}{1 + p_{12}p_{21}}\right)$. From biological viewpoint, this last equilibrium point must be in the first quadrant, i.e. $\frac{K_1 - K_2p_{12}}{1 + p_{12}p_{21}} > 0$ and $\frac{K_2 + K_1p_{21}}{1 + p_{12}p_{21}} > 0$. It follows that $K_1 - K_2p_{12} > 0$, i.e. $p_{12} < K_1/K_2$.

By the Lyapunov-Perron linearization principle, the Lyapunov asymptotic stability of a hyperbolic equilibrium point, say (x^*, y^*) , depends on the eigenvalues of the matrix of the system linearized around the point [2]. More exactly, the attractivity of (x^*, y^*) corresponds to the eigenvalues of the matrix

$$\begin{pmatrix} r_1(1 - 2x/K_1 - p_{12}y/K_1) & -r_1p_{12}x/K_1 \\ r_2p_{21}y/K_2 & r_2(1 - 2y/K_2 + p_{21}x/K_2) \end{pmatrix} \Big|_{(x^*, y^*)}. \quad (2)$$

In the following we analyze the nature of the equilibrium points and their attractivity for all possible values of the parameters p_{12} and p_{21} . Since in our case the Lyapunov stability (instability) implies attractivity (repulsivity) and,

conversely, for the sake of simplicity in the sequel we refer only to attractivity and repulsivity.

$\mathbf{p}_{12} < \mathbf{K}_1/\mathbf{K}_2$. In this case there exist four equilibria; the equilibrium O is a repulsive node, because the eigenvalues of the matrix (2) are $\lambda_1 = r_1 > 0$, $\lambda_2 = r_2 > 0$. For the equilibrium point E_1 the eigenvalues of the matrix (2) are $\lambda_1 = -r_1 < 0$, $\lambda_2 = r_2(1 + p_{21}K_1/K_2) > 0$, therefore E_1 is a saddle. Similarly, for the equilibrium point E_2 the eigenvalues of the matrix (2) are $\lambda_1 = -r_2 < 0$, $\lambda_2 = r_1(1 - p_{12}K_2/K_1) > 0$, hence E_2 is a saddle, too.

For the fourth equilibrium point, E_3 , the eigenvalues of the matrix (2) are the roots of the characteristic equation $\lambda^2 - \text{tr } \mathbf{A} \lambda + \det \mathbf{A} = 0$, where

$$\mathbf{A} = \frac{1}{1 + p_{12}p_{21}} \begin{pmatrix} r_1(p_{12}K_2 - K_1)/K_1 & r_1p_{12}(p_{12}K_2 - K_1)/K_1 \\ r_2p_{21}(p_{21}K_1 + K_2)/K_2 & -r_2(p_{21}K_1 + K_2)/K_2 \end{pmatrix}. \quad (3)$$

We have

$$\det \mathbf{A} = -\frac{r_1r_2}{K_1K_2} \cdot \frac{(p_{12}K_2 - K_1)(p_{21}K_1 + K_2)}{1 + p_{12}p_{21}} > 0, \quad (4)$$

therefore λ_1 și λ_2 have the same sign (if they are real), so, we have to study the sign of $\text{tr } \mathbf{A}$, too. We have

$$\text{tr } \mathbf{A} = \frac{1}{1 + p_{12}p_{21}} \left[\frac{r_1(p_{12}K_2 - K_1)}{K_1} - \frac{r_2(p_{21}K_1 + K_2)}{K_2} \right].$$

The curve H of the Hopf bifurcation values is the straight line defined by $\text{tr } \mathbf{A} = 0$, i.e. by the equation $p_{21} = K_2/(r_2K_1)(r_1K_2p_{12}/K_1 - r_1 - r_2)$, which for $p_{12} < K_1/K_2$ have $p_{21} < 0$, therefore this is not in the first quadrant. It follows that for positive parameters p_{12} , p_{21} there are no Hopf singularities. For $p_{12} < K_1/K_2$ we have $\text{tr } \mathbf{A} < 0$. Since $\det \mathbf{A} > 0$, it follows that E_3 is an attractive node.

$\mathbf{p}_{12} = \mathbf{p}_{21} = \mathbf{0}$. The equilibria are: $O(0, 0)$, $E_1(K_1, 0)$, $E_2(0, K_2)$, $E_3(K_1, K_2)$.

$\mathbf{p}_{12} = \mathbf{0}$, $\mathbf{p}_{21} \neq \mathbf{0}$. The equilibria are: $O(0, 0)$, $E_1(K_1, 0)$, $E_2(0, K_2)$ and $E_3(K_1, K_1p_{21} + K_2)$.

$\mathbf{p}_{12} \neq \mathbf{0}$, $\mathbf{p}_{21} = \mathbf{0}$. The equilibria are: $O(0, 0)$, $E_1(K_1, 0)$, $E_2(0, K_2)$ and $E_3(K_1 - p_{12}K_2, K_2)$. In all these situations the equilibria have the same type as in the case $p_{12} < K_1/K_2$.

$\mathbf{p}_{12} > \mathbf{K}_1/\mathbf{K}_2$. In this case, from the biological viewpoint, there exist only three equilibria, the fourth equilibrium point being in the second quadrant.

The equilibrium O is an repulsive node (the eigenvalues of the matrix (2) being $\lambda_1 = r_1 > 0$, $\lambda_2 = r_2 > 0$). The equilibrium point E_1 is a saddle (the eigenvalues of the matrix (2) are $\lambda_1 = -r_1 > 0$, $\lambda_2 = r_2(1 + p_{21}K_1/K_2) > 0$); E_2 is an attractive node (the eigenvalues of the matrix (2) being $\lambda_1 = -r_2 < 0$, $\lambda_2 = r_1(1 - p_{12}K_2/K_1) > 0$). The fourth equilibrium point (which has only a mathematical existence) is a saddle.

$p_{12} = \mathbf{K}_1/\mathbf{K}_2$. In this case (1) assumes the form

$$\begin{cases} \dot{x} &= r_1x(1 - x/K_1 - y/K_2), \\ \dot{y} &= r_2y(1 - y/K_2 - p_{21}x/K_2). \end{cases} \quad (5)$$

The equilibria of the (5) are: $O(0,0)$ (repulsive node), $E_1(K_1,0)$ (saddle) and $E_2(0,K_2)$ (saddle-node, it is a double point appeared when E_3 and E_2 coalesce).

In the following we study the nature of the saddle-node using the normal form method [1].

Proposition 2.1. *The normal form of (5) at the point $E_2(0, K_2)$ is*

$$\begin{cases} \dot{n}_1 &= r_1(p_{21}/K_2 + 1/K_1)n_1^2 + O(\mathbf{n}^3), \\ \dot{n}_2 &= -r_2n_2 + [p_{21}(r_1 - r_2)/K_2]n_1n_2 + O(\mathbf{n}^3), \end{cases} \quad (6)$$

therefore, E_2 is a nondegenerated saddle-node equilibrium.

Proof. First, we translate the point E_2 at the origin by means of the change $u_1 = x$, $u_2 = y - K_2$. Let $\mathbf{u} = (u_1, u_2)^T$. Then, in \mathbf{u} , (5) reads

$$\begin{cases} \dot{u}_1 &= -(r_1/K_1)u_1^2 - (r_1/K_2)u_1u_2, \\ \dot{u}_2 &= r_2p_{21}u_1 - r_2u_2 + (r_2p_{21}/K_2)u_1u_2 - (r_2/K_2)u_2^2. \end{cases} \quad (7)$$

The eigenvalues of the matrix defining the linear terms in (7) are $\lambda_1 = 0$, $\lambda_2 = -r_2$ and the corresponding eigenvectors read $\mathbf{u}_{\lambda_1} = (1, p_{21})^T$ and $\mathbf{u}_{\lambda_2} = (0, 1)^T$. Thus, with the change of coordinates $\begin{pmatrix} u_1 \\ u_2 \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ p_{21} & 1 \end{pmatrix} \begin{pmatrix} v_1 \\ v_2 \end{pmatrix}$, (7) achieves the form

$$\begin{cases} \dot{v}_1 &= -Bv_1^2 - (r_1/K_2)v_1v_2, \\ \dot{v}_2 &= -r_2v_2 + p_{21}Bv_1^2 - Cv_1v_2 - (r_2/K_2)v_2^2, \end{cases} \quad (8)$$

where $B = r_1(p_{21}/K_2 + 1/K_1)$ and $C = p_{21}(r_2 - r_1)/K_2$, such that the matrix defining the linear part is diagonal. In order to reduce the second order non-resonant terms in (8) we determine the transformation $\mathbf{v} = \mathbf{n} + \mathbf{h}(\mathbf{n})$, where $\mathbf{v} = (v_1, v_2)^T$ and $\mathbf{n} = (n_1, n_2)^T$, suggested by the Table 1, found by applying the normal form method.

m_1	m_2	$X_{\mathbf{m},1}$	$X_{\mathbf{m},2}$	$\Lambda_{\mathbf{m},1}$	$\Lambda_{\mathbf{m},2}$	$h_{\mathbf{m},1}$	$h_{\mathbf{m},2}$
2	0	$-B$	$p_{21}B$	0	r_2	-	$p_{21}B/r_2$
1	1	$-r_1/K_2$	$-C$	$-r_2$	0	$r_1/(r_2K_2)$	-
0	2	0	$-r_2/K_2$	$-2r_2$	$-r_2$	0	$1/K_2$

Table 1.

Here $\Lambda_{\mathbf{m},1}, \Lambda_{\mathbf{m},2}$ are the eigenvalues of the associated Lie operator, while $X_{\mathbf{m}}$ is the second order homogenous vector polynomial in (8).

We find the transformation

$$\begin{cases} v_1 = n_1 + [r_1/(r_2K_2)]n_1n_2, \\ v_2 = n_2 + (Bp_{21}/r_2)n_1^2 + (1/K_2)n_2^2, \end{cases}$$

carrying (8) into (6). We have $r_1(p_{21}/K_2 + 1/K_1) \neq 0$. By [1], the equilibrium point E_2 corresponding the dynamical system generated by a s.o.d.e. of the form (6) is a nondegenerated saddle-node. ■

3. THE DYNAMIC BIFURCATION DIAGRAM

From Section 2 it follows that the strata of the parameter space are determined by the curves $S = \{(p_{12}, p_{21}) | p_{12} = K_1/K_2\}$ and $H_{\mathbb{R}} = \{(p_{12}, p_{21}) | p_{21} = K_2/(r_2K_1)(r_1K_2p_{12}/K_1 - r_1 - r_2)\}$.

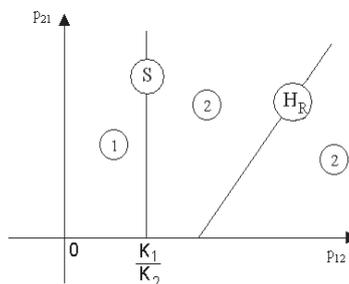


Fig. 1. The parametric portrait.

In fig. 1 the parametric portrait is represented. The regions 1 and 2 contain the axes, too.

In fig. 2 the phase portraits corresponding to the strata from the parametric portrait are presented. The coordinate axes represent the two species: x the abscissa, and y the ordinate. The portraits from the zone 2 and the zone $H_{\mathbb{R}}$ are topological equivalent (in the zone 2 the point E_3 is a saddle, while on the curve $H_{\mathbb{R}}$ it is a neutral saddle).

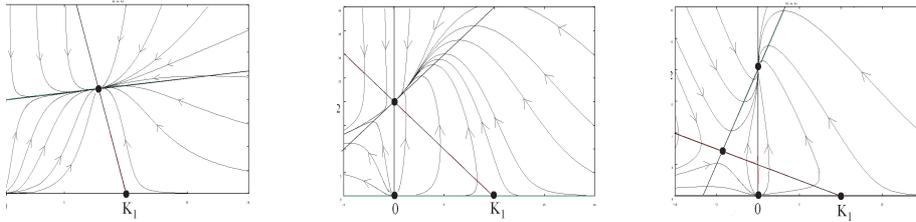


Fig. 2. The phase portraits for the strata from fig. 1.

Examining the phase portrait we conclude that for some values of the parameters p_{12} and p_{21} the two species go to a coexistence situation (zone 1). However, for other values of the same parameter, in time, the prey population x will be exterminated by the predator population y (zones S , 2 and $H_{\mathbb{R}}$).

References

- [1] Arrowsmith, D. K., Place, C. M., *Ordinary differential equations*, Chapman and Hall, London, 1982.
- [2] Georgescu, A., Moroianu, M., Oprea, I. *Bifurcation theory. Principles and applications*, Ed. Univ. Pitesti, Pitesti, 1999. (Romanian)
- [3] Giurgițeanu, N., *Computational economical and biological dynamics*, Europa, Craiova, 1997. (Romanian)
- [4] Murray, J. D., *Mathematical biology, 2nd corr. ed.*, Springer, Berlin, 1993 (first ed. 1989).