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Multiple limit cycles for the continuous model of the rock–scissors–paper game between bacteriocin producing bacteria

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ABSTRACT

In this paper we construct two limit cycles with a heteroclinic polycycle for the three-dimensional continuous model of the rock–scissors–paper (RSP) game between bacteriocin producing bacteria. Our construction gives a partial answer to an open question posed by Neumann and Schuster (2007) concerning how many limit cycles can coexist for the RSP game.

1. Introduction

There are anti-bacterial substances produced by bacteria–the bacteriocins. Interestingly, some bacteria produce bacteriocins not only against other bacterial species but also against other strains of the same species. It has been realized that the“warfare” using bacteriocins can lead to a situation that can be described by game-theoretical methods. Game theory has been used in theoretical biology for a long time to study important evolutionary phenomena such as the evolution of cooperative behavior, strategies in conflicts and fights, host-parasite interactions and the evolution of biochemical pathways. A frequently observed situation in the competition using bacteriocins is the following. One species (or strain) produces a particular toxin, a second species (or strain) does not produce the toxin but is resistant, and a third species (or strain) is sensitive to the toxin.

In this paper we consider the following spatially homogeneous model involving three-dimensional Lotka–Volterra (LV) equations for the rock–scissors–paper (RSP) game between bacteriocin-producing/resistant/sensitive bacteria.

$$\begin{cases} \dot{x}_1 = x_1(\alpha - \kappa_1 x_1 - \mu x_2 - \mu x_3), \\ \dot{x}_2 = x_2(\beta - (\mu + \gamma)x_1 - \kappa_2 x_2 - \mu x_3), \\ \dot{x}_3 = x_3(\epsilon - \mu x_1 - \mu x_2 - \kappa_3 x_3), \end{cases} \tag{1}$$

where $x_1 \geq 0$, $x_2 \geq 0$ and $x_3 \geq 0$ represent the resistant strain, the producer strain and the sensitive strain, respectively. $\mu > 0$ stands for the cross-correlation representing the limitation caused by the presence of the other species and the competition for the nutrients, $\alpha > 0$, $\beta > 0$ and $\epsilon > 0$ are the intrinsic growth rates, that is, the rate constants of growth when no limitation is active. The self-limitation is given by the $\kappa_i > 0$ $(i = 1, 2, 3)$. The factor $\gamma > 0$ represents the disadvantage

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(poisoning) of the sensitive strain x_2 (S) caused by the colicin producer strain x_1 (P) so that P wins over S through a sufficiently high γ-parameter if only the two of them were competing.

Recently, paper [11] showed that system (1) is structurally stable depending on the parameter values, and also system (1) has a stable state, stable limit cycle oscillations or a heteroclinic polycycle under some conditions. The later case is of interest in view of experiments with *E. coli* in mice [7], in which time-limited coexistence by consecutive displacement of three different *E. coli* strains was observed. Comparing system (1) with the following three-dimensional competitive LV system (2), there is only for a very limited parameter region the possibility of limit cycles (since $a_{12} = a_{13} = a_{23} = a_{31} = a_{32} = \mu$ and $a_{21} = \mu + \gamma$ with $\mu > 0$ and $\gamma > 0$ in system (1)). We checked that all examples of Zeeman class 27 with multiple limit cycles in [2,6,9,10] are very different to system (1). In paper [11] Neumann and Schuster posed an open question whether system (1) can have two or more limit cycles.

We note that system (1) is a special case of the following three-dimensional competitive LV systems

$$\begin{cases} \dot{x}_1 = x_1(r_1 - a_{11}x_1 - a_{12}x_2 - a_{13}x_3), \\ \dot{x}_2 = x_2(r_2 - a_{21}x_1 - a_{22}x_2 - a_{23}x_3), \\ \dot{x}_3 = x_3(r_3 - a_{31}x_1 - a_{32}x_2 - a_{33}x_3), \end{cases} \tag{2}$$

where all parameters r_i and a_{ij} are positive.

Hirsch [4] has shown that all nontrivial orbits of a three-dimensional competitive LV system (2) approach a "carrying simplex" Σ, a Lipchitz two-dimensional manifold-with-corner homeomorphic to the standard simplex in $\mathbb{R}^3_+$. This then leads to a Poincaré–Bendixson theorem for three-dimensional systems (see Smith [12]). Thus, the long-term behavior of system (2) is determined by the dynamics on Σ, and the nonzero forward limit sets in $\mathbb{R}^3_+$ all lie on Σ. Based on the remarkable result of Hirsch, Zeeman [15] defined a combinatorial equivalence relation on the set of all three-dimensional competitive LV systems and identified 33 stable equivalence classes. Of these, classes 1–25 and classes 32–33 exhibit convergence to an equilibrium for all orbits while limit cycles are possible for the remaining six classes, i.e., in classes 26 to 31 (see [13,15]). The Hopf bifurcation theorem shows that the remaining classes 26–31 can possess isolated periodic orbits (i.e. limit cycles).

Two limit cycles for class 27 were constructed by Hofbauer and So [6] and by Xiao and Li [14] based on Hirsch's monotone flow theorem, the center manifold theorem, and the Hopf bifurcation theorem. Lu and Luo [9] constructed two limit cycles in classes 26, 28, and 29 in Zeeman's classification, Gyllenberg and Yan [1] constructed two limit cycles in classes 30 and 31 in Zeeman's classification (without a heteroclinic polycycle), Lu and Luo [10] constructed three limit cycles in class 27 (with a heteroclinic polycycle), Gyllenberg et al. [3] constructed three limit cycles in class 29 (without a heteroclinic polycycle).

In the case of a heteroclinic polycycle on the boundary of the carrying simplex Σ of three-dimensional competitive LV systems (2), we have (see Hofbauer and Sigmund [5]):

(i) The heteroclinic polycycle is repelling if

$$L := \lambda_{12}\lambda_{23}\lambda_{31} + \lambda_{21}\lambda_{13}\lambda_{32} > 0,$$

where $\lambda_{ij} = r_j - \frac{a_{ji}r_i}{a_{ii}}$, $i = 1, 2, 3$, $j = 1, 2, 3$.

(ii) The heteroclinic polycycle is attracting if $L < 0$.

(iii) The heteroclinic polycycle is neutrally stable if $L = 0$.

In this paper, we construct two limit cycles in system (1) with an unstable heteroclinic polycycle (class 27 in Zeeman's classification). Our result gives a partial answer to Neumann and Schuster's question about how many limit cycles can coexist for system (1). However, it is much more difficult to give such an example of system (1) with two limit cycles because system (1) is a special case of the general three-dimensional competitive LV systems (2).

We denote by $\mathbb{R}^3_+$ and Int$\mathbb{R}^3_+$ the closed and open positive cone, respectively. The restriction of system (2) to the ith coordinate axis is the logistic equation $\dot{x}_i = x_i(r_i - a_{ii}x_i)$, which has a fixed point R_i at the carrying capacity r_i/a_{ii}. Note that we are abusing notation here, allowing R_i to denote a point in $\mathbb{R}_+$ or in $\mathbb{R}^3_+$ as dictated by the context.

It is easy to see that the origin is a repelling fixed point of system (2), and that the basin of repulsion of 0 in $\mathbb{R}^3_+$ is bounded. The boundary of that basin is called the carrying simplex of system (2), and is denoted by Σ. We refer to Hirsch [4] and Zeeman [15] for more details.

The following theorem of Hirsch [4] shows that Σ is topologically and geometrically simple and that all the nonzero equilibria and other ω-limit sets of system (2) lie on Σ. In particular, the equilibria R_i and any nontrivial periodic orbit lie on Σ.

We start by introducing some notation. A vector x is called positive if $x \in \mathbb{R}^3_+$, strictly positive if $x \in \text{Int}\mathbb{R}^3_+$. Two points $u, v \in \mathbb{R}^3$ are related if either $u - v$ or $v - u$ is strictly positive. A set S is called balanced if no two distinct points of S are related. The unit simplex, $\triangle$, in $\mathbb{R}^3_+$ has the standard meaning of $\Pi \cap \mathbb{R}^3_+$, where Π denotes the plane with equation $\sum_{i=1}^{3} x_i = 1$.

Theorem 1.1 (Hirsch)**.** *Given system (2), every trajectory in $\mathbb{R}^3_+ \setminus 0$ is asymptotic to one in Σ, and Σ is a balanced Lipschitz submanifold, homeomorphic to the unit simplex in $\mathbb{R}^3_+$ by radial projection.*