Proceedings of the *International Conference on Theory and Application of Mathematics and Informatics ICTAMI 2005* - Alba Iulia, Romania

BIFURCATION IN A MODEL OF THE POPULATION DYNAMICS

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Abstract. The static bifurcation diagram (sbd) and the global dynamic bifurcation diagram (dbd) around some nonhyperbolic equilibria are provided for the Odell model which depends on one parameter. The biological interpretation is then presented.

2000 *Mathematics Subject Classification*: 37N25, 34C23.

1. The mathematical model

Predator-prey models govern many phenomena in population dynamics, immunology, medicine etc. We assume that there are only two competing species: one species (predator) feeds on another species (prey), which in turn feeds on other things. We deal with a particular case of the model consisting of a Cauchy problem $x(0) = x_0,\ y(0) = y_0$, for the following system of ordinary differential equations (sode), which was studied by Odell in 1980 [6]

$$\begin{cases} \dot{x} &= x[x(1-x) - y], \\ \dot{y} &= y(x-a), \end{cases} \tag{1}$$

where x and y represent the population numbers of the prey and the predator, respectively, and a is a nonnegative parameter. The presence of this parameter is the source of a rich dynamics generated by (1) and of its qualitative changes as a crosses some values on the real axis.

In this paper we study only the biologically realistic case $a > 0$ and we treat the bifurcation from a new perspective [3].

Also by biological reasons, the phase space must be the first quadrant (without axes of coordinates). However, for mathematical (namely bifurcation) reasons we consider, in addition, the origin, the half-axes and the other quadrants.

2. The static bifurcation diagram

If $a \notin \{0,1\}$ there exist three equilibrium points: $O(0,0)$, $E_1(1,0)$, $E_2(a, a(1-a))$. If $a = 1$ the point E_1 collides with E_2 and, in this way, there are only two equilibrium points, O and E_1.

We recall that the attractivity properties of an equilibrium point (x^*, y^*) is determined by the real part of the eigenvalues of the matrix $\mathbf{A}$ defining the linearized sode about this point. In our case

$$\mathbf{A} = \begin{pmatrix} 2x - 3x^2 - y & -x \\ y & x - a \end{pmatrix}. \tag{2}$$

Therefore, O is a saddle-node (the eigenvalues of $\mathbf{A}$ are $\lambda_1 = 0$, $\lambda_2 = -a$) and E_1 is a saddle for $a < 1$, a saddle-node for $a = 1$ and an attractive node for $a > 1$ (the eigenvalues of $\mathbf{A}$ are $\lambda_1 = -1$, $\lambda_2 = 1 - a$). For the third equilibrium point, E_2, the eigenvalues of the matrix $\mathbf{A}$ are the roots of the characteristic equation

$$\lambda^2 - \text{tr } \mathbf{A}\ \lambda + \det \mathbf{A} = 0, \tag{3}$$

with tr $\mathbf{A} = a(1-2a)$, $\det \mathbf{A} = a^2(1-a)$ and $\Delta = a^2(4a-3)$. Therefore, the point E_2 is a repulsive focus for $a \in (0, 1/2)$, a Hopf singularity for $a = 1/2$, an attractive focus for $a \in (1/2, 3/4)$, a sink for $a = 3/4$, an attractive node for $a \in (3/4, 1)$, a saddle-node for $a = 1$ and a saddle for $a > 1$. In this last case, the point E_2 is in the fourth quadrant.

As a consequence, as we said in the above, we can construct the sbd, represented in fig. 1 from two perspectives.

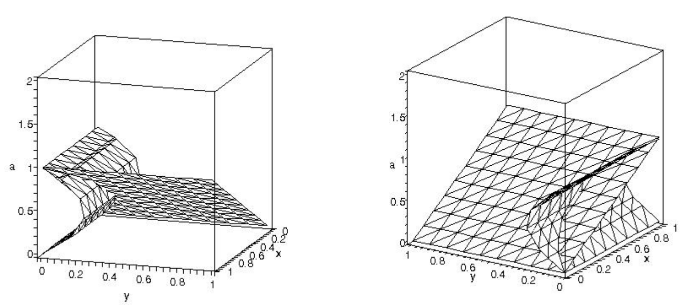

Figure 1: The static bifurcation diagram

Owing to the Hartman-Grobman theorem, we are interested only in non-hyperbolic equilibria: the saddle-node O for $a \in \mathbb{R}_+ \setminus \{0\}$, the saddle-node E_1 for $a = 1$ and the Hopf singularity E_2 for $a = 1/2$.

3.The nature of the nonhyperbolic equilibrium points

In order to see whether a nonhyperbolic equilibrium point is a degenerated or a nondegenerated singularity we have to derive the normal form of (1) at that point [1].

Proposition 1. *The normal form of (1) at $O(0,0)$ for $a \neq 0$ is*

$$\begin{cases} \dot{n}_1 &= n_1^2 + O(\mathbf{n}^3), \\ \dot{n}_2 &= -an_2 + n_1 n_2 + O(\mathbf{n}^3), \end{cases} \tag{4}$$

and, thus, O is a nondegenerated saddle-node.

The system (1) is equivalent to

$$\begin{cases} \dot{x} &= x^2 - xy + O(x^3), \\ \\ \dot{y} &= -ay + xy, \end{cases} \tag{5}$$

whose matrix of the linear terms is diagonal. In order to reduce the second order nonresonant terms in (5) we determine the transformation $\mathbf{X} = \mathbf{n} + \mathbf{h}(\mathbf{n})$, where $\mathbf{X} = (x, y)^T$ and $\mathbf{n} = (n_1, n_2)^T$, suggested by the Table 1.

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	1	0	0	a	-	0
1	1	-1	1	$-a$	0	$1/a$	-
0	2	0	0	$-2a$	$-a$	0	0

Table 1.

Here $\Lambda_{\mathbf{m},1}$, $\Lambda_{\mathbf{m},2}$ are the eigenvalues of the associated Lie operator, and $X_{\mathbf{m}}$ is a second order vector polynomial in (5). We find the transformation

$$\begin{cases} x &= n_1 + (1/a) n_1 n_2, \\ y &= n_2, \end{cases}$$

carrying (5) into (4). By [1], the equilibrium point $O(0,0)$ corresponding the dynamical system generated by a sode of the form (4) is a nondegenerated saddle-node.

Proposition 2. *The normal form of (1) at* $E_1(1,0)$ *for* $a=1$ *is*

$$\left\{\begin{array}{lcl}\dot{n}_1 & = & -n_1-4n_1n_2+O(\mathbf{n}^3),\\ \dot{n}_2 & = & n_2^2+O(\mathbf{n}^3),\end{array}\right. \tag{6}$$

and, thus, E_1 *is a nondegenerated saddle-node.*

Proof. First, we translate the point E_1 at the origin with the aid of the change $u_1=x-1,\ u_2=y$. Let $\mathbf{u}=(u_1,u_2)^T$. Then, in $\mathbf{u}$, (1) reads

$$\left\{\begin{array}{lcl}\dot{u}_1 & = & -u_1-u_2-2u_1^2-u_1u_2-u_1^3,\\ \dot{u}_2 & = & u_1u_2.\end{array}\right. \tag{7}$$

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

$$\left\{\begin{array}{lcl}\dot{v}_1 & = & -v_1-2v_1^2-4v_1v_2-2v_2^2+O(\mathbf{v}^3),\\ \dot{v}_2 & = & v_1v_2+v_2^2,\end{array}\right. \tag{8}$$

involving a diagonal matrix of the linear terms. In order to reduce the second order nonresonant 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 2.

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	-2	0	-1	-2	2	0
1	1	-4	1	0	-1	-	-1
0	2	-2	1	1	0	-2	-

Table 2.

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

$$\left\{\begin{array}{lcl}v_1 & = & n_1+2n_1^2-2n_2^2,\\ v_2 & = & n_2-n_1n_2,\end{array}\right.$$

carrying (8) into (6). By [1], the equilibrium point $E_1(1,0)$ corresponding the dynamical system generated by a sode of the form (6) is a nondegenerated saddle-node.

PROPOSITION 3. *The normal form of (1) at* $E_2(1/2,1/4)$ *for* $a=1/2$ *is*

$$\begin{pmatrix} \dot{w}_1 \\ \dot{w}_2 \end{pmatrix} = \begin{pmatrix} 0 & -\sqrt{2}/4 \\ \sqrt{2}/4 & 0 \end{pmatrix} - (w_1^2+w_2^2)\left[\frac{1}{2}\begin{pmatrix} w_1 \\ w_2 \end{pmatrix} + \frac{31\sqrt{2}}{18}\begin{pmatrix} -w_2 \\ w_1 \end{pmatrix}\right] + O(w^4) \tag{9}$$

and, thus, E_2 *is a nondegenerated Hopf singularity.*

Proof. First, we translate the point E_2 at the origin with the aid of the change $u_1 = x - 1/2,\ u_2 = y - 1/4$. Let $\mathbf{u} = (u_1,u_2)^T$. Then, in $\mathbf{u}$, (1) reads

$$\begin{cases} \dot{u}_1 &= -\frac{1}{2}u_2 - \frac{1}{2}u_1^2 - u_1u_2 - u_1^3, \\ \dot{u}_2 &= \frac{1}{4}u_1 + u_1u_2. \end{cases} \tag{10}$$

The eigenvalues of the matrix defining the linear terms in (10) are $\lambda_1 = \overline{\lambda_2} = \sqrt{2}i/4$ and, let $\mathbf{u}_{\lambda_1} = (i\sqrt{2},1)^T$ be an eigenvector corresponding to the positive eigenvalue. We have $\mathbf{u}_{\lambda_1} = (0,1)^T + i(\sqrt{2},0)^T$. Thus, with the change of the coordinates $\begin{pmatrix} u_1 \\ u_2 \end{pmatrix} = \mathbf{P}\mathbf{M}_{\mathbb{C}}\begin{pmatrix} v_1 \\ v_2 \end{pmatrix}$, where $\mathbf{P} = \begin{pmatrix} \sqrt{2} & 0 \\ 0 & 1 \end{pmatrix}$ and $\mathbf{M}_{\mathbb{C}} = \frac{1}{2}\begin{pmatrix} 1 & 1 \\ -i & i \end{pmatrix}$, i.e. $\begin{pmatrix} u_1 \\ u_2 \end{pmatrix} = \frac{1}{2}\begin{pmatrix} \sqrt{2} & \sqrt{2} \\ -i & i \end{pmatrix}\begin{pmatrix} v_1 \\ v_2 \end{pmatrix}$, (10) achieves the complex form

$$\begin{cases} \dot{v}_1 &= \frac{\sqrt{2}i}{4}v_1 + \left(\frac{\sqrt{2}}{8} + \frac{i}{4}\right)v_1^2 - \frac{\sqrt{2}}{4}v_1v_2 - \left(\frac{3\sqrt{2}}{8} + \frac{i}{4}\right)v_2^2 - \frac{1}{4}(v_1+v_2)^3, \\ \dot{v}_2 &= \frac{-\sqrt{2}i}{4}v_2 - \left(\frac{3\sqrt{2}}{8} - \frac{i}{4}\right)v_1^2 - \frac{\sqrt{2}}{4}v_1v_2 + \left(\frac{\sqrt{2}}{8} - \frac{i}{4}\right)v_2^2 - \frac{1}{4}(v_1+v_2)^3, \end{cases} \tag{11}$$

involving a diagonal matrix of the linear terms. In order to reduce the second order resonant terms in (11) 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 3.

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	M	$\overline{N}$	$\sqrt{2}i/4$	$3\sqrt{2}i/4$	P	$\overline{Q}$
1	1	$\sqrt{2}/4$	$-\sqrt{2}/4$	$-\sqrt{2}i/4$	$\sqrt{2}i/4$	$-i$	i
0	2	N	$\overline{M}$	$-3\sqrt{2}i/4$	$-\sqrt{2}i/4$	Q	$\overline{P}$

Table 3.

Here $\Lambda_{\mathbf{m},1}$, $\Lambda_{\mathbf{m},2}$ are the eigenvalues of the associated Lie operator, $X_{\mathbf{m}}$ is a second order vector polynomial in (11) $M = \dfrac{\sqrt{2}}{8} + \dfrac{i}{4}$, $N = -\dfrac{3\sqrt{2}}{8} - \dfrac{i}{4}$, $P = \dfrac{\sqrt{2}}{2} - \dfrac{i}{2}$ and $Q = \dfrac{\sqrt{2}}{6} - \dfrac{i}{2}$.

We find the transformation

$$\begin{cases} v_1 = n_1 + \left(\dfrac{\sqrt{2}}{2} - \dfrac{i}{2}\right) n_1^2 - in_1n_2 + \left(\dfrac{\sqrt{2}}{6} - \dfrac{i}{2}\right) n_2^2, \\ v_2 = n_2 + \left(\dfrac{\sqrt{2}}{6} + \dfrac{i}{2}\right) n_1^2 + in_1n_2 + \left(\dfrac{\sqrt{2}}{2} + \dfrac{i}{2}\right) n_2^2, \end{cases}$$

carrying (11) into

$$\begin{cases} \dot{n}_1 = \dfrac{\sqrt{2}i}{4} n_1 + \left(\dfrac{1}{6} - \dfrac{\sqrt{2}i}{2}\right) n_1^3 - \left(\dfrac{1}{2} + \dfrac{31\sqrt{2}i}{18}\right) n_1^2 n_2 - \\ \quad - \left(\dfrac{1}{6} + \dfrac{7\sqrt{2}i}{6}\right) n_1 n_2^2 - \left(\dfrac{5}{6} + \dfrac{\sqrt{2}i}{2}\right) n_2^3 + O(n^4), \\ \dot{n}_2 = \dfrac{-\sqrt{2}i}{4} n_2 - \left(\dfrac{5}{6} - \dfrac{\sqrt{2}i}{2}\right) n_1^3 - \left(\dfrac{1}{6} - \dfrac{7\sqrt{2}i}{6}\right) n_1^2 n_2 - \\ \quad - \left(\dfrac{1}{2} - \dfrac{31\sqrt{2}i}{18}\right) n_1 n_2^2 + \left(\dfrac{1}{6} + \dfrac{\sqrt{2}i}{2}\right) n_2^3 + O(n^4). \end{cases} \tag{12}$$

Thus we eliminated the nonresonant second order terms. Now, we have to reduce the third order nonresonant terms in (12). This reduces to determine the transformation $\mathbf{n} = \mathbf{s} + \mathbf{h}(\mathbf{s})$, where $\mathbf{n} = (n_1, n_2)^T$ and $\mathbf{s} = (s_1, s_2)^T$, suggested by the Table 4.

m_1	m_2	$X_{\mathbf{m},1}$	$X_{\mathbf{m},2}$	$\Lambda_{\mathbf{m},1}$	$\Lambda_{\mathbf{m},2}$	$h_{\mathbf{m},1}$	$h_{\mathbf{m},2}$
3	0	R	$\overline{Z}$	$\sqrt{2}i/2$	$\sqrt{2}i$	C	$\overline{E}$
2	1	S	$\overline{T}$	0	$\sqrt{2}i/2$	-	$\overline{D}$
1	2	T	$\overline{S}$	$-3\sqrt{2}i/2$	0	D	-
0	3	Z	$\overline{R}$	$-\sqrt{2}i$	$-\sqrt{2}i/2$	E	$\overline{C}$

Table 4.

Here $X_{\mathbf{m}}$ is a third order vector polynomial in (11) $R = \frac{1}{6} - \frac{\sqrt{2}i}{2}$, $S = -\frac{1}{2} - \frac{31\sqrt{2}i}{18}$, $T = -\frac{1}{6} - \frac{7\sqrt{2}i}{18}$, $Z = -\frac{5}{6} - \frac{\sqrt{2}i}{2}$, $C = -1 - \frac{\sqrt{2}i}{6}$, $D = \frac{7}{3} - \frac{\sqrt{2}i}{6}$, and $E = \frac{1}{2} - \frac{5\sqrt{2}i}{12}$.

We find the transformation

$$\begin{cases} n_1 = s_1 - \left(1 + \frac{\sqrt{2}i}{6}\right) s_1^3 + \left(\frac{7}{3} - \frac{\sqrt{2}i}{6}\right) s_1 s_2^2 + \left(\frac{1}{2} - \frac{5\sqrt{2}i}{12}\right) s_2^3, \\ n_2 = s_2 + \left(\frac{1}{2} + \frac{5\sqrt{2}i}{12}\right) s_1^3 + \left(\frac{7}{3} + \frac{\sqrt{2}i}{6}\right) s_1^2 s_2 - \left(1 - \frac{\sqrt{2}i}{6}\right) s_2^3, \end{cases}$$

carrying (12) into

$$\begin{cases} \dot{s}_1 = \frac{\sqrt{2}i}{4} s_1 - \left(\frac{1}{2} + \frac{31\sqrt{2}i}{18}\right) s_1^2 s_2 + O(s^4), \\ \dot{s}_2 = \frac{-\sqrt{2}i}{4} s_2 - \left(\frac{1}{2} - \frac{31\sqrt{2}i}{18}\right) s_1 s_2^2 + O(s^4). \end{cases} \tag{13}$$

Let us come back to the real state functions by denoting $s_1 = w_1 + iw_2$, $\overline{s_2} = w_1 - iw_2$ [4]. In this way we obtain

$$\begin{cases} \dot{w}_1 = -\frac{\sqrt{2}i}{4} w_2 - (w_1^2 + w_2^2)\left(\frac{1}{2} w_1 - \frac{31\sqrt{2}i}{18} w_2\right) + O(w^4), \\ \dot{w}_2 = \frac{\sqrt{2}i}{4} w_1 - (w_1^2 + w_2^2)\left(\frac{1}{2} w_1 - \frac{31\sqrt{2}i}{18} w_2\right) + O(w^4), \end{cases} \tag{14}$$

or, equivalently,

$$\begin{pmatrix} \dot{w}_1 \\ \dot{w}_2 \end{pmatrix} = \begin{pmatrix} 0 & -\sqrt{2}/4 \\ \sqrt{2}/4 & 0 \end{pmatrix} - (w_1^2 + w_2^2) \left[\frac{1}{2} \begin{pmatrix} w_1 \\ w_2 \end{pmatrix} + \frac{31\sqrt{2}}{18} \begin{pmatrix} -w_2 \\ w_1 \end{pmatrix} \right] + O(w^4)$$

This is the normal form of (10). By [1], the equilibrium point $E_2(1/2, 1/4)$ corresponding the dynamical system generated by a sode of the form (9) is a nondegenerated supercritical Hopf singularity.

4.The global dynamic bifurcation diagram

The discussion in Section 2 shows on the real $a-$axis (which represents the parametric portrait) seven regions corresponding to topologically equivalent dynamical systems are determined (fig. 2). In fig. 3 we represent the phase portraits corresponding to each stratum of the parametric portrait. This shows that, in spite of their unrealistic significance for the population dynamics, the equilibria O, E_1 and E_2 for $a > 1$ heavily contribute to the changes in the phase portraits and, so, to the dynamic bifurcation diagram (which consists of figs 1 and 2).

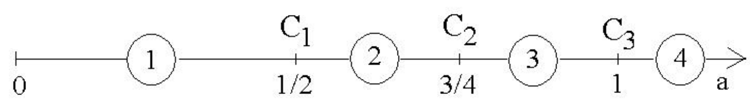

Figure 2: The parametric portrait

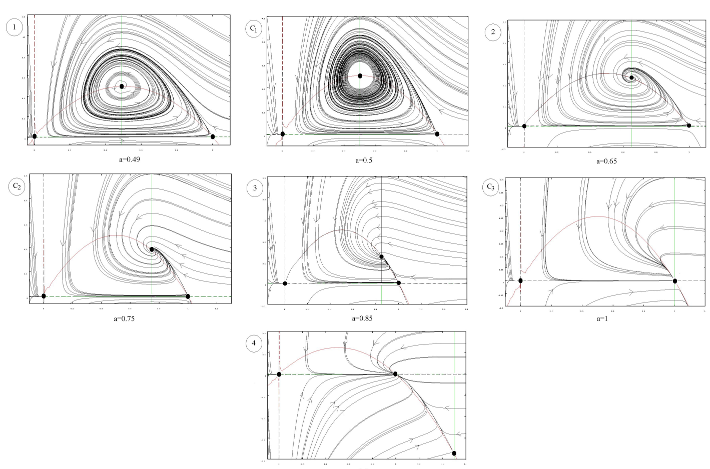

Figure 3: Phase portrait for various strata in fig.2.

The equilibria in it can be described at follows: the equilibrium O is always a saddle-node and it exists for every value of the parameter a; the equilibrium

E_1 is a saddle for any $a < 1$, a saddle-node for $a = 1$ and an attractive node for $a > 1$; the equilibrium E_2 is a repulsive focus, a Hopf singularity, an attractive focus, a sink, an attractive node, respectively, for different values of the parameter $a < 1$. When $a = 1$, the equilibrium E_2 collides with E_1 and it becomes a saddle-node and, then, for $a > 1$ it has a negative component, so, from the biological point of view, we can say that it disappears.

5.The biological interpretation

For mathematical reasons we studied the population dynamics for the entire real plane. However, for biology purposes we give the biological interpretation only for the fist quadrant. As a consequence, if x_0 and/or y_0 are negative we say that the corresponding equilibrium $\mathbf{x}_0 = (x_0, y_0)$ does not exist.

Analyzing the portraits in fig. 3 we can conclude that, if one or both initial populations do not exist, they will not exist for ever and if the initial populations are at any equilibrium point, then the populations remain constant at any subsequent time. For all other initial values the subsequent populations vary in various manners, depending the values of the parameter a. The paths described by these values are phase space trajectories corresponding to transient regimes between some equilibrium state or/and periodic regime.

Thus, for the zones C_1 and 2 the numbers of the subsequent populations are oscillatory but not periodic (firstly both populations increase, then only y increases and x decreases, then only x increases and y decreases with the amplitudes smaller and smaller, and again both populations increase and so on) until they reach the equilibrium point E_2. In the zone 2 the increase (decrease) of the populations are faster than in zone C_1 where the increase (decrease) of the population is very very slow. For zones C_3 and 3 the subsequent populations are very little oscillatory until they come to an equilibrium point E_2. For the zone 1, the equilibrium points are repulsive and the populations go to a limit cycle where they become periodic.

Finally, we can conclude that the prey $x(t)$ flourish in the absence of the predator. Theoretically, the predator can destroy all the prey so that the latter becomes extinct. However, if this happens the predator $y(t)$ will also become extinct since, as we assume, it depends on the prey for its existence. In addition, our parametric portrait shows where all these phenomena occur.

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