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On the complete classification of nullcline stable competitive three-dimensional Gompertz models ☆

Jifa Jiang [a,*], Lei Niu [a,*], Daojun Zhu [b]

[a] *Mathematics and Science College, Shanghai Normal University, Shanghai 200234, People's Republic of China*

[b] *Department of Mathematics, Tongji University, Shanghai 200092, People's Republic of China*

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ABSTRACT

We investigate a competitive model of three species, each of which, in isolation, admits Gompertz growth. A well-known theorem by M.W. Hirsch guarantees the existence of carrying simplex. Based on this, we compare three dimensional competitive Gompertz models with three dimensional competitive Lotka–Volterra models, and we find that each Gompertz model has a corresponding Lotka–Volterra model with identical nullclines. We then present the complete classification of nullcline stable models and arrive at a total of 33 stable nullcline classes, and show that in 27 of these classes all the compact limit sets are equilibria. Despite the common results, we go on to show that the behavior on the carrying simplex of Gompertz systems is subtly different from that on Lotka–Volterra systems. The number of limit cycles is finite in 5 of the remaining 6 classes, and that only the classes 26 and 27 admit Hopf bifurcations and the other 4 do not. The class 27, which has a heteroclinic cycle, contains a system having May–Leonard phenomenon: the existence of nonperiodic oscillation, and still admitting at least two limit cycles. The numerical simulation reveals that there are some systems in class 28 with two limit cycles.

1. Introduction

There is an extensive literature in population ecology on deterministic models of the Kolmogorov form

$$\frac{dx_i}{dt} = x_i f_i(x_1, x_2, \dots, x_n), \quad 1 \le i \le n,\ x_i \ge 0, \tag{1}$$

where x_i represents the population density of the ith species and $f_i(x)$ represents the *per capita* growth rate of the ith species. The system (1) is called *competitive* if $f(x)$ is continuously differentiable and $\frac{\partial f_i}{\partial x_j} \le 0$ on the closed positive cone $\mathbf{R}^n_+$ for $i \ne j$, and *totally competitive* if $\frac{\partial f_i}{\partial x_j} < 0$ on $\mathbf{R}^n_+$ for all i, j. Much of the literature on Kolmogorov systems (1) has focused on competitive systems. Smale [1] showed that any vector field on the standard $(n-1)$-simplex in $\mathbf{R}^n$ can be embedded in a smooth totally competitive system on $\mathbf{R}^n_+$, for which the simplex is an attractor. Hirsch [2] proved that every positive limit set lies in an invariant open $(n-1)$-cell, and that the flow in any limit set of system (1) is conjugate to the flow in some

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* Corresponding authors. Tel.: +86 13916538425.
E-mail addresses: jiangjf@shnu.edu.cn (J. Jiang), 1000342830@smail.shnu.edu.cn, 2012_niulei@tongji.edu.cn (L. Niu).

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invariant set of a Lipschitz vector field in $\mathbf{R}^{n-1}$. Hirsch [3] showed that if system (1) is totally competitive and dissipative on $\mathbf{R}^n_+$ with the origin as a repeller, then every trajectory is asymptotic to one in Σ, where Σ is homeomorphic to the standard $(n-1)$-simplex Δ^{n-1} by radial projection. According to Zeeman [4], the Σ is called *carrying simplex*. This theory is very powerful for a three-dimensional competitive system: Smith [5] proved that the Poincaré–Bendixson Theorem holds for three-dimensional competitive systems, and Hirsch [6] and Smith [7] provided the classification for limit sets of three-dimensional competitive systems in some sense.

In ecology, the most frequently used model is the Lotka–Volterra system, that is, each per capita growth function f_i is affine and chosen as the logistic growth. In this circumstance, system (1) reads as

$$\frac{dx_i}{dt} = x_i\left(r_i - \sum_{j=1}^{n} a_{ij}x_j\right), \quad 1 \le i \le n,\ x_i \ge 0. \tag{2}$$

The system (2) is a totally competitive system if all parameters r_i, a_{ij} are positive. The set CLV(3) of all these three dimensional competitive Lotka–Volterra systems corresponds to parameter space $\mathrm{int}\mathbf{R}^{12}_+$ in a one-to-one way. Based on the theory of the carrying simplex, Zeeman [4] used a geometric analysis of nullclines of a Lotka–Volterra system to define a combinatorial equivalence relation on the space, named *nullcline equivalence*, by simple algebraic inequalities on the parameters. A vector field $F \in$ CLV(3) is said to be *nullcline stable* if its equivalence class is an open set in CLV(3). In [4] only relative position of equilibria in classes 1 through 25 is given, but whether any two LV systems in the same class are topologically equivalent was formulated as Conjecture 2.17. She also proved that Hopf bifurcations occur in each of six stable nullcline classes among the remaining eight classes but not in the other two. Van den Driessche and Zeeman [8] ruled out periodic orbits in the last two classes. This is due to Zeeman's fundamental classification theory, and many researchers have investigated multiplicity of limit cycles, see Hofbauer and So [9], Xiao and Li [10], Lu and Luo [11,12], Gyllenberg and Yan [13], Gyllenberg, Yan and Wang [14]. Classification results for other three-dimensional competitive systems in this spirit were provided by Li and Smith [15] and van den Driessche and Zeeman [16].

Note that, the logistic growth is not suitable for some populations, while a lot of works, such as Burton [17], Laird [18], Simpson-Herren and Lloyd [19], Steel [20] and Sullivan and Salmon [21], showed the suitability of the Gompertz growth law (that is, the per capita growth rate is the logarithm $\ln\frac{K}{x}$ developed by Gompertz [22] which was derived from the actuarial model) to tumor growth. They got the results mainly by curve fitting with actual data. The Gompertz law shows a better data fit than other growth laws such as the logistic model when tumor data involves a wide range of sizes [20]. It seems that no strong biological or physical argument can interpret the reason that the Gompertz model fits actual tumor data primely. Gompertz equation even aided in the design of successful clinical trials [23,24] though the frequent use is empirical and based upon data fitting, and it is often accepted in the study of cancer and the therapy. For survey article we refer to [25]. A lot of research on mobile communications has been carried out with particular emphasis on their diffusion at national as well as at international level during recent years. Note that the Gompertz function reaches the maximum rate of growth at an earlier phase than the logistic, so it is the best chosen to exhibit the dynamics of the diffusion process whose growth is so rapid at an early phase, while slows relatively when approaching the saturation level. It becomes visible that the Gompertz model is appropriate enough for precise fitting and predicting the diffusion of mobile telephony in this case, see [26–30]. When the competition is among several regions or countries, it is reasonable to use multidimensional Gompertz equations. Yu, Wang and Lu [31] proposed the three-dimensional Gompertz model

$$\begin{aligned}
\frac{dx_1}{dt} &= x_1 \ln\frac{b_1}{x_1 + a_{12}x_2 + a_{13}x_3},\\
\frac{dx_2}{dt} &= x_2 \ln\frac{b_2}{a_{21}x_1 + x_2 + a_{23}x_3},\\
\frac{dx_3}{dt} &= x_3 \ln\frac{b_3}{a_{31}x_1 + a_{32}x_2 + x_3},
\end{aligned} \tag{3}$$

and then they analyzed the existence of local stability of all equilibria, ruled out the existence of periodic solutions and obtained global stability for some cases.

This paper will present the complete classification of nullcline stability for competitive three-dimensional Gompertz models by using the idea of Zeeman [4]. We compare three-dimensional competitive Gompertz models with competitive Lotka–Volterra models, and we find that each Gompertz model has a corresponding Lotka–Volterra model with identical nullclines. There are exactly 33 stable equivalence classes of three dimensional Gompertz models, in 27 of which all their trajectories converge to equilibria. All equilibria are hyperbolic except the interior equilibrium in classes 26 and 27. Despite the common results, we go on to show that the behavior on the carrying simplex of Gompertz systems is subtly different from that on Lotka–Volterra systems. We shall prove that in only two classes (classes 26 and 27) Hopf bifurcation can occur. It is shown that the number of limit cycles of system (3) is finite if it has no heteroclinic cycle in $\mathbf{R}^3_+$. In the class admitting a heteroclinic cycle (class 27), we provide the criteria for the interior equilibrium to be globally asymptotically stable and for the system to possess May–Leonard phenomenon: the existence of nonperiodic oscillation, and exhibit the results to bifurcate one or two limit cycles. The numerical stimulation reveals that there are some systems in class 28 with two limit