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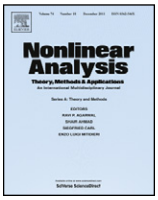

Global qualitative analysis of a non-smooth Gause predator–prey model with a refuge

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ABSTRACT

The present paper aims to provide a detailed qualitative analysis of a non-smooth Gause predator–prey model. In this model, the saturating functional response function with a discontinuity at a critical prey density was employed to show the effects of a prey refuge on the population dynamic behavior. Analysis of this model revealed rich dynamics including locally (or globally) stable canard cycles, a locally (globally) stable pseudo-equilibrium, unbounded trajectories in which both populations go to infinity or the prey goes to infinity and the predator dies out eventually. The main purpose of the present work is to carry out a completely qualitative analysis for this model. In particular, two sets of sufficient conditions drive both populations to approach infinity and the sufficient and necessary conditions for all of the other main results are presented.

1. Introduction

Stimulated by the implications of the Lotka–Volterra equation which was formulated in the mid 1920s, Gause [1] performed the first detailed experiments to look for evidence of population cycles between *Paramecium* (prey) and *Didinium* (predator) in a microcosm experiment [1]. If both species were placed together in a test tube containing clear medium, then *Didinium* over-ate *Paramecium* and exterminated it, and then starved to death itself. If some sediment (refuge for the prey) was added to the medium, then *Didinium* went extinct, but the *Paramecium* population survived. In a third experiment, Gause introduced new individuals of each species at regular intervals; such pulse releasing strategies resulted in two complete cycles of prey and predator. Employing *Paramecium aurelia* as the predator and *Saccharmyces exiguus* as the prey, Gause [2] carried out other experiments and obtained nearly three complete cycles [1,2]. Huffaker [3] performed similar laboratory experiments and expanded on those of Gause by examining how both the factors of migration and spatial heterogeneity lead to predator–prey oscillations [4,3].

The above experiments confirmed that a certain threshold concentration of prey staying within the sediment on the bottom of the arena cannot be destroyed by predators. This is because the prey may avoid the predator via a habitat shift by moving to the refuge at the bottom if their concentration is low, which indicates that the prey individuals were effectively protected in a refuge when at low concentrations [4]. Once the density of prey increased and exceeded the threshold density, they re-appeared in the water column and once again became accessible to predators [5]. Under such circumstances, the prey and predator may coexist and oscillate periodically. In order to take into account the observed experimental results theoretically, Gause et al. [2] extended the classical Lotka–Volterra model by using a piecewise saturating function to replace the linear consumption rate.

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With $x(t)$ and $y(t)$ denoting the density of prey and predator populations, respectively, the following predator–prey model was proposed by Gause et al. [2]

$$\begin{cases} \dfrac{dx(t)}{dt} = rx(t) - \phi(x)y, \\ \dfrac{dy(t)}{dt} = k\phi(x)y - \delta y(t), \end{cases} \tag{1}$$

where r represents the intrinsic growth rate of the prey population in the absence of the predator, k denotes the efficiency rate with which captured prey are converted to new predators, δ is the death rate of the predator, and $\phi(x)$ is the piecewise Gause functional response function which is described as follows: (a) below a critical prey population threshold (denoted by x_c) prey cannot be consumed, i.e. $\phi(x) = 0$ for $x < x_c$, which indicates that below the threshold the density of prey increases and that of the predator decreases; (b) the consumption function $\phi(x)$ has a discontinuity at the threshold at $x = x_c$; (c) the consumption function $\phi(x)$ is a monotonic increasing function with respect to prey density x for $x > x_c$ [2,5].

Therefore, the piecewise Gause functional response function can be defined as follows

$$\phi(x) = \begin{cases} 0, \quad x < x_c, \\ \dfrac{bx}{1+bhx}, \quad x > x_c. \end{cases} \tag{2}$$

Here parameter b describes the search rate of a predator and h is the handling time, i.e. the time between prey being encountered and search being resumed. x_c is the critical prey density below which prey are not accessible to predators. Thus, for above-critical prey density, ϕ is the Holling type II functional response.

If the densities of the prey population are less than the threshold ($x < x_c$), then the prey cannot be consumed by predators and their population grows exponentially, while that of the predator decreases exponentially. Thus the model (1) becomes

$$\begin{cases} \dfrac{dx(t)}{dt} = rx(t), \\ \dfrac{dy(t)}{dt} = -\delta y(t), \end{cases} \quad x < x_c. \tag{3}$$

If the densities of the prey population are larger than the threshold ($x > x_c$), then the population dynamics are given by the Lotka–Volterra model with the Holling type II functional response, i.e. we have

$$\begin{cases} \dfrac{dx(t)}{dt} = rx(t) - \dfrac{bx(t)y(t)}{1+bhx(t)}, \\ \dfrac{dy(t)}{dt} = \dfrac{kbx(t)y(t)}{1+bhx(t)} - \delta y(t), \end{cases} \quad x > x_c. \tag{4}$$

Denote $H(Z) = x - x_c$ with $Z = (x, y)^T \in R_+^2$ and let

$$\epsilon = \begin{cases} 0, \quad H(Z) = x - x_c < 0, \\ 1, \quad H(Z) = x - x_c > 0. \end{cases} \tag{5}$$

Then the models (3) and (4) can be rewritten as the following non-smooth dynamic system or Filippov system [6,7]

$$\begin{cases} \dfrac{dx(t)}{dt} = rx(t) - \dfrac{\epsilon bx(t)y(t)}{1+bhx(t)}, \\ \dfrac{dy(t)}{dt} = \dfrac{\epsilon kbx(t)y(t)}{1+bhx(t)} - \delta y(t). \end{cases} \tag{6}$$

This model has been investigated by Gause et al. [2] and they pointed out that the model (6) exists a limit cycle. However, by employing both numerical and qualitative methods Křivan [5] showed that model (6) could present six different qualitative dynamics including:

- all trajectories converge to a stable canard cycle (defined later);
- all trajectories tend to a pseudo-equilibrium (defined later);
- some trajectories tend to a locally stable canard cycle and the others tend to infinity, i.e. (∞, ∞);
- some trajectories tend to a locally stable pseudo-equilibrium and the others tend to infinity, i.e. (∞, ∞);
- all trajectories approach $(\infty, 0)$;
- all trajectories tend to infinity, i.e. (∞, ∞).

For further details, see Fig. 2 in Ref. [5]. Recently, Non-smooth dynamic systems or Filippov systems have been widely used in many fields of science and engineering [8–17]. In particular, all codimension one sliding bifurcations in generic planar Filippov systems (or nonsmooth systems) have been extensively discussed by Kuznetsov et al. [15], Bernardo et al. [8,18] and Buzzi et al. [19,20].

The main purpose of the present work is to provide rigorous proofs of the above six results for the non-smooth Gause model (6). Furthermore, the sufficient and necessary conditions for the first five results are provided and two groups of sufficient conditions for the last result are also given.