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Limit cycles for competitor–competitor–mutualist Lotka–Volterra systems[☆]

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Abstract

It is known that a limit cycle (or periodic coexistence) can occur in a competitor–competitor–mutualist Lotka–Volterra system

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

where r_i, a_{ij} are positive real constants [X. Liang, J. Jiang, The dynamical behavior of type-K competitive Kolmogorov systems and its applications to 3-dimensional type-K competitive Lotka–Volterra systems, Nonlinearity 16 (2003) 785–801]. In this paper, we shall construct an example with at least two limit cycles, and furthermore, we will show that the number of periodic orbits (and hence a fortiori of limit cycles) is finite. It is also shown that, contrary to three-dimensional competitive Lotka–Volterra systems, nontrivial periodic coexistence does occur even if none of the three species can resist invasion from either of the others. In this case, new amenable conditions are given on the coefficients under which the system has no nontrivial periodic orbits. These conditions imply that the positive equilibrium, if it exists, is globally asymptotically stable.

Keywords: Competitor–competitor–mutualist; Lotka–Volterra systems; Limit cycles; Hopf bifurcation

1. Introduction

Consider a community of $n \geq 2$ interacting populations modeled by the Lotka–Volterra system

$$\dot{x}_i = x_i \left(r_i + \sum_{j=1}^{n} a_{ij} x_j \right), \quad i = 1, 2, \ldots, n, \tag{1}$$

where x_i is the density of the ith population, r_i is the intrinsic growth rate of the ith population and the coefficient a_{ij} describes the influence of the jth population upon the ith population (Hofbauer and Sigmund [13]). The signs of a_{ij} and a_{ji} determine the nature of the interaction between the populations i and j: the system (1) can describe all of the three basic types of interactions, viz., competition, collaboration (mutualism) and host–parasite (predator–prey) interactions.

The dynamics of two-dimensional Lotka–Volterra systems is well understood. Bomze [2] gave a complete classification of all possible phase portraits for this case. In particular, there are no limit cycles in two-dimensional Lotka–Volterra systems: if there

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is a periodic orbit, then the equilibrium in Int $\mathbb{R}^2_+$ is a center (that is, it is surrounded by a continuum of periodic orbits). As is well known, this is the case in the classical Lotka–Volterra predator–prey system [13]. It should, however, be noted that the phase portrait does not reveal the whole dynamics. For example, the solution may blow up in finite time (this is clear because the system (1) contains the system $\dot{x}_i = x_i^2$ as a special case).

As one steps from two to higher dimensions the situation becomes far more complicated and difficult as numerical simulations reveal. Many of the well-known phenomena in discrete dynamical systems generated by the quadratic map, such as the period-doubling route to chaos, have also been observed for the continuous system (1) with $n \geq 3$.

For three-dimensional competitive Lotka–Volterra systems, the dynamical possibilities are more restricted: Hirsch [12] has shown that all nontrivial orbits approach a "carrying simplex", a Lipshitz two-dimensional manifold-with-corner, homeomorphic to the standard simplex ($\triangle = \{x : x = (x_1, x_2, x_3), x_1 + x_2 + x_3 = 1$ and $x_i \geq 0$ for all $i\}$) in $\mathbb{R}^3_+ = \{x : x = (x_1, x_2, x_3)$ and $x_i \geq 0$ for all $i\}$. Based on this, Zeeman [30] used geometric analysis of the surfaces $\dot{x}_i = 0$ $(i = 1, 2, 3)$ of a system to define a combinatorial equivalence relation by inequalities on the parameters. A classification of 33 stable equivalence classes for three-dimensional competitive Lotka–Volterra systems was given in [30]. Of these, only classes 26–31 may have limit cycles (see [30]). Hofbauer and So [14], and Xiao and Li [29] have presented examples of three-dimensional competitive Lotka–Volterra systems with at least two limit cycles, and Lu and Luo [19] and Gyllenberg et al. [11] have constructed examples with three limit cycles.

Recently Liang and Jiang [17] have classified the three-dimensional type-K competitive Lotka–Volterra systems, much in the spirit of Zeeman's work [30]. Type-K competitive systems are Lotka–Volterra systems (1) that satisfy a certain monotonicity condition. For instance competitor–competitor–mutualist systems are type-K competitive and in [17] special attention was given to this case. A more detailed study of the existence and number of limit cycles analogous to the ones in [10,11,14,19,29,31] for competitive systems is still missing.

In this paper, we focus on limit cycles for competitor–competitor–mutualist Lotka–Volterra systems. The specific system we consider models two competing populations which both collaborate with a third one. Such systems occur frequently in nature. For instance two plant species competing for the same insectile pollinators or two fungal species competing for the roots of the same tree species to form mycorrhiza form such competitor–competitor–mutualist systems. These systems are also fundamental for understanding the evolution of mutualism by natural selection. A mutant arriving to a mutualistic community will compete with the resident type of its species. The dynamics after the invasion attempt by the mutant is therefore described by a competitor–competitor–mutualist system, with the mutant and resident of the same species being the competitors. A mathematical framework for treating questions of invasion and evolution that explicitly takes the population dynamics into account is *adaptive dynamics* [6–8,20,21].

In the following sections, we shall prove that the number of nontrivial periodic orbits (and hence a fortiori of limit cycles) is finite in competitor–competitor–mutualist Lotka–Volterra systems. We also construct an example of a system of this type with at least two limit cycles by using local Hopf bifurcation and the Poincaré–Bendixson theorem.

It also deserves to be noted that it is under the assumption $M_{12} := a_{11}a_{22} - a_{12}a_{21} < 0$ that Liang and Jiang [17] obtained the existence of a nontrivial limit cycle, generated by Hopf bifurcation, in competitor–competitor–mutualist Lotka–Volterra systems [17, Theorem 5.5]. The biological interpretation of the condition $M_{12} < 0$ is that, in the competitive subcommunity of two species 1 and 2, at least one can resist invasion by the other [13, pp. 56–58]. For the three-dimensional competitive Lotka–Volterra systems, van den Driessche and Zeeman [5] have shown that if none of the species can resist invasion by either of the others, then there is no periodic orbit and therefore limit cycles do not exist and the global dynamics is completed determined. For a competitor–competitor–mutualist system, it is obvious that none of the species can resist invasion by the other in the mutualistic subcommunity of two species with one of the competitors missing. Therefore, it is a very interesting question whether there exist periodic orbits in competitor–competitor–mutualist Lotka–Volterra systems if none of the species can resist invasion by the other in the competitive subcommunity of two competitors. In this paper, we shall answer this question by providing an example of a stable limit cycle. Meanwhile, new amenable conditions are also given on the coefficients r_i, a_{ij}, under which system (1) has no periodic orbits if none of the species can resist invasion from either of the others. When these conditions are satisfied all trajectories converge to equilibria. Based on this, we also present an example of global stability for a positive equilibrium, but the Volterra multipliers method [17, Theorem 5.6] cannot be applied.

The paper is organized as follows. In Section 2 we formulate the model and provide a review of some relevant related results. The main results are presented in Section 3 and full proofs are given in Sections 4 and 5.

2. Background material

The Lotka–Volterra system (1) modeling a competitor–competitor–mutualist interaction as described in the introduction takes the form

$$\begin{cases} \dot{x}_1 = x_1(r_1 - a_{11}x_1 - a_{12}x_2 + a_{13}x_3) = x_1 f_1(x) \equiv F_1(x), \\ \dot{x}_2 = x_2(r_2 - a_{21}x_1 - a_{22}x_2 + a_{23}x_3) = x_2 F_2(x) \equiv F_2(x), \\ \dot{x}_3 = x_3(r_3 + a_{31}x_1 + a_{32}x_2 - a_{33}x_3) = x_3 f_3(x) \equiv F_3(x), \end{cases} \tag{2}$$