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ON THE OCCURRENCE OF LIMIT CYCLES IN THE VOLTERRA–LOTKA EQUATION

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1. INTRODUCTION

The paper deals with the following problem: For which dimension n do limit cycles occur in the classical Volterra–Lotka differential equation

$$\dot{x}_i = x_i\left(a_{i0} + \sum_{j=1}^{n} a_{ij}x_j\right), \quad i = 1, \ldots, n \tag{1.1}$$

defined on $\mathbb{R}^n_+ = \{x = (x_1, \ldots, x_n) \in \mathbb{R}^n: x_i \geq 0 \text{ for all } i\}$.

It is a classical result (see [1, p, 213] or [2, p. 300]) that for $n = 2$ isolated periodic orbits are not possible. We will show that Hopf bifurcations and hence stable limit cycles occur for dimensions $n \geq 3$.

This will be done by showing in Section 2 that (1.1) is equivalent to a certain differential equation on the simplex S_{n+1}, the "replicator equation"

$$\dot{y}_i = y_i\left(\sum_j a_{ij}y_j - \sum_{k,l} a_{kl}y_k y_l\right), \quad i = 0, 1, \ldots, n \tag{1.2}$$

which arises in such different fields as population genetics ($a_{ij} = a_{ji}$ in the Fisher–Wright–Haldane model), prebiotic evolution [3] and game dynamics [12, 14]. For this equation Hopf bifurcations were found for $n \geq 3$ in [5], whereas Zeeman [14] disproved occurrence of Hopf bifurcations for $n = 2$. His paper was the starting point for this investigation.

In dimensions $n \geq 3$ there are only few results on (1.1), apart from the special case $a_{ij} = -a_{ji}$, which allows a constant of motion and was treated already extensively by Volterra [13]. For the case $a_{ij} = a_{ji}$, MacArthur [6] has found a global Lyapunov function. Rescigno's paper [9] deals with the three-dimensional case. His discussion is confined to a classification of parameter values for which at least one of the 8 equilibrium points is stable. But, as observed by May and Leonard [8], unlike the two dimensional case there remain a lot of combinations of the interaction coefficients a_{ij} where all fixed points are unstable. In particular, May and Leonard study the equation

$$\begin{aligned}
\dot{x}_1 &= x_1(1 - x_1 - \alpha x_2 - \beta x_3),\\
\dot{x}_2 &= x_2(1 - \beta x_1 - x_2 - \alpha x_3),\\
\dot{x}_3 &= x_3(1 - \alpha x_1 - \beta x_2 - x_3),
\end{aligned} \tag{1.3}$$

and indicate that for certain values of the parameters α, β almost all orbits tend to nonperiodic oscillations of bounded amplitude but ever increasing cycle time. See also [10] for an exact description of the attractor of (1.3) which lies on the boundary of $\mathbb{R}^3_+$. Equation (1.3) however is too special to allow stable limit cycles. Nevertheless we will see in section 3 that higher dimensional versions of (1.3) admit Hopf bifurcations.

Finally we mention that Fujii [4] found a stable limit cycle by numerical integration in a two-prey–one-predator system modelled by equation (1.1) for $n = 3$.

2. AN EQUIVALENT SYSTEM

The n-dimensional Volterra–Lotka equation (1.1) is defined on the positive octant $\mathbb{R}^n_+$.

Let us compactify this region introducing homogeneous coordinates by setting $x_0 = 1$ and

$$y_i = \frac{x_i}{\sum_{j=0}^{n} x_j}, \quad i = 0, \dots, n.$$

Then $y = (y_0, y_1, \dots, y_n)$ lies on the simplex

$$S_{n+1} = \left\{ y \in \mathbb{R}^{n+1}, y_i \geq 0, \sum_{i=0}^{n} y_i = 1 \right\}.$$

The inverse transformation is given by

$$x_i = \frac{y_i}{y_0}, \quad i = 1, \dots, n.$$

Equation (1.1) then transforms into

$$\begin{aligned} \dot{y}_i &= \frac{\dot{x}_i}{\Sigma x_j} - \frac{x_i \Sigma \dot{x}_j}{(\Sigma x_j)^2} \\ &= x_i \left(\sum_{j=0}^{n} a_{ij} x_j \right) y_0 - x_i \left(\sum_{j,k} x_j a_{jk} x_k \right) y_0^2 \\ &= y_i \left(\sum_{j=0}^{n} a_{ij} y_j - \sum_{j,k=0}^{n} y_j a_{jk} y_k \right) \frac{1}{y_0}, \end{aligned}$$

if we agree to set $a_{0j} = 0$ which is in accordance with (1.1) if one sets $x_0 \equiv 1$. Up to the factor $1/y_0$ which means only a change of velocity this is just the differential equation

$$\dot{y}_i = y_i \left(\sum_j a_{ij} y_j - \sum_{k,l} y_k a_{kl} y_l \right), \quad i = 0, \dots, n \tag{2.1}$$

on the simplex S_{n+1}, called "replicator equation " in [12]. It is easy to see that (2.1) remains unchanged (on S_{n+1}), if we add an arbitrary constant to each column of the matrix (a_{ij}). Hence we always may assume the 0th row to be zero ($a_{0j} = 0$) and can conversely write (2.1) in the equivalent form (1.1).

For some results on the replicator equation we refer to [5, 11], the occurrence of Hopf bifurcation and limit cycles for $n \geq 3$ was shown in [5]. Recently Zeeman [14] proved the nonexistence of Hopf bifurcations and gave a complete description of all possible stable flows arising from (2.1) for $n = 2$, under the assumption that it allows no limit cycles. This gap is now closed and one can apply Zeeman's result to describe completely the possible flows arising from the two-dimensional Volterra–Lotka equation.

Finally we want to draw attention upon a differential equation similar to the two-dimensional Volterra–Lotka equation, namely

$$\dot{x} = x(1-x)(a+bx+cy), \qquad (2.2)$$

$$\dot{y} = y(1-y)(d+ex+fy),$$

defined on the square $0 \leq x \leq 1$, $0 \leq y \leq 1$. This equation occurring in neural network theory and game dynamics, has been treated extensively in [12]. It is an instructive example showing how implantation of higher order nonlinearities manifests itself in a higher complexity of the dynamics. Indeed (2.2) allows stable limit cycles in contrast to the two-dimensional Volterra–Lotka equation. Furthermore it can be shown that (2.2) occurs as an invariant subsystem of the three- (and of course higher-) dimensional Volterra–Lotka equation.

3. CYCLIC SYMMETRY

In the following we will treat explicitely and in a similar manner to [5] the higher dimensional versions of the example of May and Leonard (1.3) which also give rise to Hopf bifurcations for dimension $n \geq 4$.

Following May and Leonard we assume the matrix a_{ij} to be circulant, (indices are counted cyclically modulo n):

$$\dot{x}_i = x_i\left(1 - \sum_{j=1}^{n} c_j x_{i+j}\right), \quad i = 1, \ldots, n. \qquad (3.1)$$

For $n = 3$ we obtain (1.3) with $c_0 = 1$, $c_1 = \alpha$, $c_2 = \beta$. Let us write $\gamma_k = \Sigma_{j=0}^{n-1} c_j \lambda^{jk}$ with $\lambda = \exp 2\pi i/n$ and assume $\gamma_o = \Sigma_{j=1}^{n} c_j > 0$. This guarantees the existence of the fixed point

$$\bar{x}_1 = \bar{x}_2 = \ldots = \bar{x}_n = (\Sigma c_j)^{-1} = \gamma_0^{-1}. \qquad (3.2)$$

The Jacobian at $\bar{x}$ is given by

$$-\frac{1}{\gamma_0}\begin{bmatrix} c_0 & c_1 & \ldots & c_{n-1} \\ c_{n-1} & c_0 & \ldots & c_{n-2} \\ \ldots & \ldots & \ldots & \ldots \end{bmatrix}$$

and using a wellknown formula, the eigenvalues take the form

$$\omega_k = -\gamma_k/\gamma_0, \quad k = 1, \ldots, n. \qquad (3.3)$$

Note that $\overline{\omega}_{n-k} = \omega_k$ for $k = 1, \ldots, n-1$.

We will prove the following:

THEOREM: If Re $\omega_1 \leq 0 (\omega_1 \neq 0)$ and Re $\omega_k < 0$ for $k = 2, \ldots, n-2$, then x is a global attractor. In particular, $\bar{x}$ is asymptotically stable.

COROLLARY 1. If $\bar{x}$ is a sink, it is a global attractor.

COROLLARY 2. If Re $\omega_k < 0$ $(k = 2, \ldots, n-2)$ and Re $\omega_1 > 0$ and sufficiently small then there is a stable limit cycle near the (unstable) fixed point $\bar{x}$.

This follows from Hopf bifurcation theory [7].

Proof. We will construct a global Lyapunov function.
Let $P = x_1x_2 \ldots x_n$, $S = \Sigma_{i=1}^n x_i$ and $Q = \Sigma_{i,j=1}^n c_{j-i}x_ix_j$.
Then (3.1) implies

$$\dot{P} = P(n - \gamma_o S), \tag{3.4}$$

$$\dot{S} = S - Q, \tag{3.5}$$

$$(PS^{-n})^{\cdot} = PS^{-n-1}(nQ - \gamma_0 S^2). \tag{3.6}$$

We claim that PS^{-n} is a global Lyapunov function under the assumptions of the Theorem. To see this we introduce new variables

$$y_p = \sum_{i=1}^{n} \lambda^{ip} x_i, \quad p = 0, \ldots, n-1$$

which obviously represent the eigenvectors corresponding to the eigenvalues ω_p in (3.3). This vector $y = (y_0, \ldots, y_{n-1})$ is just the Fourier transform of $x = (x_1, \ldots, x_n)$ on the cyclic group $\mathbb{Z}_n$ of indices modulo n.

Using the inverse relations

$$x_i = \frac{1}{n} \sum_{p=0}^{n-1} \lambda^{ip} y_p$$

and the well-known identity $\Sigma_{j=0}^{n-1} \lambda^{jm} = \delta_{0,m}$, a short calculation (quite similar to that in [5]) transforms (3.1) into

$$\dot{y}_p = y_p - \frac{1}{n} \sum_{m=0}^{n-1} \gamma_m y_{-m} y_{p+m}. \tag{3.7}$$

Since $y_0 = S$, a comparison of (3.7) (for $p = 0$) with (3.5) yields

$$Q = \frac{1}{n} \sum_{m=0}^{n-1} \gamma_m |y_m|^2 = \frac{1}{n} \sum_{m=0}^{n-1} \operatorname{Re} \gamma_m |y_m|^2.$$

Hence (3.6) takes the form

$$(PS^{-n})^{\cdot} = PS^{-n-1} \sum_{m=1}^{n-1} \operatorname{Re} \gamma_m |y_m|^2. \tag{3.8}$$

Therefore $(PS^{-n})^{\cdot} \geqslant 0$ if $\operatorname{Re} \gamma_m \geqslant 0$ (i.e., $\operatorname{Re} \omega_m \leqslant 0$) for $m = 1, \ldots, n-1$.

Using the well-known Lyapunov stability theorem every orbit tends to an invariant set contained in $\{x\colon (PS^{-n})^{\cdot} = 0\}$. We have to show that this is just the fixed point $\bar{x}$, which is given by $(n/\gamma_0, 0, \ldots, 0)$ in y-space. This is obvious, if all $\operatorname{Re} \gamma_m > 0$.

If $\operatorname{Re} \gamma_m > 0$ holds only for $m = 2, \ldots, n-2$ and $\operatorname{Re} \gamma_1 = 0$, but $\gamma_1 \neq 0$, then

$$\{(PS^{-n})^{\cdot} = 0\} = bd\, \mathbb{R}_+^n \cup \{y_2 = y_3 = \ldots = y_{n-2} = 0\}. \tag{3.9}$$

The assumption $\dot{y}_i \equiv 0$ for $i = 2, \ldots, n-2$ makes (3.7) for $n \geqslant 5$ to

$$0 = \dot{y}_2 = -\frac{1}{n}\sum_{m=0}^{n-1} \gamma_m y_{-m} y_{m+2} = -\frac{1}{n}\gamma_{-1} y_1^2 \tag{3.10}$$

and hence $y_1 = 0$. Again the line $x_1 = x_2 = \ldots = x_n$ is the maximal invariant subset of (3.9), but only $\bar{x}$ itself can arise as ω-limit of an orbit. For $n = 4$ (3.10) takes another form, but it leads to the same result.

For $n = 3$ however (3.8) reduces to

$$(PS^{-3})^{\cdot} = PS^{-4} \cdot 2\,\mathrm{Re}\,\gamma_1 |y_1|^2 = PS^{-4}\left(c_0 - \frac{c_1 + c_2}{2}\right)[(x_1 - x_2)^2 + (x_2 - x_3)^2 + (x_3 - x_1)^2].$$

Hence, as seen already by May and Leonard [8] and in a more precise and general way by Schuster, Sigmund and Wolff [10], for $2c_0 > c_1 + c_2, \bar{x}$ is globally stable, for $2c_0 = c_1 + c_2$ all orbits lie on cones with $PS^{-3} = const.$ and tend to periodic orbits lying in the plane $x_1 + x_2 + x_3 = 3/(c_0 + c_1 + c_2)$ and finally for $2c_0 < c_1 + c_2$, each orbit (apart from the three orbits on the line $x_1 = x_2 = x_3$) approaches the boundary and oscillates with ever increasing period.

Hence, combining the results of Sections 2 and 3 we have proved:

THEOREM. The n-dimensional Volterra–Lotka equation (1.1) admits stable limit cycles iff $n \geqslant 3$.

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REFERENCES

1. ANDRONOV A. A. *et al.*, *Qualitative Theory of Second Order Dynamic Systems*, Wiley, New York (1973).
2. COPPEL W. A., A Survey of quadratic systems, *J. diff. Eqns.* **2**, 293–304 (1966).
3. EIGEN M. & SCHUSTER P., *The Hypercycle—A Principle of Natural Self-Organization*, Springer, Berlin (1979).
4. FUJII K., Complexity–Stability relationship of two-prey–one-predator species system model: local and global stability, *J. theor. Biol.* **69**, 613–623 (1977).
5. HOFBAUER J., SCHUSTER P., SIGMUND K. & WOLFF R., Dynamical Systems under constant organization II: Homogeneous growth functions of degree p = 2, *SIAM J. appl. Math.* **C38**, 282–304 (1980).
6. MACARTHUR R., Species packing and competitive equilibrium for many species, *Theor. Popul. Biology* **1**, 1–11 (1970).
7. MARSDEN J. & MCCRACKEN M., The Hopf bifurcation and its applications, *Applied Mathematical Sciences*, Vol. 19, Springer, New York (1976).
8. MAY R. M. & LEONARD W. J., Nonlinear aspects of competition between three species, *SIAM J. appl. Math.* **29**, 243–253 (1975).
9. RESCIGNO A., The struggle for life: II, Three competitors, *Bull. math. Biophys.* **30**, 291–298 (1968).
10. SCHUSTER P., SIGMUND K. & WOLFF R., On ω-limits for competition between three species, *SIAM J. appl. Math.* **37**, 49–54 (1979).
11. SCHUSTER P., SIGMUND K. & WOLFF R., Mass action kinetics of selfreplication in flow reactors, *J. math. Analysis Applic.* **78**, 88–112 (1980).
12. SCHUSTER P., SIGMUND K., HOFBAUER J. & WOLFF R., Self-regulation of behaviour in animal societies, *Biological Cybernetics* **40**, 1–25 (1981).
13. SCUDO F. M. & ZIEGLER J. R., The Golden Age of Theoretical Ecology: 1923–1940, Lecture Notes in Biomathematics **22**, Springer, Berlin (1978).
14. ZEEMAN E. C., Population dynamics from game theory, in *Global Theory of Dynamical Systems*, Lecture Notes in Mathematics **819**, Springer (1980).