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Multiple Limit Cycles for Three Dimensional Lotka-Volterra Equations

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Abstract—A 3D competitive Lotka-Volterra equation with two limit cycles is constructed.

Keywords—Lotka-Volterra equations, Competitive systems, Limit cycles, Hopf bifurcation.

INTRODUCTION

It is a classical result (due to Moisseev 1939 and/or Bautin 1954, see [1, p. 213, Section 12, Example 7] or [2, 18.2]) that 2D Lotka-Volterra equations cannot have limit cycles: if there is a periodic orbit, then the interior fixed point is a center (i.e., surrounded by a continuum of periodic orbits). Hence, a center is a codimension one phenomenon for 2D Lotka-Volterra equations, like for linear equations. On the other hand, 3D Lotka-Volterra equations allow already complicated dynamics (see [3–5]): The period doubling route to chaos and many other phenomena known from the iteration of the quadratic map have been observed by numerical simulations.

For 3D *competitive* systems, the dynamical possibilities are more restricted: According to Hirsch [6, Theorem 1.7], there is an invariant manifold (called the carrying simplex) that is homeomorphic to the two-dimensional simplex and that attracts all orbits except the origin. Therefore in 3D competitive systems, the Poincaré-Bendixson theorem holds. Based on this, M. L. Zeeman [7] has given a classification of all possible stable phase portraits of 3D competitive Lotka-Volterra equations, thus extending a related classification of the game dynamical equation [8]. However, the question of how many limit cycles can surround the interior fixed point was left open and is still open. Up to now only examples with at most one limit cycle seem to have appeared in the literature.

In this paper, we will give an example where the (locally stable) interior equilibrium is surrounded by (at least) two limit cycles.

The idea for constructing such an example with multiple limit cycles is as follows: We consider a competitive LV-system which is *permanent* (i.e., the boundary of $\mathbb{R}^3_+$ is repelling) and where the unique interior fixed point has a pair of purely imaginary eigenvalues, but is repelling on its center manifold (which is part of the carrying simplex). This implies the existence of an

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Typeset by $\mathcal{A}\mathcal{M}\mathcal{S}$-TEX asymptotically stable (or a pair of semistable) limit cycle(s) on the carrying simplex. If we now change the parameters slightly, the fixed point will undergo a *subcritical Hopf bifurcation.* The interior equilibrium becomes stable and will be surrounded by another, smaller, unstable limit cycle.

Essentially the same idea had been applied in [9] to construct multiple limit cycles in predator-prey systems. However, the analysis is more involved here since we are dealing with 3D systems.

LOTKA-VOLTERRA EQUATIONS

Lotka-Volterra equations are given as

$$\dot{u}_i = u_i \left(r_i - \sum_{j=1}^{n} a_{ij} u_j \right). \tag{1}$$

Without loss of generality, we can assume that $E = (1, 1, \dots, 1)$ is a fixed point of (1). This way we can get rid of the r_i, which are then given by $r_i = \sum_j a_{ij}$. (If there is no interior fixed point, then the dynamics of (1) is trivial: every orbit converges to the boundary [2, 9.2]; if $u^* > 0$ is an interior fixed point of (1), a linear rescaling $v_i = u_i/u_i^*$ will move u^* to E.)

Set $x_i = u_i - 1$. Then (1) reads

$$\dot{x}_i = -(1 + x_i) \left(\sum_{j=1}^{n} a_{ij} x_j \right). \tag{2}$$

This form is convenient for the *local analysis* around the fixed point $u = E$ or $x = 0$. The Jacobian of (2) at $x = 0$ is just the matrix $-A$. With the abbreviations

$$\begin{aligned} T &= -a_{11} - a_{22} - a_{33}, \\ M &= a_{11}a_{22} - a_{12}a_{21} + a_{11}a_{33} - a_{13}a_{31} + a_{22}a_{33} - a_{23}a_{32}, \\ D &= -\det A, \end{aligned}$$

the fixed point is stable if

$$T < 0, D < 0 \quad \text{and} \quad TM < D, \tag{3}$$

and a Hopf bifurcation occurs (i.e., there is a pair of purely imaginary eigenvalues) if

$$T < 0, D < 0 \quad \text{and} \quad TM = D. \tag{4}$$

Whether this Hopf bifurcation is sub- or super-critical is determined by the *focal values* which depend on the higher order terms. The expression for the first focal value is well known for 2D systems if the linear part is in the normal form $\begin{pmatrix} 0 & \omega \\ -\omega & 0 \end{pmatrix}$, see [10] or [11]. In order to avoid the linear transformation to normal form, it is often more convenient to have an expression for the focal value at hand for a general linear part $\begin{pmatrix} a & b \\ c & -a \end{pmatrix}$ where we need $a^2 + bc < 0$. The corresponding formula can be found in [10, p. 253]. The next step is to consider 3D systems whose linear part is in the block diagonal form $\begin{pmatrix} a & b & 0 \\ c & -a & 0 \\ 0 & 0 & e \end{pmatrix}$. This can be reduced to the 2D case by computing the center manifold

$$x_3 = F(x_1, x_2) = p_{20}x_1^2 + p_{11}x_1x_2 + p_{02}x_2^2 + O(3)$$

up to second order terms. Solving for the p_{ij}'s and substituting leads to a rather lengthy expression for the first focal value.

If A is an arbitrary 3×3 matrix with a pair of purely imaginary eigenvalues, then its trace is an eigenvalue. Solving for its right and left eigenvectors one can transform A to the above block diagonal form. The obtained expression for the focal value is much too long to be reproduced here. It is known that the equilibrium is (weakly) repelling right at the bifurcation point and the Hopf bifurcation is subcritical provided the first focal value is positive.

In order to test the *uniform persistence* or *permanence* of (1), we restrict our attention to the case when there is no two-species equilibrium in the 3D system. The external eigenvalue at the one-species equilibrium F_i where $\bar{u}_i = r_i/a_{ii}$ in the direction j is given by

$$\left.\frac{\dot{u}_j}{u_j}\right|_{F_i} = r_j - \frac{a_{ji}r_i}{a_{ii}} =: \lambda_{ij}. \tag{5}$$

If λ_{ij} and λ_{ji} have different sign, then the $i-j$-subsystem does not have an interior equilibrium. If $\lambda_{12}, \lambda_{23}, \lambda_{31} > 0$ and $\lambda_{21}, \lambda_{13}, \lambda_{32} < 0$ (respectively with the inequalities reversed), the system has a *heteroclinic cycle* $F_1 \longrightarrow F_2 \longrightarrow F_3 \longrightarrow F_1$ of May-Leonard type (respectively with the arrows reversed). System (1) is then uniformly persistent provided this heteroclinic cycle is repelling. This will be the case as long as

$$P := \lambda_{12}\lambda_{23}\lambda_{31} + \lambda_{21}\lambda_{13}\lambda_{32} > 0 \tag{6}$$

or, equivalently,

$$\sum_{i=1}^{3} \frac{a_{ii}}{r_i} > 1, \tag{7}$$

which means geometrically that E lies above the plane spanned by F_1, F_2, F_3 (see [2, Ch. 22.1]).

AN EXAMPLE

With these preparations, we are able to find the following numerical example. Choose the interaction matrix

$$A = \begin{pmatrix} 2 & 5 & .5 \\ .5 & 1 & \mu \\ 1 & .5 & 1 \end{pmatrix}.$$

At $\mu = 71/48 = 1.479666\ldots$ there is a subcritical Hopf bifurcation: The first focal value is positive. (Its exact value was computed as a *rational* number using MAPLE and the procedure described above.) For μ slightly less than $71/48$, the equilibrium E is stable and surrounded by an unstable limit cycle; for $\mu > 71/48$, E is unstable. Computing the external eigenvalues (5), we see that the system has a heteroclinic cycle for $1 < \mu < 7/2$. From (6) or (7) this heteroclinic cycle is unstable for $\mu < 3/2$. Hence, near the Hopf bifurcation, the system is permanent. This implies the existence of another (large and presumably stable) limit cycle.

Figure 1 shows the bifurcating branch of periodic orbits (and their periods), computed numerically with the package COLCON developed by G. Bader and P. Kunkel (Applied Mathematics, University Heidelberg): A pair of periodic orbits is born at $\mu = 1.4764619\ldots$. As μ increases, the inner (unstable) periodic orbit shrinks to the fixed point at which it merges: $\mu = 1.479666\ldots$. The outer (stable) limit cycle grows, until at $\mu = 1.5$, it reaches the boundary and disappears in a heteroclinic or 'blue sky' bifurcation. (We are grateful to Alois Steindl, Institut für Mechanik, TU Wien, for this numerical computation).

DISCUSSION

We have presented an example of a 3D competitive Lotka-Volterra equation with two limit cycles. Admittedly, the parameter range where the two limit cycles coexist, is rather small, and they would be hard to find by numerical integration. More importantly however, we have given a

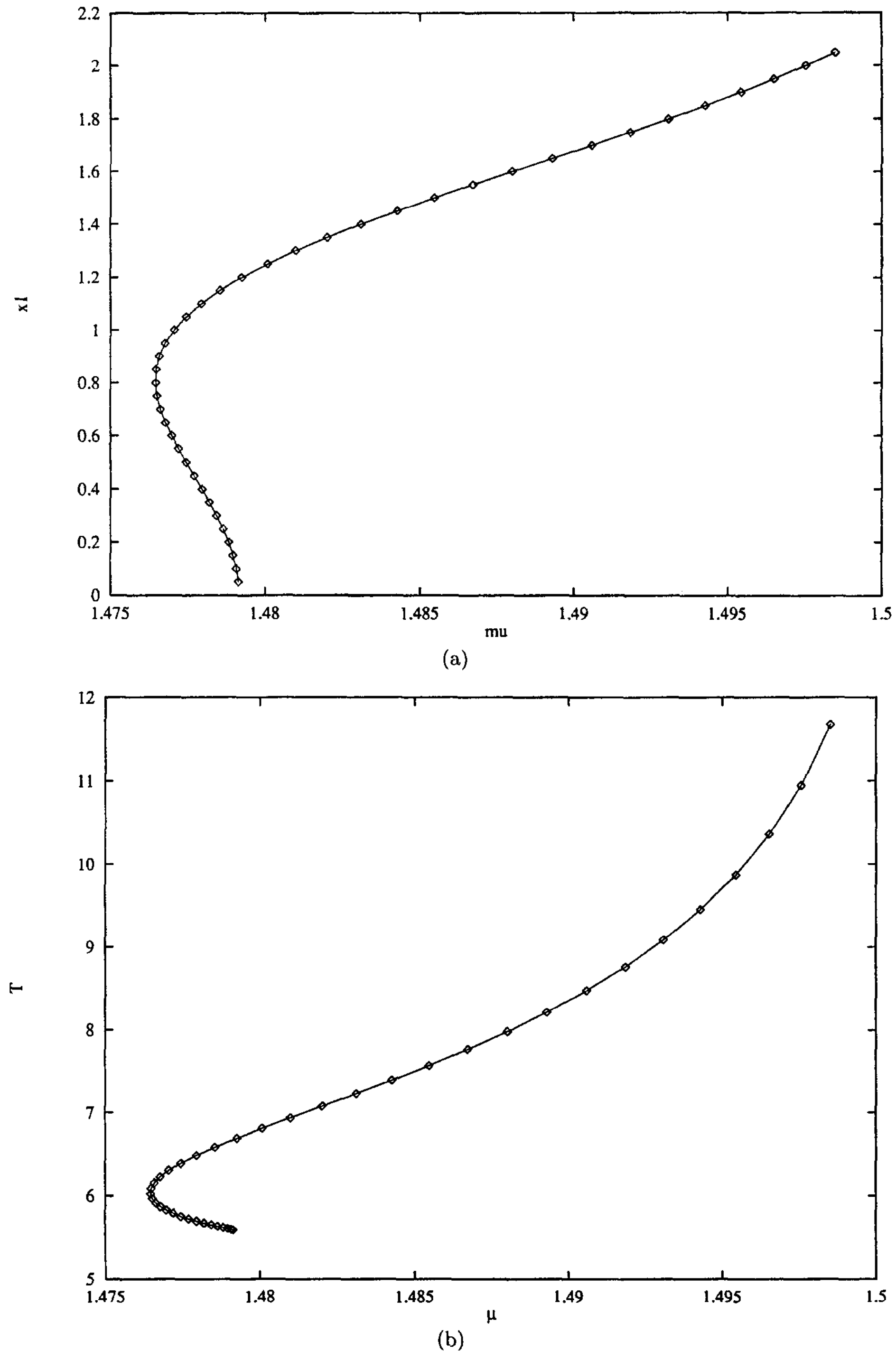

Figure 1. The bifurcation diagram and the period.

rigorous proof that such behavior exists (the computations for the relevant quantities were done symbolically, using rational numbers). It is likely that other concrete examples, that are more robust numerically, can be given.

The consequence is that higher dimensional Lotka-Volterra equations are more complicated as one might think. Lotka-Volterra equations have a bad reputation among biologists as being oversimplified and simplistic. This is true, but much of this disregard stems from the usual focus in textbooks on the 2 species case, where the dynamics is easy. In particular, our example shows that it is rather hopeless to characterize global stability for Lotka-Volterra equations: the boundary is repelling, the interior fixed point is asymptotically stable, yet not globally stable.

Hopf bifurcations for Lotka-Volterra equations were also discussed in [12,13] and [4]. These papers consider special cases where only supercritical Hopf bifurcations occur. The latter gives a detailed analysis of the subclass of those interaction matrices which are diagonally equivalent to a normal matrix. For such matrices, local stability implies VL-stability (i.e., Volterra's Lyapunov function works), and hence, global stability. This shows that any Hopf bifurcation occurring within this class is supercritical (or degenerate). It is therefore unlikely to have two limit cycles in this subclass of competitive Lotka-Volterra equations.

The main question now is whether there can be more than two limit cycles in 3D competitive Lotka-Volterra equations. We believe the answer is no. Besides this probably very difficult problem, it would also be of interest to determine which other classes in Zeeman's classification [7,8] (defined by boundary behavior) besides the heteroclinic cycle case to which we confined ourselves, can have two or more limit cycles.

A related question is the *center problem*: *For which parameters r and A does* (1) *have a two-dimensional invariant manifold filled with periodic orbits?* There are two codimension 3 families possessing such a center:

(A) If $r_1 = r_2 = r_3$, then the dynamics of (1) is essentially homogeneous and can be reduced to a replicator equation on the two-dimensional simplex S_3 or equivalently to a two-dimensional Lotka-Volterra equation. Furthermore, if an interior fixed point with a pair of purely imaginary eigenvalues exists, then there is a center. The corresponding constant of motion is of the form $\prod x_i^{\alpha_i} (\sum c_i x_i)^{-\sum \alpha_i}$.

(B) The plane spanned by the three one-species equilibria is invariant under (1). This is the case if and only if the eigenvalues λ_{ij} in (5) satisfy the three relations $\lambda_{ij} + \lambda_{ji} = 0$ for $1 \leq i < j \leq 3$.

Cases (A) and (B) may not exhaust all examples of centers. In the case of a heteroclinic cycle on the boundary, we believe that the following three conditions are equivalent to having a center:

(a) There is a pair of purely imaginary eigenvalues at E.

(b) The first focal value vanishes.

(c) There is equality in (6) resp. (7), i.e., the heteroclinic cycle is neutrally stable.

Here the last condition (c) might be replaced by the (computationally intractable?) condition

(c′) The second focal value vanishes.

Then the maximum order of a focus would be 2 and one could not generate more than two limit cycles from local bifurcations. This motivates our belief that two is the maximum number of limit cycles in these systems.

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