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Journal of Nonlinear Sciences and Applications (JNSA)

Print: ISSN 2008-1898 Online: ISSN 2008-1901

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Profile for

Journal of Nonlinear Sciences and Applications. JNSA

Journal Details

Title	Journal of Nonlinear Sciences and Applications. JNSA
Abbreviation	J. Nonlinear Sci. Appl.
Publisher	Int. Sci. Res. Publ.
Websites	isr-publications.com
ISSN (Print)	2008-1898
ISSN (Online)	2008-1901
Frequency	6 issues/vol./yr.
Publications Listed	1 738

Recent Issues

[2023, vol. 16, no. 4](#)
[2023, vol. 16, no. 3](#)
[2023, vol. 16, no. 2](#)

[List All Issues](#)

Journal Title History

Title	Start	End
J. Nonlinear Sci. Appl.	2008	—

[View Details](#)

Reference Lists	N/A
Latest Issue	2023, vol. 16, no. 4
Earliest Issue	2008, vol. 1, no. 1
Note	Published by the Journal of Nonlinear Sciences and Applications through 2016.
Publications Cited	866 (49,8% of publications)
Citations	2 872 from 2 122 publications

Mathematical Citation Quotient

Graph 

Table 

All MCQ Table 

Description 

MCQ

0.35
0.3

■ Journal MCQ
 ■ All Journal Median MCQ



MR4577529

Summary

 [Article](#)  [Cite](#)  [Review PDF](#)

Degla, Guy A. (BN-UAC-IMP); Degbo, Seyive J. (BN-UAC-IMP); Dossou-Yovo, Marie-Louise (BN-UAC-IMP)

Auto-oscillation of a generalized Gause type model with a convex constraint. (English summary) [Corrected title: Auto-oscillation of a generalized Gause type model with a convex constraint]

J. Nonlinear Sci. Appl. **16** (2023), no. 1, 60–78.

Classifications

92D25 - Population dynamics (general)

37G15 - Bifurcations of limit cycles and periodic orbits in dynamical systems

37N25 - Dynamical systems in biology

92D40 - Ecology

Citations

From References: 0

From Reviews: 0

Summary

"In this paper, we study the generalized Gause model in which the functional and numerical responses of the predators need not be monotonic functions and the intrinsic mortality rate of the predators is a variable function. As a result, we have established sufficient conditions for the existence, uniqueness and global stability of limit cycles confined in a closed convex nonempty set, by relying on a recent Lobanova and Sadovskii theorem. Moreover, we prove sufficient conditions for the existence of Hopf bifurcation. Eventually using scilab, we



Auto-oscillation of a generalized Gause type model with a convex constraint



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Abstract

In this paper, we study the generalized Gause model in which the functional and numerical responses of the predators need not be monotonic functions and the intrinsic mortality rate of the predators is a variable function. As a result, we have established sufficient conditions for the existence, uniqueness and global stability of limit cycles confined in a closed convex nonempty set, by relying on a recent Lobanov and Sadvovskii theorem. Moreover, we prove sufficient conditions for the existence of Hopf bifurcation. Eventually using scilab, we illustrate the validity of the results with numerical simulations.

Keywords: Generalized Gause model, nonmonotonic numerical responses, nonconstant death rate, convex constraint, global stability, limit cycle, Hopf bifurcation, first Lyapunov number.

2020 MSC: 92F05, 92B05, 37N25, 37G15.

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1. Introduction

In recent years, there has been a renewed interest in the development and analysis of models of interacting species in ecosystems. A well-studied category of these models is the interaction between two species, so-called predator-prey models, which have been of crucial importance for the analysis of the dynamics of complex ecological systems such as food chains, since their introduction by Lotka-Volterra. One of the models in this category that has been progressively revised is the Gause-type predator-prey model whose variants focus on the functional and numerical responses of the predator to describe the effects of environmental changes, including those reflected in prey density and on population dynamics. Indeed, as prey density increases, the predator's functional and numerical responses may change in a variety of ways such as linearly, decelerating, sigmoidally, or initially increasing to a maximum rate and then decreasing and saturating to a minimum rate (group defense). Understanding how predators respond to varying ecological conditions is essential for predicting the consequences of predator-prey interactions on the ecosystem. The objects allowing to make such prediction are the periodic solutions, in particular the limit cycles whose existence, uniqueness and stability remain very open problems now even in dimension two (see [12]).

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doi: [10.22436/jnsa.016.01.06](https://doi.org/10.22436/jnsa.016.01.06)

Received: 2022-11-06 Revised: 2023-03-12 Accepted: 2023-03-22

In a Gause type predation model where the functional and numerical responses of the predators are regular and monotonic functions and where the mortality rate of the predators in the absence of the prey is constant, the existence of a limit cycle has been studied by several authors such as Freedman [10], using the Poincaré-Bendixson theorem. The uniqueness and stability conditions have also been studied by several authors such as Liou and Cheng [18], Hasik [13], Cheng [5], Kuang and Freedman [16], Huang and Merrill [15], Hwang [14] by the method of isocline symmetry of prey or by the Lienard transformation.

Moreover, the stability of such a limit cycle when it exists can be studied according to the sign of the Liapunov coefficient which is sometimes very difficult to calculate (see [19, 21]).

The main objective of this paper is first to establish sufficient conditions for the existence, uniqueness, and global stability of the limit cycle confined in a nonempty, closed, convex set for a generalized Gause model in which the functional and numerical responses of the predators need not be monotonic functions and the intrinsic mortality rate of the predators is a variable function. Moreover, we establish a sufficient condition for the existence of Hopf bifurcation for the same model. Finally, we illustrate the validity of the results with numerical simulations.

This paper is organized as follows. Section 1 is devoted to the introduction. In section 2, we present the mathematical model that we have studied. In section 3, we prove a theorem on the existence, uniqueness and global stability of limit cycle for our mathematical model. In section 4, we apply our theorem to some particular models and illustrate it with numerical simulations. We give the conditions for the existence of Hopf bifurcation in section 5. Finally, in section 6 we have concluded.

2. Mathematical model

The first generalization of the prey-predator or Lotka-Volterra model is due to the zoologist G.F. Gause. The general model proposed by Gause is the following

$$(S_0) \begin{cases} \dot{x} = rx - yg(x), \\ \dot{y} = -\delta y + yp(x), \end{cases} \quad (2.1)$$

where $x(t) := x$ and $y(t) := y$ denote respectively the densities of prey and predators at time t and the functions g and p stand as follows:

- g is the functional response of the predator population, i.e. $g(x)$ is the number of prey consumed per unit of time by a predator, it is differentiable on \mathbb{R}_+ and verifies

$$g(0) = 0 \text{ and for all } x \geq 0, \frac{dg(x)}{dx} > 0.$$

- $p(x)$ is the rate of conversion of prey to predators. The function p is differentiable on \mathbb{R}_+ and verifies:

$$p(0) = 0, \text{ and for all } x > 0, p(x) > 0, \text{ and } \frac{dp(x)}{dx} > 0.$$

- δ is the death rate of the predator in the absence of prey.
- $r > 0$ is the intrinsic growth rate of prey in the absence of predator.

Note that to make Gause's model more realistic, Malthus' prey growth function defined by $m(x) = rx$ is replaced by Verhulst's logistic growth function defined by $V(x) = xf(x)$. In order to make Gause's model ever more realistic, the entomologist C.S. Holling after several experiments, imposes other conditions on the functions g and p . Indeed, with the following hypotheses,

- $f(x)$ is the growth rate of the prey population in the absence of predators, it is differentiable for all $x \geq 0$ and verifies $f(0) > 0$ and if the environment has a limit capacity, there exists $k > 0$ such that

$$f(k) = 0 \quad \text{and} \quad (x - k)f(x) < 0 \quad \text{for} \quad x \neq k.$$

- g is the functional response of the predator population, i.e. $g(x)$ is the number of prey consumed per unit of time by a predator, it is differentiable on \mathbb{R}_+ and there exists $l_0 \in \mathbb{R}_+^*$ such that ,

$$\lim_{x \rightarrow +\infty} g(x) \leq l_0, \quad g(0) = 0 \quad \text{and} \quad \text{for all } x \geq 0, \quad \frac{dg(x)}{dx} > 0.$$

- p is the conversion rate function of the prey population to predators, it is differentiable on \mathbb{R}_+ and there exists a positive real l_1 such that,

$$\lim_{x \rightarrow +\infty} p(x) \leq l_1, \quad p(0) = 0 \quad \text{and} \quad \text{for all } x \geq 0, \quad \frac{dp(x)}{dx} > 0.$$

We obtain the system:

$$(S_0) \begin{cases} \dot{x} = xf(x) - yg(x), \\ \dot{y} = -\delta y + yp(x). \end{cases} \quad (2.2)$$

Recent researches have shown that when certain species (prey) are in large numbers, they develop a collective defense behavior towards predators, which considerably impacts the dynamics of predators. Indeed, faced with this defensive character of the prey, the functional response g and the numerical response p of the predator become nonmonotonic functions [1, 3, 9, 20, 21, 23]. In the same way, some experiments and observations have shown that in the absence of prey, the mortality rate of predators is not always constant [4, 6–8, 22, 24]. Therefore, in this paper, we propose the following general Gause model

$$(S_1) \begin{cases} \dot{x} = xf(x) - byg(x), \\ \dot{y} = y(cp(x) - h(y)), \end{cases} \quad (2.3)$$

where the function g , h and p are defined as follows:

- g is the functional response of the predator which is positive, continuous, differentiable on \mathbb{R}_+ and there exists a positive real number l_0 such that

$$g(0) = 0 \quad \text{and} \quad \lim_{x \rightarrow +\infty} g(x) \leq l_0.$$

- p is the conversion rate function of the prey population to predators which is positive, continuous, differentiable on \mathbb{R}_+ and there exists a positive real number l_1 such that

$$p(0) = 0 \quad \text{and} \quad \lim_{x \rightarrow +\infty} p(x) \leq l_1.$$

- h is the death rate function of the predator in the absence of preys, it is positive, continuous, differentiable on \mathbb{R}_+ and such that there exist two positive constant real numbers k_1 and k_2 such that

$$k_1 \leq k_2, \quad h(0) = k_1, \quad \text{for all } y \geq 0, \quad \frac{dh(y)}{dy} \geq 0, \quad \text{and} \quad \lim_{y \rightarrow +\infty} h(y) = k_2. \quad (2.4)$$

3. Auto-Oscillation of (2.3)

In this section, we prove a theorem for auto-oscillations of (2.3) using Lobanov-Sadovskii theorem [17] on a nonempty closed and convex set K of \mathbb{R}^2 . Indeed, for any positive input $X_0 = (x_0, y_0) \in (0, +\infty)^2$, we obtain for the system (2.3) a positive output of $\dot{X} = F(X)$. We assume that the system (2.3) admits a positive equilibrium point $U^* = (x_* ; y_*)$ inside \mathbb{R}_+^2 defined by

$$y_* = \frac{x_* f(x_*)}{bg(x_*)} > 0 \text{ and } cp(x_*) = h(y_*). \tag{3.1}$$

In the sequel, we set

$$\alpha_2 = \alpha_2(x_*) = f(x_*) + x_* f'(x_*) - \frac{x_* f(x_*) g'(x_*)}{g(x_*)}, \tag{3.2}$$

$$\alpha_3 = \alpha_3(x_*) = bg(x_*), \tag{3.3}$$

$$\beta_2 = \beta_2(y_*) = -y_* h'(y_*), \tag{3.4}$$

$$\beta_3 = \beta_3(U^*) = cy_* p'(x_*), \tag{3.5}$$

$$\tag{3.6}$$

and make the following change of coordinates. Let $Z \in \mathbb{R}^2$ such that $Z + U^* \in \mathbb{R}_+^2$, then $Z \in \mathbb{R}_+^2 - U^*$. Let

$$K = [-\delta, +\infty)^2, \text{ where } \delta := \frac{\min\{x_*, y_*\}}{q}, \text{ } q \geq 2$$

First of all, we translate the interior equilibrium $U^* = (x_* ; y_*)$ to the origin and linearize the system (2.3) around the origin. Let $Z = (z_1, z_2) \in K$, then there exists $X = (x ; y) \in \mathbb{R}_+^2$ such that

$$z_1 = x - x_* \text{ and } z_2 = y - y_*.$$

Hence, the system (2.3) can be rewritten as

$$\begin{cases} \dot{z}_1 = \alpha_2 z_1 - \alpha_3 z_2 + o(\|(z_1, z_2)\|), \\ \dot{z}_2 = \beta_3 z_1 + \beta_2 z_2 + o(\|(z_1, z_2)\|). \end{cases} \tag{3.7}$$

Now, we consider the following system

$$\dot{Z} = \tau_Z L(Z), \tag{3.8}$$

where $L = (L_1, L_2)$ is the vector field denoted by

$$L_1(Z) = \alpha_2 z_1 - \alpha_3 z_2 \text{ and } L_2(Z) = \beta_3 z_1 + \beta_2 z_2$$

and τ_Z is the metric projection on the tangent cone T_Z to K at the point Z , confer [2, 17]. Let

$$d_0 = \max \left\{ \frac{-2\gamma\alpha_2\beta_3}{\alpha_3(\alpha_2 + \beta_2 + 2\beta_3)} ; -\gamma\sqrt{\frac{\beta_3}{\alpha_3}} \right\}, \text{ } d_1 = \frac{-2\gamma\beta_2}{\alpha_2 + \beta_2 - 2\alpha_3},$$

$$Q_1(x_*, y_*) = \alpha_3(\beta_2 + \beta_3) + \beta_3(\alpha_3 - \alpha_2), \text{ } Q_2(x_*, y_*) = \beta_3(\alpha_2 + \beta_2 - 2\alpha_3)^2 - 4\alpha_3\beta_2^2.$$

Theorem 3.1. *If there are some real numbers a, b, c, d and γ such that the system (2.3) admits a positive equilibrium point X_* , and there holds:*

$$\beta_3 > 0 \text{ and } 2 \min \{ \beta_3 ; \alpha_3 \} > \alpha_2 - \beta_2, \tag{3.9}$$

$$\alpha_2 > 0, 0 < \alpha_2 + \beta_2 < 2\alpha_3, Q_1(x_*, y_*) > 0, Q_2(x_*, y_*) > 0, \text{ and } d_0 < d < d_1, \tag{3.10}$$

and

$$\forall Z \in \partial K, \exists u \in T_Z, \langle u, f(Z) \rangle > 0, \tag{3.11}$$

then the system (2.3) admits a unique closed trajectory Γ of which orbit is a globally stable limit cycle in $K + X_*$.

Proof. We check that $O \in \overset{\circ}{K}$; K is a closed and convex set. Moreover, L is locally Lipschitz on K because its components L_1 and L_2 are polynomial functions.

Now let us find $r_0 > 0$ such that for all $Z \in K, \langle JZ, L(Z) \rangle \geq r_0 \|Z\|^2$; where J is a map from \mathbb{R}^2 to \mathbb{R}^2 defined by

$$J(z_1; z_2) = (-z_2; z_1).$$

Let $Z \in K$, we have

$$\langle JZ, L(Z) \rangle = \beta_3 z_1^2 + \alpha_3 z_2^2 + (\beta_2 - \alpha_2) z_1 z_2.$$

Moreover, we have

$$|z_1 z_2| \leq \frac{1}{2} (z_1^2 + z_2^2). \tag{3.12}$$

Then

$$\begin{aligned} \langle JZ, L(Z) \rangle &\geq \left(\beta_3 - \frac{\alpha_2 - \beta_2}{2} \right) z_1^2 + \left(\alpha_3 - \frac{\alpha_2 - \beta_2}{2} \right) z_2^2 \\ &\geq \frac{1}{2} \left(2\beta_3 - (\alpha_2 - \beta_2) \right) z_1^2 + \frac{1}{2} \left(2\alpha_3 - (\alpha_2 - \beta_2) \right) z_2^2. \end{aligned}$$

From (3.9), we have

$$2\beta_3 - (\alpha_2 - \beta_2) > 0 \text{ and } 2\alpha_3 - (\alpha_2 - \beta_2) > 0.$$

Hence, we obtain

$$|\langle JZ, L(Z) \rangle| \geq \frac{1}{2} \min \left\{ 2\beta_3 - (\alpha_2 - \beta_2), 2\alpha_3 - (\alpha_2 - \beta_2) \right\} \|Z\|^2.$$

Then there exists $r_0 = \frac{1}{2} \min \left\{ 2\beta_3 - (\alpha_2 - \beta_2), 2\alpha_3 - (\alpha_2 - \beta_2) \right\} > 0$, such that for all $Z \in K$,

$$|\langle JZ, L(Z) \rangle| \geq r_0 \|Z\|^2.$$

Next we prove that there exists a real positive definite matrix B and an application

$$\mu : (0, +\infty) \rightarrow (0, +\infty) \text{ such that for all } Z \in K, \langle BZ, f(Z) \rangle \geq \mu(\|Z\|).$$

Let $(a, \gamma, d) \in (0; +\infty)^2 \times (-\infty, 0)$, $a = \frac{\gamma\beta_3}{\alpha_3}$, and $B = \begin{pmatrix} a & d \\ d & \gamma \end{pmatrix}$. From (3.10), we have $a\gamma > d^2$, then B is a symmetric positive definite matrix. Let $Z \in K$, we have

$$\langle BZ, L(Z) \rangle = (a\alpha_2 + d\beta_3)z_1^2 + (\gamma\beta_2 - d\alpha_3)z_2^2 + d(\alpha_2 + \beta_2)z_1 z_2.$$

According to (3.12), we have

$$\begin{aligned} \langle BZ, L(Z) \rangle &\geq \left(a\alpha_2 + d\beta_3 - \frac{|d|}{2}(\alpha_2 + \beta_2) \right) z_1^2 + \left(\gamma\beta_2 - d\alpha_3 - \frac{|d|}{2}(\alpha_2 + \beta_2) \right) z_2^2 \\ &\geq \left(a\alpha_2 + \frac{d}{2}(2\beta_3 + \alpha_2 + \beta_2) \right) z_1^2 + \left(\gamma\beta_2 + \frac{d}{2}(\alpha_2 + \beta_2 - 2\alpha_3) \right) z_2^2 \end{aligned}$$

$$\langle \text{BZ}, L(Z) \rangle \geq \min \left\{ \alpha \alpha_2 + \frac{d}{2}(2\beta_3 + \alpha_2 + \beta_2), \gamma \beta_2 + \frac{d}{2}(\alpha_2 + \beta_2 - 2\alpha_3) \right\} \|Z\|^2.$$

From (3.10), we have $\alpha \alpha_2 + \frac{d}{2}(2\beta_3 + \alpha_2 + \beta_2) > 0$ and $\gamma \beta_2 + \frac{d}{2}(\alpha_2 + \beta_2 - 2\alpha_3) > 0$. Hence, we can take $\mu_0 = \min \left\{ \alpha \alpha_2 + \frac{d}{2}(2\beta_3 + \alpha_2 + \beta_2), \gamma \beta_2 + \frac{d}{2}(\alpha_2 + \beta_2 - 2\alpha_3) \right\} > 0$ and $\mu(r) = \mu_0 r^2$, for all $r > 0$.

Therefore, for all $Z \in K$, $\langle \text{BZ}, L(Z) \rangle \geq \mu(\|Z\|)$.

Now, we prove that for all $Z \in K \setminus \{O_{\mathbb{R}^2}\}$, $L(Z) \notin N_Z$; where N_Z is the normal cone to K at Z .

Case1:

If $Z \in \overset{\circ}{K}$, then $N_Z = \{O\}$. Thus, $L(Z) \in N_Z$ if and only if $L(Z) = O$. Moreover, there exists $r_0 > 0$ such that for all $Z \in K$,

$$\langle \text{JZ}, L(Z) \rangle \geq r_0 \|Z\|^2.$$

So, $L(Z) \in N_Z$ implies $Z = O$. Thus, for all $Z \in \overset{\circ}{K}$, $Z \neq O_{\mathbb{R}^2}$, and $L(Z) \notin N_Z$.

Case 2:

If $Z \in \partial K$, according to the hypothesis (3.11), there exists $u \in T_Z$, such that $\langle u, L(Z) \rangle > 0$. Thus, for all $Z \in \partial K$, $L(Z) \in T_Z$. So, for all $Z \in \partial K$, $L(Z) \notin N_Z$. Thus, for all $Z \in K \setminus \{O_{\mathbb{R}^2}\}$, $L(Z) \notin N_Z$.

Hence, according to the Lobanova-Sadovskii theorem [17], the conclusion of theorem 3.1 follows. This is the end of the proof. \square

4. Applications and simulations

4.1. Application 1

As an application of Theorem 3.1, we consider

$$f(x) = r - \lambda x, \quad g(x) = \frac{x}{1+x^2}, \quad h(y) = \delta \quad \text{and} \quad p(x) = x.$$

Then we obtain the system

$$\begin{cases} \dot{x} = x(r - \lambda x) - \frac{byx}{1+x^2}, \\ \dot{y} = -\delta y + cyx, \end{cases} \quad (4.1)$$

where

$x(t) := x$ and $y(t) := y$ denote respectively the densities of prey and predators at time t .

$r > 0$ is the intrinsic growth rate of prey in the absence of predators.

$\lambda = \frac{1}{k} > 0$ with k as the carrying capacity of preys.

$b > 0$ represents the conversion efficiency of predator by consuming prey.

$c > 0$ represents the biomass conversion rate, and

$\delta > 0$ represents the mortality rate at the low density and the maximal mortality, respectively, $\delta < \beta \delta_0$.

Let

$$\begin{aligned} \lambda_0^* &= \frac{2rx_*}{1+3x_*^2}; \quad \lambda_0 = \min \left\{ \frac{r}{x_*}; \lambda_0^* \right\}, \quad b_0 = \frac{2rx_*^2}{b(1+x_*^2)}, \quad b_1 = \frac{(1+x_*^2)^2 c}{x_*^2}, \quad b_2 = \frac{x_*(1+3x_*^2)}{b(1+x_*^2)}, \\ b_3 &= \frac{2c(1+x_*^2)^2}{(1+3x_*^2)}, \quad b_4 = \frac{1}{2}(2rx_* - \lambda(1+3x_*^2)), \quad \lambda_1 = \frac{2(1+x_*^2)}{1+3x_*^2} \sqrt{\frac{c(r-x_*)}{x_*}}, \quad b_5 = \frac{b_3(r-x_*)}{x_*(\lambda_0^* - \lambda)}, \end{aligned}$$

Theorem 4.1. *If the system (4.1) admits a positive equilibrium point $X_* = (x_*, y_*)$ such that*

$$x_* < r, \lambda_0^* - \lambda_1 < \lambda < \lambda_0, b_4 < b < b_5, \quad (4.2)$$

and

$$\forall Z \in \partial K, \exists u \in T_Z, \langle u, L(Z) \rangle > 0, \quad (4.3)$$

then the system (4.1) admits a unique closed trajectory Γ of which orbit is a globally stable limit cycle in $K + \{X_*\}$.

Proof. The system (4.1) admits a unique positive equilibrium point $X_* = (x_*, y_*)$, where

$$x_* = \frac{\delta}{c} \text{ and } y_* = \frac{x_*(r - \lambda x_*)}{bg(x_*)}, \text{ with } \lambda < \frac{r}{x_*}.$$

Moreover, we have

$$\alpha_2 = \frac{2rx_*^2 - \lambda x_*(1 + 3x_*^2)}{1 + x_*^2}, \alpha_3 = \frac{bx_*}{1 + x_*^2}, \beta_2 = 0, \text{ and } \beta_3 = \frac{c(r - \lambda x_*)(1 + x_*^2)}{b}.$$

According to (4.2), we have $\alpha_2 > 0, 0 < \alpha_2 + \beta_2 < 2\alpha_3, \beta_3 > 0, 2\beta_3 - \alpha_2 > 0,$

$Q_1(x_*, y_*) = \beta_3(2\alpha_3 - \alpha_2) > 0, Q_2(x_*, y_*) = \beta_3(2\alpha_3 - \alpha_2)^2 > 0.$ That is the end of the proof. \square

4.1.1. Simulation

If $r = 7, \delta = 5, c = 3,$ then we have $x_* = \frac{5}{3}, b_4 \approx 1.866, b_5 \approx 12.3, \lambda_0 = 2.5.$ So, we can take $0 \leq \lambda = 2.1 \leq \lambda_2$ and $b_4 < b = 2 < b_5.$ We obtain $K := [-0.83, +\infty)^2.$

Let $Z \in \partial K,$ then we distinguish two cases.

Case1: Z is a corner point. In this case, the tangent cone at Z is the angular domain. For example if $Z = (-0.83, -0.83),$ then $T_Z = K$ and $N_Z = \{(z_1, z_2) \in \mathbb{R}^2, z_1 \leq -0.83 \text{ and } z_2 \leq -0.83\}.$ Moreover, we have

$$u = (1, -0.5) \in T_Z \text{ and } \langle u, L(Z) \rangle = 0.83(\alpha_3 - \alpha_2 + 0.5\beta_3) > 0.$$

Case2: Z is not a corner point. In this case the tangent cone at Z is the half-plane. For example if $Z = (0, -0.83),$ then

$$T_Z = \{(z_1, z_2) \in \mathbb{R}^2, z_1 \geq -0.83\} \text{ and } N_Z = \{(z_1, z_2) \in \mathbb{R}^2, z_1 \leq -0.83 \text{ and } z_2 = 0\}.$$

Moreover, we have

$$u = (1, -0.5) \in T_Z \text{ and } \langle u, L(Z) \rangle > 0.$$

Then, for all $Z \in \partial K,$ there exists $u \in T_Z$ such that $\langle u, L(Z) \rangle > 0.$ So, for these parameter values, the system (4.1) admits a unique closed trajectory of which orbit is stable. Let $(x(0), y(0))$ be the initial condition. We obtain the following simulation. On the Figure 2, the red and blue curves represent the evolution of prey and predators respectively.

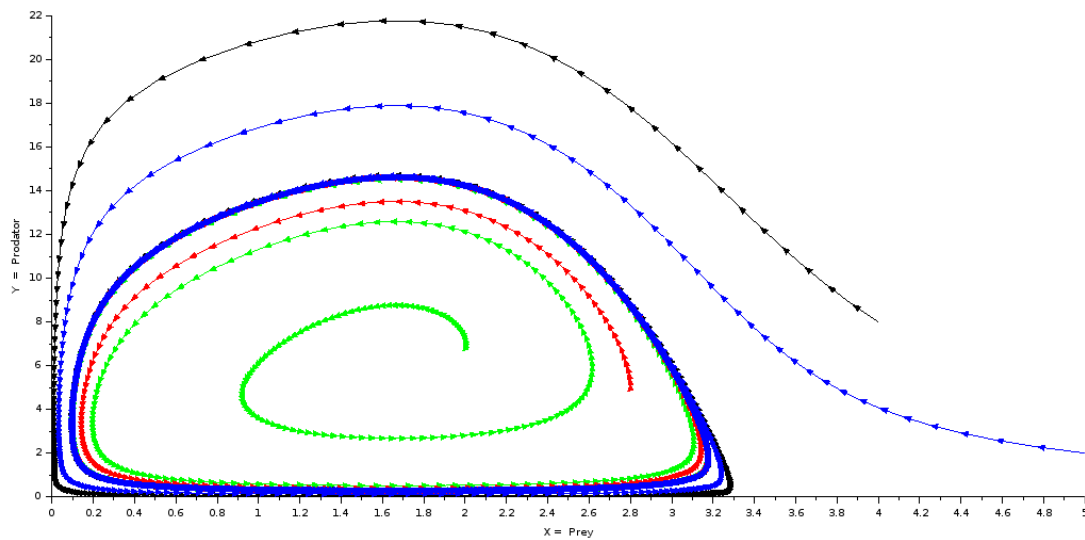


Figure 1: Phase portrait of the differential system (4.1) for $(x(0), y(0)) \in \{(4, 8), (2, 7), (2.8, 5), (5, 2)\}$.

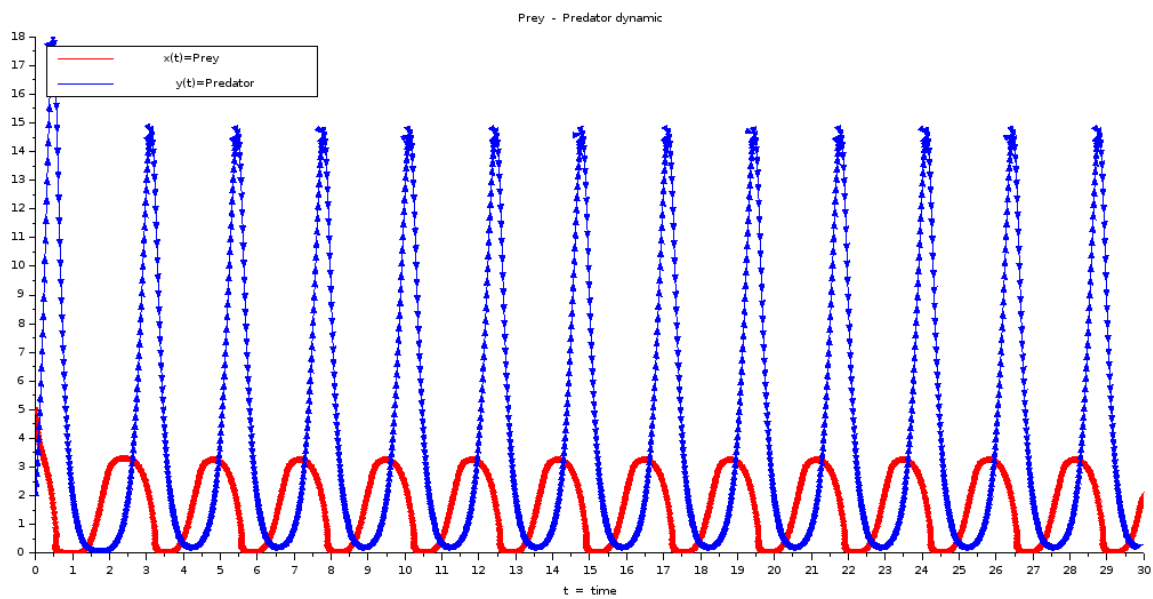


Figure 2: Chronic of the differential system (4.1) for $(x(0), y(0)) = (5, 2)$.

4.2. Application 2

As an application of the Theorem 3.1, we consider

$$f(x) = r - \lambda x, \quad p(x) = g(x) = \frac{x^n}{\alpha + x^m}, \quad \text{and} \quad h(y) = \frac{\delta + \beta \delta_0 y}{1 + \beta y}.$$

Then we obtain the system

$$\begin{cases} \dot{x} = x(r - \lambda x) - \frac{b y x^n}{\alpha + x^m}, \\ \dot{y} = y \left(-\frac{\delta + \beta \delta_0 y}{1 + \beta y} + \frac{c x^n}{\alpha + x^m} \right), \end{cases} \tag{4.4}$$

where

$x(t) := x$ and $y(t) := y$ denote respectively the densities of prey and predators at time t .

$r > 0$ is the intrinsic growth rate of preys in the absence of predators.

$\lambda = \frac{1}{k} > 0$ with k as the carrying capacity of preys.

$b > 0$ represents the conversion efficiency of predator by consuming prey.

$c > 0$ represents the biomass conversion rate.

$\delta > 0$ and $\delta_0 > 0$ represent the mortality rate at the low density and the maximal mortality, respectively, $\delta < \beta\delta_0$ and with $\beta > 0$ is a suitable real parameter.

n and m are positive real numbers such that $n \leq m$.

Let

$$x_0 = \sqrt[m]{\frac{n\alpha}{m-n}} \text{ and } x_0^* = \min\left\{\frac{r}{\lambda}, x_0\right\}, \text{ with } n < m.$$

Lemma 4.2 (Existence of positive equilibrium point).

1. If $\delta < cp\left(\frac{r}{\lambda}\right)$, then the system (4.4) admits a positive equilibrium point $X_* = (x_*, y_*)$ inside $(0, \frac{r}{\lambda}) \times (0, +\infty)$.
2. If

$$\delta < \min\left\{cp(x_0)(1 + \beta u(x_0)), cp\left(\frac{r}{\lambda}\right)\right\}, \text{ and } \beta\delta_0 < \frac{cp(x_0)(1 + \beta u(x_0)) - \delta}{u(x_0)},$$

then the system (4.4) admits a positive equilibrium point $X_* = (x_*, y_*)$ inside $(0, x_0^*) \times (0, +\infty)$.

Proof. Let

$$u(x) = \frac{x(r - \lambda x)}{bg(x)} \text{ and } H(x) = h(u(x)) - cp(x).$$

Let's solve the equation $H(x) = 0$ in $(0, \frac{r}{\lambda}) \cap (0, x_0)$. We have

$$\lim_{x \rightarrow 0^+} H(x) = \begin{cases} \delta_0, & \text{if } n > 1, \\ h\left(\frac{\alpha r}{b}\right), & \text{if } n = 1, \end{cases}$$

$$H\left(\frac{r}{\lambda}\right) = \delta - cp\left(\frac{r}{\lambda}\right), \text{ and } H(x_0) = h(u(x_0)) - cp(x_0),$$

and moreover, the function H is continuous on $(0, \frac{r}{\lambda})$. Thus according to the intermediate value theorem, the equation $H(x) = 0$ admits at least one root in $(0, \frac{r}{\lambda})$ if $H\left(\frac{r}{\lambda}\right) < 0$. We have,

$$H\left(\frac{r}{\lambda}\right) < 0 \iff \delta < cp\left(\frac{r}{\lambda}\right). \quad (4.5)$$

The function H is continuous on $(0, x_0)$, so according to the intermediate value theorem the equation $H(x) = 0$ admits at least one root in $(0, x_0)$ if $H(x_0) < 0$. Moreover,

$$H(x_0) < 0 \iff \delta < cp(x_0)(1 + \beta u(x_0)), \text{ and } \beta\delta_0 < \frac{cp(x_0)(1 + \beta u(x_0)) - \delta}{u(x_0)}. \quad (4.6)$$

This is the end of the proof. □

Let

$$\begin{aligned}
 A(x) &= \frac{(m-n)(x_0^m - x^m)}{\alpha + x^m}, \quad Q_3(x) = M(x) - \frac{2c(r-\lambda x)A(x)}{b}, \quad v(x) = r(1-A(x)) - \lambda x(2-A(x)), \\
 M(x) &= v(x) - u(x)h'(u(x)), \quad R(x) = \left(\frac{cg(x)A(x)}{x} - h'(u(x))\right)u(x) - v(x), \quad B(x) = \frac{v(x)(1+\beta u(x))^2}{u(x)}, \\
 Q(x) &= bg(x) - v(x) - u(x)h'(u(x)), \quad Q_1(x) = u(x)\left(2bcg(x)p'(x) - bg(x)h'(u(x)) - cp'(x)v(x)\right), \\
 Q_2(x) &= cu(x)p'(x)\left(v(x) - u(x)h'(u(x)) - 2bg(x)\right)^2 - 4bg(x)u(x)^2h'(u(x))^2, \quad \delta_1(x) = cp(x)(1+\beta u(x)), \\
 T_0(x) &= \frac{(2\lambda x - r)(1+\beta u(x))^2}{u(x)}, \quad T_1(x) = \frac{g(x)(1+\beta u(x))^2(c(r-\lambda x)A(x) - bv(x))}{x(r-\lambda x)}, \\
 \Delta(x) &= \frac{bg(x)(1+\beta u(x))^2}{u(x)}, \quad \Delta_1(x) = \frac{(bg(x) - v(x))(1+\beta u(x))^2}{u(x)}, \quad \delta_2 = \frac{\delta_1(\bar{x}) - \delta}{u(\bar{x})}, \quad \delta_3 = \frac{\delta_1(x_0) - \delta}{u(x_0)}, \\
 \delta_4 &= u(x_0)\delta_1(\bar{x}) - u(\bar{x})\delta_1(x_0), \quad \delta_5 = u(x_0) - u(\bar{x}), \quad \delta_7 = \frac{\delta_1(\bar{x}) - \delta_6(x_0, \bar{x})u(\bar{x})}{1+u(\bar{x})}, \\
 \delta_6(x_0, \bar{x}) &= \min\{B(x_0), B(\bar{x}), \Delta(x_0), \Delta_1(\bar{x}), T_0(x_0), T_1(\bar{x})\}, \quad \delta_{\min} = \min\{\delta_3, \delta_6(x_0, \bar{x}) + \delta\}, \\
 c_0 &= \frac{v(\bar{x})^2}{(r-\lambda\bar{x})A(\bar{x})g(\bar{x})}, \quad b_0 = \frac{v(\bar{x})}{g(\bar{x})}, \quad b_1 = \frac{c(r-\lambda\bar{x})A(\bar{x})}{v(\bar{x})}, \quad n_0(m) = \max\left\{m, \frac{(4m-1)^2-9}{m}\right\}, \\
 \bar{x} &= \frac{r(m-1)(m-n-1)}{\lambda(m+1)(m-n-2)}, \quad r(n, m) = \frac{\lambda x_0(m+1)(m-n-2)}{(m-1)(m-n-1)}, \quad r_1 = \min\{2\lambda x_0, r(n, m)\}, \\
 P_{nm}(x) &= \lambda(m-n-2)x^{m+1} + r(1-m+n)x^m - \lambda\alpha(2-n)x + r\alpha(1-n),
 \end{aligned}$$

where $f'(x) = -\lambda$, $p'(x) = g'(x) = \frac{g(x)A(x)}{x}$, $h'(y) = \frac{\beta\delta_0 - \delta}{(1+\beta y)^2}$, $u(x) = \frac{x^{1-n}(r-\lambda x)(\alpha+x^m)}{b}$, and $x_0 = \sqrt[m]{\frac{n\alpha}{m-n}}$.

Theorem 4.3. *If there exist some positive real numbers $r, \lambda, b, \delta, \beta, \delta_0, c, \alpha, n$, and m such that*

$$\delta_7 < \delta_1(x_0), \quad \delta_7 < \delta < \delta_1(x_0), \quad \delta_4 < \delta_5\delta, \quad c_0 < c, \quad b_0 < b < b_1, \quad \text{and} \quad \delta_2 < \beta\delta_0 < \delta_{\min}, \quad (4.7)$$

$$\begin{cases}
 Q_1(\bar{x}) > 0, \quad Q_2(\bar{x}) > 0, \quad Q_3(\bar{x}) < 0, \\
 \exists(x_1, x_2, x_3) \in [\bar{x}, x_0]^3, \quad Q_1(x_1) = Q_2(x_2) = Q_3(x_3) = 0, \quad x_4 = \max\{x_1, x_2\} < x_3, \\
 H(x_1) > 0, \quad H(x_2) > 0, \quad \text{and} \quad H(x_3) < 0,
 \end{cases} \quad (4.8)$$

$$1 < m, \quad n < m, \quad n_0(m) < n + 1, \quad \lambda x_0 < r < r_1, \quad P'_{nm}(x_0) > 0, \quad \text{and} \quad P_{nm}(\bar{x}) > 0, \quad (4.9)$$

$$\forall x \in [\bar{x}, x_0], \quad \frac{dM}{dx}(x) \neq 0, \quad \frac{dR}{dx}(x) \neq 0, \quad \frac{dQ}{dx}(x) \neq 0, \quad \frac{dQ_1}{dx}(x) < 0, \quad \frac{dQ_2}{dx}(x) < 0, \quad \text{and} \quad \frac{dQ_3}{dx}(x) > 0, \quad (4.10)$$

and

$$\forall Z \in \partial K, \quad \exists u \in T_Z, \quad \langle u, L(Z) \rangle > 0, \quad (4.11)$$

then the system (4.4) admits a unique closed trajectory Γ of which orbit is a globally stable limit cycle inside $K + \{X_*\}$.

Proof. From (4.7) and (4.9), we have $1 < m < n + 1$, $r < r(n, m)$, $\delta_7 < \delta < \delta_1(x_0)$ and $\delta_2 < \beta\delta_0 < \delta_3$, then $0 < \bar{x} < x_0$, $H(\bar{x}) > 0$, and $H(x_0) < 0$. So, from by Lemma 4.2, the system (4.4) admits a positive equilibrium point $X_* = (x_*; y_*)$ inside of $(\bar{x}, x_0) \times (0, +\infty)$. In particular, according to (4.8), $X_* = (x_*; y_*) \in (x_4, x_3) \times (0, +\infty)$.

• For all $x \in (0, x_0)$, $p'(x) > 0$. Since $x_* \in (0, x_0)$, then $\beta_3 = cy_*p'(x_*) > 0$.

Remark that

$$\alpha_2 = v(x)|_{x=x_*}, \quad \alpha_2 + \beta_2 = M(x)|_{x=x_*}, \quad \beta_3 - \alpha_2 + \beta_2 = R(x)|_{x=x_*}, \quad \alpha_3 - \alpha_2 + \beta_2 = Q(x)|_{x=x_*},$$

$$\alpha_3(\beta_2 + \beta_3) + \beta_3(\alpha_3 - \alpha_2) = Q_1(x)|_{x=x_*}, \quad \beta_3(\beta_2 + \beta_3 - 2\alpha_3)^2 - 4\alpha_3\beta_2^2 = Q_2(x)|_{x=x_*}, \quad \text{and}$$

$$\alpha_2 + \beta_2 - 2\alpha_3 = Q_3(x)|_{x=x_*}.$$

Let us now study the sign of v , M , R , Q , Q_1 , Q_2 , and Q_3 on (\bar{x}, x_0) .

• **Sign of $v(x)$ on (\bar{x}, x_0) .**

Note that

$$v(x) > 0 \iff P_{nm}(x) > 0.$$

The function P_{nm} is a continuous and differentiable function on $[0, x_0]$ and we have

$$\forall x \in [0, x_0], \quad P''_{nm}(x) = \lambda m(m+1)(m-n-2)x^{m-2}(x-\bar{x}).$$

Since, $1 < m < n + 1$, and $r < r(n, m)$, then $0 < \bar{x} < x_0$, and $\forall x \in [\bar{x}, x_0]$, $P''_{nm}(x) < 0$.

Thus, $P'_{nm}([\bar{x}, x_0]) = [P'_{nm}(x_0), P'_{nm}(\bar{x})]$. According to (4.9) $P'_{nm}(x_0) > 0$, then $\forall x \in [\bar{x}, x_0]$, $P'_{nm}(x) > 0$.

Thus, $P_{nm}([\bar{x}, x_0]) = [P_{nm}(\bar{x}), P_{nm}(x_0)]$. Moreover, according to (4.9), we have $P_{nm}(\bar{x}) > 0$, then $\forall x \in [\bar{x}, x_0]$, $P_{nm}(x) > 0$. Since $x_* \in (\bar{x}, x_0)$, then $\alpha_2 > 0$.

• **Sign of $M(x)$ on $(0, x_0)$.**

The function M is a continuous and differentiable function on $(0, x_0)$ and we have

$$M(x_0) = v(x_0) - u(x_0)h'(u(x_0)), \quad \text{and} \quad M(\bar{x}) = v(\bar{x}) - u(\bar{x})h'(u(\bar{x})).$$

From (4.7), we have

$$b_0 < b, \quad \text{and} \quad \beta\delta_0 - \delta < \min\{B(x_0), B(\bar{x})\},$$

which implies that $M(x_0) > 0$ and $M(\bar{x}) > 0$. Moreover, from (4.10), we have $\forall x \in [\bar{x}, x_0]$, $\frac{dM}{dx}(x) \neq 0$, thus $M([\bar{x}, x_0]) \subset (0, +\infty)$. Therefore,

$$\forall x \in (\bar{x}, x_0), \quad M(x) > 0.$$

Since, $x_* \in (\bar{x}, x_0)$, then $\alpha_2 + \beta_2 > 0$.

• **Sign of $R(x)$ on (\bar{x}, x_0)**

The function R is a continuous and differentiable function on (\bar{x}, x_0) and we have

$$R(x_0) = (2\lambda x_0 - r) - u(x_0)h'(u(x_0)), \quad R(\bar{x}) = \left(\frac{cg(\bar{x})A(\bar{x})}{\bar{x}} - h'(u(\bar{x})) \right) u(\bar{x}) - v(\bar{x}).$$

From (4.7), we have

$$b < \frac{c(r - \lambda\bar{x})A(\bar{x})}{v(\bar{x})}, \quad \text{and} \quad \beta\delta_0 - \delta < \min\{T_0(x_0), T_1(\bar{x})\},$$

which implies that $R(x_0) > 0$ and $R(\bar{x}) > 0$. Moreover, from (4.10), we have $\forall x \in [\bar{x}, x_0]$, $\frac{dR}{dx}(x) \neq 0$, thus $R([\bar{x}, x_0]) \subset (0, +\infty)$. Therefore,

$$\forall x \in (\bar{x}, x_0), R(x) > 0.$$

Since, $x_* \in (\bar{x}, x_0)$, then $0 < \beta_3 - \alpha_2 + \beta_2 < 2\beta_3 - \alpha_2 + \beta_2$.

• **Sign of $Q(x)$ on (\bar{x}, x_0) .**

The function Q is a continuous and differentiable function on (\bar{x}, x_0) and we have

$$Q(x_0) = bg(x_0) - u(x_0)h'(u(x_0)), \text{ and } Q(\bar{x}) = bg(\bar{x}) - v(\bar{x}) - u(\bar{x})h'(u(\bar{x})).$$

From (4.7), we have

$$\frac{v(\bar{x})}{g(\bar{x})} < b, \text{ and } \beta\delta_0 - \delta < \min\{\Delta(x_0), \Delta_1(\bar{x})\},$$

which implies that $Q(x_0) > 0$, $Q(\bar{x}) > 0$. Moreover, from (4.10), we have $\forall x \in [\bar{x}, x_0]$, $\frac{dQ}{dx}(x) \neq 0$, thus $Q([\bar{x}, x_0]) \subset (0, +\infty)$. Therefore,

$$\forall x \in (\bar{x}, x_0), Q(x) > 0.$$

Since, $x_* \in (\bar{x}, x_0)$, then $0 < \alpha_3 - \alpha_2 + \beta_2 < 2\alpha_3 - \alpha_2 + \beta_2$.

• **Sign of $Q_1(x)$ on (\bar{x}, x_0) .**

The function Q_1 is a continuous and differentiable function on (\bar{x}, x_0) and we have

$$Q_1(x_0) = -bg(x_0)u(x_0)h'(u(x_0)) < 0.$$

From (4.10), we have $\forall x \in [\bar{x}, x_0]$, $\frac{dQ_1}{dx}(x) < 0$, thus $Q_1([\bar{x}, x_0]) = [Q_1(x_0), Q_1(\bar{x})]$. Moreover, from (4.8), $Q_1(\bar{x}) > 0$, then there exists $x_1 \in [\bar{x}, x_0]$ such that

$$Q_1(x_1) = 0 \text{ and } \forall x \in (x_1, x_0], Q_1(x) > 0.$$

Since, $H(x_1) > 0$, and $H(x_0) < 0$, then $x_* \in (x_1, x_0)$. Therefore, $Q_1(x_*) = \alpha_3(\beta_2 + \beta_3) + \beta_3(\alpha_3 - \alpha_2) > 0$.

• **Sign of $Q_2(x)$ on (\bar{x}, x_0) .**

The function Q_2 is a continuous and derivable function on (\bar{x}, x_0) and we have

$$Q_2(x_0) = -4bg(x_0)u(x_0)^2h'(u(x_0))^2 < 0.$$

From (4.10), we have $\forall x \in [\bar{x}, x_0]$, $\frac{dQ_2}{dx}(x) < 0$, thus $Q_2([\bar{x}, x_0]) = [Q_2(x_0), Q_2(\bar{x})]$.

Moreover, from (4.8), $Q_2(\bar{x}) > 0$ and so, there exists a unique element $x_2 \in [\bar{x}, x_0]$ such that

$$Q_2(x_2) = 0 \text{ and } \forall x \in (x_2, x_0], Q_2(x) > 0.$$

Since, $H(x_2) > 0$, and $H(x_0) < 0$, then $x_* \in (x_2, x_0)$. Therefore, $Q_2(x_*) = \beta_3(\beta_2 + \beta - 2\alpha_3)^2 - 4\alpha_3\beta_2^2 > 0$.

• **Sign of $Q_3(x)$ on (\bar{x}, x_0) .**

The function Q_3 is a continuous and differentiable function on (\bar{x}, x_0) and we have

$$Q_3(x_0) = M(x_0), \text{ and } Q_3(\bar{x}) = M(\bar{x}) - \frac{2c(r - \lambda\bar{x})A(\bar{x})}{b}.$$

From (4.10), we have $\forall x \in [\bar{x}, x_0]$, $\frac{dQ_3}{dx}(x) > 0$, thus $Q_3([\bar{x}, x_0]) = [Q_3(\bar{x}), Q_3(x_0)]$.

From (4.8), we have $Q_3(\bar{x}) < 0$. Thus, there exists a unique element $x_3 \in [\bar{x}, x_0]$ such that

$$Q_3(x_3) = 0 \text{ and } \forall x \in (\bar{x}, x_3), Q_3(x) < 0.$$

Since, $H(\bar{x}) > 0$ and $H(x_3) < 0$, then $x_* \in (\bar{x}, x_3)$. Therefore, $\alpha_2 + \beta_2 - 2\alpha_3 = Q_3(x_*) < 0$. This is the end of the proof. \square

4.2.1. Simulation

For $n = 1.3 < m = \frac{\ln(3)}{\ln(2)}$, $\alpha = 0.5$, $\beta = 1$, $\lambda = 0.13$, we have

$$x_0 \cong 1.6824886, 0.1666653 < r = 0.43 < 2\lambda x_0 = 0.437447, b_0 \cong 0.1594231 < b = 1, c_0 \cong 0.9164583 < c = 1,$$

$$\delta = 0.522 < 1.0626609, \delta_0 = 0.54 < 0.5436387.$$

Hence, according to the theorem 4.3, the system (4.4) admits a unique closed trajectory Γ of which orbit is a globally stable limit cycle inside $K + \{X_*\}$, where $X_* = (0.57, 0.38)$, and $K := [-0.19, +\infty)^2$.

Let $Z \in \partial K$, then we distinguish two cases.

Case1: Z is a corner point. In this case the tangent cone at Z is the angular domain. For example if $Z = (-0.19, -0.19)$, then $T_Z = K$ and $N_Z = \{(z_1, z_2) \in \mathbb{R}^2, z_1 \leq -0.19 \text{ and } z_2 \leq -0.19\}$. Moreover, we have

$$u = (1, -0.1) \in T_Z \text{ and } \langle u, L(Z) \rangle = 0.19(\alpha_3 - \alpha_2 + 0.1\beta_3) > 0.$$

Case2: Z is not a corner point. In this case the tangent cone at Z is the half plane. For example if $Z = (-0.19, 0)$, then

$$T_Z = \{(z_1, z_2) \in \mathbb{R}^2, z_1 \geq -0.19\} \text{ and } N_Z = \{(z_1, z_2) \in \mathbb{R}^2, z_1 \leq -0.19 \text{ and } z_2 = 0\}.$$

Moreover, we have

$$u = (1, -0.1) \in T_Z \text{ and } \langle u, L(Z) \rangle > 0.$$

Then, for all $Z \in \partial K$, there exists $u \in T_Z$ such that $\langle u, L(Z) \rangle > 0$. Let $(x(0), y(0))$ be the initial condition, then we obtain the following simulation. In figure 4, the red and blue curves represent the evolution of prey and predators respectively.

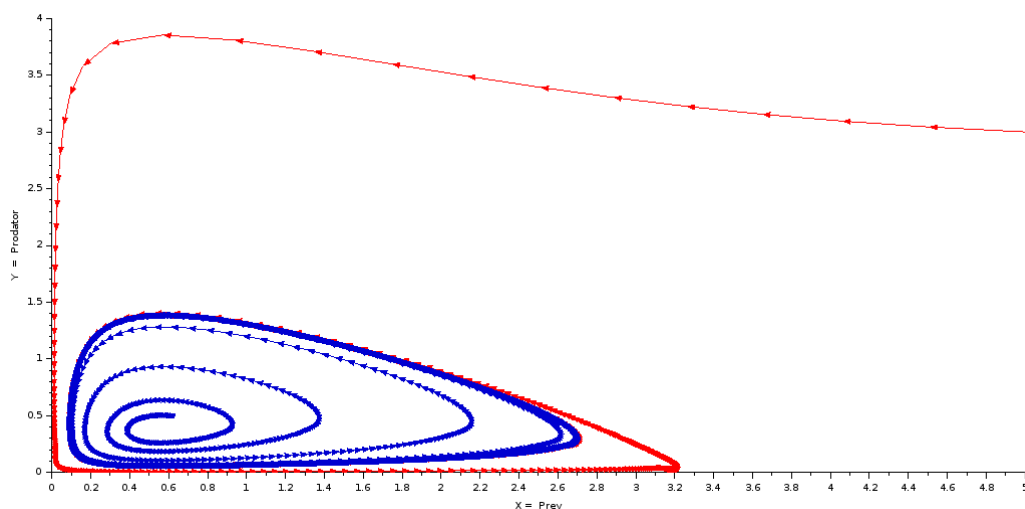


Figure 3: Phase portrait of the differential system (4.4) with $(x(0), y(0)) \in \{(0.6, 0.5); (5, 3)\}$.

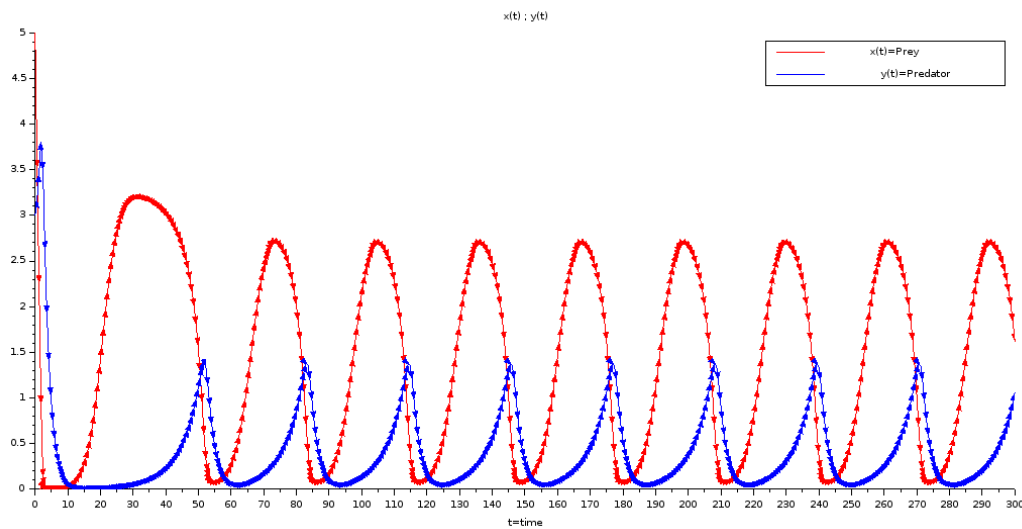


Figure 4: Chronic of the differential system (4.4) with $(x(0) ; y(0)) = (5 , 3)$.

5. Hopf bifurcation

Let us recall that there is no regular method to study the limit cycles of the systems in the plane. Perhaps, one of the most important approaches, together with the Poincaré-Bendixson theory, is the Poincare-Andronov-Hopf bifurcation [11, 13, 19], which is the only genuinely two dimensional bifurcation (i.e., it cannot be observed in systems of dimension 1), which can occur in generic two dimensional autonomous systems depending on one parameter (co-dimension 1 bifurcation).

In this section, we give the conditions for the existence of Hopf bifurcation in the neighborhood of a positive equilibrium point of the system (2.3). For all $(a, x) \in \mathbb{R}_+^2$, let $T(a, x) = \alpha_2(a, x) + \beta_2(a, x)$, $D(a, x) = \alpha_2(a, x)\beta_2(a, x) + \alpha_3(a, x)\beta_3(a, x)$, $\Delta(a, x) = (\alpha_2(a, x) - \beta_2(a, x))^2 - 4\alpha_3(a, x)\beta_3(a, x)$, where a is a real parameter of the system (2.3).

Theorem 5.1. *If the system (2.3) admits a positive equilibrium point $X_* = (x_* , y_*)$ such that*

$$\beta_3(a , x_*) > 0 \text{ and } \Delta(a , x_*) < 0 , \tag{5.1}$$

there exists a positive real number a_ such that*

$$T(a_* , x_*) = 0 , \text{ and } \left. \frac{T(a , x_*)}{da} \right|_{a=a_*} \neq 0 , \tag{5.2}$$

then the system (2.3) admits a Hopf bifurcation in a neighborhood of (X_ , a_*) .*

Proof. The Jacobian matrix of system (2.3) at the neighborhood of X_* is

$$W(X_*) = \begin{pmatrix} \alpha_2(a, x_*) & -\alpha_3(a, x_*) \\ \beta_3(a, x_*) & \beta_2(a, x_*) \end{pmatrix}$$

which trace and determinant are respectively $T_0(X_*) = T(a, x_*)$ and $D_0(X_*) = D(a, x_*)$. Let $\Delta_0(X_*) = T_0(X_*)^2 - 4D_0(X_*)$ be the discriminant of the characteristic polynomial of $N(X_*)$.

We have $\Delta_0(X_*) = \Delta(a, x_*)$. According to (5.1), $\Delta(a, x_*) < 0$, then the matrix $N(X_*)$ admits two conjugate complex eigenvalues $z(a) = \gamma(a) + i\omega(a)$ and $\bar{z}(a) = \gamma(a) - i\omega(a)$, with

$$\gamma(a) = \frac{\Gamma(a, x_*)}{2} \quad \text{and} \quad \omega(a) = \frac{\sqrt{-\Delta(a, x_*)}}{2}.$$

According to (5.2), we obtain $\left. \frac{d\gamma(a)}{da} \right|_{a=a_*} \neq 0$. Moreover, according to (5.1) and (5.2), we have

$$\gamma(a_*) = 0, \quad \text{and} \quad \omega(a_*) = 2\sqrt{D(a_*)} > 0.$$

Likewise, for $a = a_*$, the only eigenvalues of $W(X_*)$ are $z(a_*) = i\omega(a_*)$ and $\bar{z}(a_*) = -i\omega(a_*)$. Thus, according to the Poincaré-Andronov-Hopf theorem [11, 13], the system (2.3) admits a Hopf bifurcation in a neighborhood of (X_*, a_*) . For the stability of the limit cycle, we need to calculate the first Lyapunov number $\Sigma(a_*, x_*)$ at X_* first. Letting $X = x - x_*$, $Y = y - y_*$ to transform X_* to $(0, 0)$, and we rewrite model (2.3) as

$$\begin{cases} \dot{X} = a_{10}X + a_{01}Y + a_{11}XY + a_{20}X^2 + a_{21}X^2Y + a_{30}X^3 + \Gamma_1(X, Y), \\ \dot{Y} = b_{10}X + b_{01}Y + b_{11}XY + b_{20}X^2 + b_{21}X^2Y + b_{30}X^3 + b_{03}Y^3 + \Gamma_2(X, Y), \end{cases} \quad (5.3)$$

where $\Gamma_1(X, Y) = \sum_{i+j \geq 4} a_{ij}X^iY^j$ and $\Gamma_2(X, Y) = \sum_{i+j \geq 4} b_{ij}X^iY^j$,

$$\begin{aligned} a_{11} &= -bg'(x_*), \quad a_{01} = -\alpha_3, \quad a_{10} = \alpha_2, \quad a_{20} = \frac{1}{2}(2f'(x_*) + x_*f''(x_*) - by_*g''(x_*)), \\ a_{21} &= -\frac{b}{2}g''(x_*), \quad a_{30} = \frac{1}{6}(3f''(x_*) + 2x_*f^{(3)}(x_*)), \quad b_{10} = \beta_3, \quad b_{11} = cp'(x_*), \\ b_{01} &= \beta_2, \quad b_{02} = -\frac{1}{2}(2h'(y_*) + y_*h''(y_*)), \quad b_{20} = \frac{c}{2}y_*p''(x_*), \quad b_{21} = \frac{c}{2}p''(x_*), \\ b_{03} &= -\frac{1}{6}(3h''(y_*) + 2y_*h^{(3)}(y_*)), \quad b_{30} = \frac{c}{3}y_*p^{(3)}(x_*). \end{aligned}$$

The Liapunov number [19] of the system (2.3) at X_* is defined by

$$\Sigma(a_*, X_*) = -\frac{3\pi}{2a_{01}\sqrt{D_0(X_*)^3}} [\sigma_1 + \sigma_2 + \sigma_3 + \sigma_4],$$

where

$$\begin{aligned} \sigma_1 &= a_{10}b_{10}(a_{11}^2 + a_{11}b_{02} + a_{02}b_{11}) + a_{10}a_{01}(b_{11}^2 + b_{11}a_{20} + a_{11}b_{02}), \\ \sigma_2 &= b_{10}^2(a_{11}a_{02} + 2a_{02}b_{02}) - 2a_{10}b_{10}(b_{02}^2 - a_{20}a_{02}) - 2a_{10}a_{01}(a_{20}^2 - b_{20}b_{02}), \\ \sigma_3 &= -a_{01}^2(2a_{20}b_{20} + b_{11}b_{20}) + (a_{01}b_{10} - 2a_{10}^2)(b_{11}b_{02} - a_{11}a_{20}), \\ \sigma_4 &= -(a_{10}^2 + a_{01}b_{10})(3(b_{10}b_{03} - a_{01}a_{30}) + 2a_{10}a_{21} + (b_{10}a_{12} - a_{01}a_{21})), \end{aligned}$$

and $D_0(X_*) = D(a_*, x_*)$. The limit cycle is stable via a supercritical Hopf bifurcation if $\Sigma(a_*, x_*) < 0$, and it is unstable via a subcritical Hopf bifurcation if $\Sigma(a_*, x_*) > 0$. □

5.1. Application

As application of the Theorem 5.1, we consider the sytem (4.1). Let

$$\begin{aligned} R_0 &= \frac{\delta(1+x_*^2)^2}{x_*^2(1+3x_*^2)}, \quad R_1 = \frac{\delta(1+x_*^2)}{x_*^2}, \quad R_2 = \frac{bx_*(1-x_*^2)(1-3x_*^2)}{(1+x_*^2)^3(1+3x_*^2)}, \quad A_0 = \frac{4rx_*^2}{1+x_*^2}(r-R_1), \\ A_1 &= \frac{2x_*^3(1+3x_*^2)}{(1+x_*^2)^2}(R_0-r), \quad A_2 = \frac{x_*(1+3x_*^2)}{1+x_*^2}, \quad \lambda_* = \frac{2rx_*}{1+3x_*^2}, \quad \text{and} \quad a_{01}a_{21} = -\frac{b^2x_*^2(3-x_*^2)}{(1+x_*^2)^4}. \end{aligned}$$

Theorem 5.2. *If*

$$\begin{cases} \lambda < \min \left\{ \frac{r}{x_*}, \frac{\sqrt{A_1 - A_2^2 A_0 - A_1}}{A_2^2} \right\}, \\ r < \min\{R_0, R_1\}, \end{cases} \quad \text{or} \quad \begin{cases} \lambda < \min \left\{ \frac{r}{x_*}, \frac{\sqrt{A_1 - A_2^2 A_0 - A_1}}{A_2^2} \right\}, \\ r > R_0, \end{cases} \quad (5.4)$$

then the system (4.1) admits a Hopf bifurcation in a neighborhood of (X_*, λ_*) , where $\alpha = \lambda$ is the bifurcation parameter. The limit cycle is stable via a supercritical Hopf bifurcation if

$$\begin{cases} r < \frac{a_{01} a_{21}}{R_2}, \\ \frac{\sqrt{3}}{3} < x_* < 1, \end{cases} \quad \text{or} \quad \begin{cases} \frac{a_{01} a_{21}}{R_2} < r, \\ x_* \in (0, \frac{\sqrt{3}}{3}) \cup (1, +\infty), \end{cases} \quad \text{or} \quad x_* \in \left\{ 1, \frac{\sqrt{3}}{3} \right\}, \quad (5.5)$$

and it is unstable via a subcritical Hopf bifurcation if

$$\begin{cases} r < \frac{a_{01} a_{21}}{R_2}, \\ \sqrt{3} < x_*, \end{cases} \quad \text{or} \quad \begin{cases} \frac{a_{01} a_{21}}{R_2} < r, \\ \frac{\sqrt{3}}{3} < x_* < 1. \end{cases} \quad (5.6)$$

Proof. The system (4.1) admits a unique positive equilibrium point $X_* = (x_*, y_*)$ such that

$$x_* = \frac{\delta}{c} \quad \text{and} \quad y_* = \frac{x_*(r - \lambda x_*)}{bg(x_*)}, \quad \text{with} \quad \lambda < \frac{r}{x_*}.$$

Moreover, we have $\alpha_2 = A_2(\lambda_* - \lambda)$, $\alpha_3 = \frac{bx_*}{1+x_*^2}$, $\beta_2 = 0$, $\beta_3 = \frac{c(r-\lambda x_*)(1+x_*^2)}{b}$,

$$T(\lambda, x_*) = \alpha_2(\lambda, x_*), \quad D(\lambda, x_*) = \alpha_3(\lambda, x_*)\beta_3(\lambda, x_*), \quad \Delta(\lambda, x_*) = A_2\lambda^2 + 2A_1\lambda + A_0.$$

According to (5.4), we have $\Delta(\lambda, x_*) < 0$. Moreover, if $\lambda = \lambda_*$, we obtain

$$T(\lambda_*, x_*) = 0, \quad D(\lambda_*, x_*) = \frac{r\delta(1+x_*^2)}{1+3x_*^2} > 0 \quad \text{and} \quad \frac{dT(\lambda, x_*)}{d\lambda} \Big|_{\lambda=\lambda_*} = -A_2 < 0.$$

Then the system (4.1) admits a Hopf bifurcation at the neighborhood of (λ_*, X_*) . The Liapounov number is given by

$$\Sigma(\lambda_*, x_*) = \frac{3\pi\beta_3}{2\sqrt{D_0(X_*)^3}} [a_{01} a_{21} - R_2 r].$$

Hence, $\Sigma(\lambda_*, x_*) > 0$ if and only if $\begin{cases} r < \frac{a_{01} a_{21}}{R_2}, \\ \sqrt{3} < x_*, \end{cases}$ or $\begin{cases} \frac{a_{01} a_{21}}{R_2} < r, \\ \frac{\sqrt{3}}{3} < x_* < 1, \end{cases}$ and

$\Sigma(\lambda_*, x_*) < 0$ if and only if

$$\begin{cases} r < \frac{a_{01} a_{21}}{R_2}, \\ \frac{\sqrt{3}}{3} < x_* < 1, \end{cases} \quad \text{or} \quad \begin{cases} \frac{a_{01} a_{21}}{R_2} < r, \\ x_* \in (0, \frac{\sqrt{3}}{3}) \cup (1, +\infty), \end{cases} \quad \text{or} \quad x_* \in \left\{ 1, \frac{\sqrt{3}}{3} \right\}.$$

That is the end of the proof. □

5.2. Simulation

For $b = 7$, $\delta = 5$, $c = 3$, we obtain $1 < x_* = \frac{5}{3}$, and Hopf bifurcation at $\lambda_* \approx 0.7142857$ and we can take

$$\frac{a_{01} a_{21}}{R_2} \approx -0.3035 < r = 2 < \min\{R_0, R_1\} = 2.752381, \quad \lambda < 1.0278859.$$

Let's denote by $(x(0), y(0))$ the initial condition. Taking $(x(0), y(0)) \in \{(2, 2); (1.5, 0.3)\}$, we obtain the following figures.

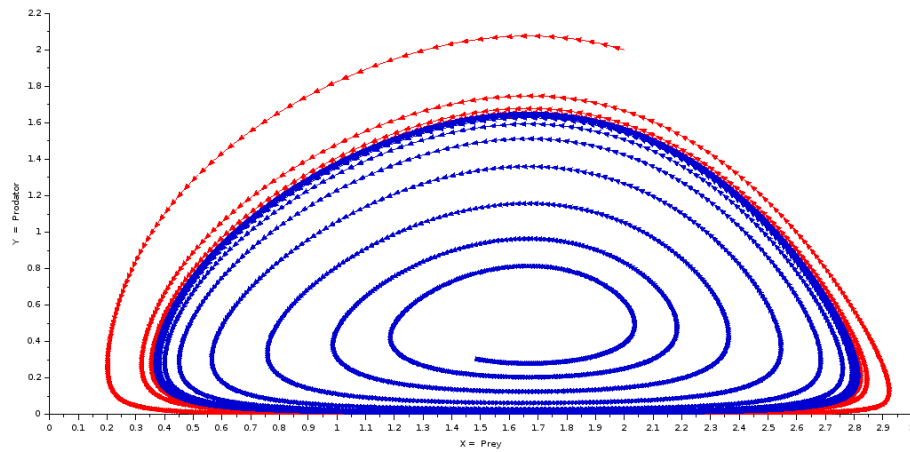


Figure 5: For $\lambda = 0.65 < \lambda_*$.

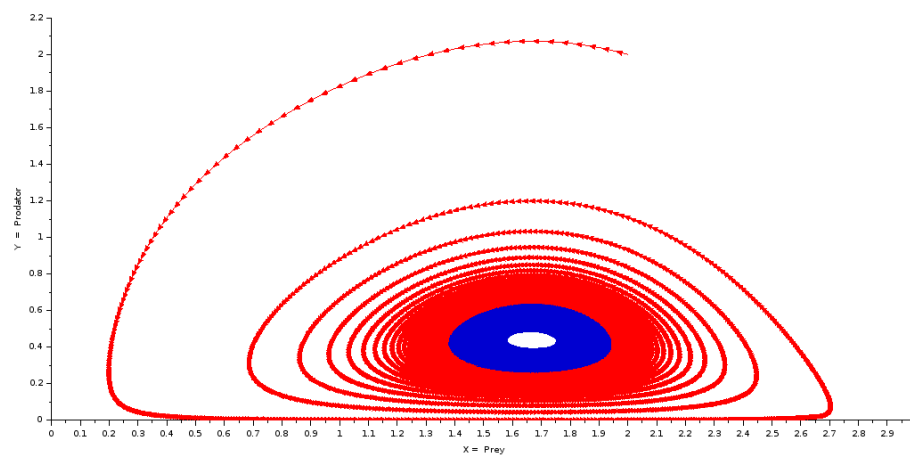


Figure 6: For $\lambda = \lambda_*$.

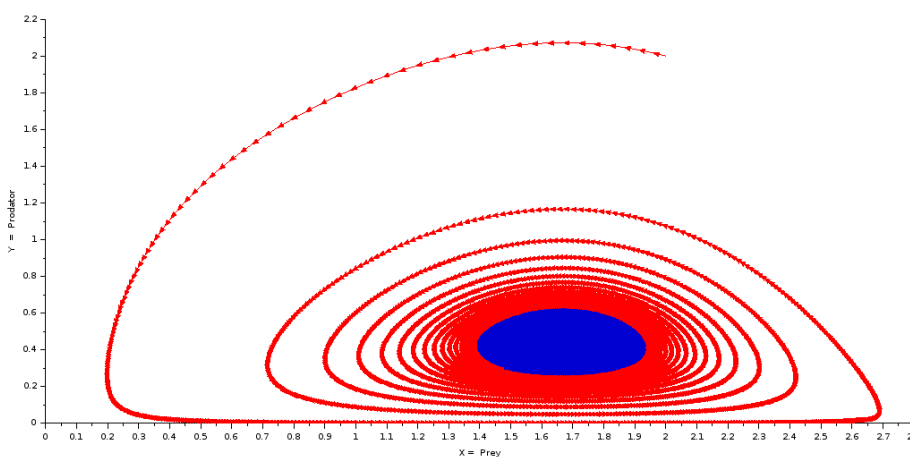


Figure 7: For $\lambda = 0.719 \geq \lambda_*$.

6. Conclusion

In this work, we have studied on a nonempty, convex and closed set the existence, uniqueness and global stability of limit cycles for the generalized Gause model in which the functional and numerical responses of the predators are not necessarily monotonic functions and where the intrinsic mortality rate of the predators is can be a nonconstant function. The result obtained is applied theoretically to two particular models and validated by simulations. We have established a Hopf bifurcation result for the studied model. This bifurcation result is also applied to a particular model and validated by simulations. The results established in this paper are applicable to all prey-predator systems of the Gause type.

Author Contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by **Guy Degla**, **S. Jean-Marie Degbo** and **Marie-Louise Dossou-Yovo**. The first draft of the manuscript was written by **Seyive Jean-Marie Degbo** and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Acknowledgment

We thank all reviewers for their valuable comments. The first author is grateful to the Deutscher Akademischer Austauschdienst German Academic Exchange Service (DAAD) for its fellowship. The other authors acknowledge the grant of The World Academy of Sciences (TWAS) for the advancement for science in developing countries.

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