

EFFECT OF VIRAL INFECTION ON THE GENERALIZED GAUSE MODEL OF PREDATOR-PREY SYSTEM

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The generalized Gause model of predator-prey system is revisited with an introduction of viral infection on prey population. Stability behavior of such modified system is carried out to observe the change of dynamical behavior of the system. To substantiate the analytical results of this generalized susceptible prey, infected prey and predator population, numerical simulations of the model with specific growth and response functions are performed. Our observations suggest that the disease on prey population has a destabilizing or stabilizing effect depending on the level of force of infection and may act as a biological control for the persistence of the species.

Keywords: Gause predator-prey model; viral infection; stability; biological control.

1. Introduction

Mathematical ecology and mathematical epidemiology are major fields of study in their own right. The study which includes ecology and epidemiology is now termed as eco-epidemiology. Even though the importance of transmissible disease in ecological situations has been shown to induce major behavioral changes in the species, little attention has been paid to describe such situations theoretically that may predict useful implications in both dynamics and control. Few theoretical studies have been carried out in such systems [1–5, 8, 11, 12] where the effect of viral infection has been explored.

1.1. *The main motivation*

Beltrami and Carroll [1] proposed and analyzed a predator-prey system in which some of the susceptible phytoplankton cells were infected by viral infection and formed an infected group. They concluded that only a minute amount of infectious agent can destabilize the otherwise stable trophic configuration. Venturino [11] considered a predator-prey system and the analysis included SI and SIS models with mass action and standard incidence type. He concluded that under suitable

assumptions the disease can act as a control for the persistence of the system. Chattopadhyay and Pal [3] modified the model of Beltrami and Carroll [1] and the model of Venturino [11]. They observed that if the contact rate follows the law of mass action, there is a possibility for the coexistence of the species but on the other hand if the contact rate follows the law of standard incidence, only a minute amount of infectious agent can destabilize the otherwise stable system. Finally, Chattopadhyay and Pal [3] concluded that behavior of such system is very much model dependent and the progress of this sensitive and important issue depends on the responsibility of the researchers. Hence the study with generalized predator-prey model may be useful to have some insight on this complex system.

Gause [6] model on predator-prey dynamics is one of the pioneering work on population dynamics. A considerable amount of research papers have appeared in the literature based on this work. The role of disease in such systems can not be ignored and we like to revisit the generalized Gause type predator-prey model with viral infection on prey population only. The main objective of this article is to observe the role of the disease in the original Gause model.

2. Gause Model and Main Results

Let us consider a generalized Gause Model [6, 7] for predator-prey interactions, e.g.,

$$\begin{aligned}\frac{dx}{dt} &= xg(x) - yp(x), \\ \frac{dy}{dt} &= y\{-\gamma + q(x)\},\end{aligned}\tag{2.1}$$

where, $g(x)$ is the specific growth rate of the prey in the absence of any predators and $p(x)$ is the predator response function for the predator with respect to that particular prey. We also adopt the general assumption (for the theoretical as well as for the biological validity) on the functions $g(x), p(x)$ and $q(x)$, i.e.,

- 1a. $g(x)$ is continuously differentiable for $x \geq 0$, $g_x(x) \leq 0$ and $g(0) > 0$.
- 1b. There exists K such that $g(K) = 0$ on $0 \leq x < K$, K being the carrying capacity of the environment and $g(x) < 0$ on $x > K$.
2. $p(x)$ and $q(x)$ are both continuously differentiable for $x \geq 0$, $p_x(x), q_x(x) > 0$ and $p(0) = q(0) = 0$.

As a consequence of above assumptions, $0 < \lim_{x \rightarrow \infty} p(x) = p_\infty$ and $0 < \lim_{x \rightarrow \infty} q(x) = q_\infty$ are true; we also consider $p_x(0) = p'_0$ and $q_x(0) = q'_0$. A unique positive interior equilibrium (x^*, y^*) , exists if $0 < x^* < K$ such that $q(x^*) = \gamma$ and $\lim_{y \rightarrow \infty} y > \max_{0 \leq x \leq K} \left\{ \frac{xq(x)}{p(x)} \right\}$ (see [9]). Conditions for local asymptotic stability and instability of the system (2.1) around the positive interior equilibrium (x^*, y^*) is

$$\begin{aligned}H(x^*) < 0 &\Rightarrow (x^*, y^*) \text{ stable,} \\ > 0 &\Rightarrow (x^*, y^*) \text{ unstable,} \\ = 0 &\text{ undecided,}\end{aligned}\tag{2.2a}$$

where,

$$\begin{aligned} H(x^*) &= x^*g(x^*) + g(x^*) - y^*p_x(x^*), \\ y^* &= \frac{x^*g(x^*)}{p(x^*)}. \end{aligned} \quad (2.2b)$$

□

2.1. The modified Gause model

We shall now modify the Gause predator-prey model by introducing viral infection on prey population. The following basic assumptions are made:

- In the absence of virus disease the prey population grows with specific growth function $g(x)$.
- In the presence of virus the prey population is divided into two classes, namely, susceptible prey, denoted by x_1 and infected prey, denoted by x_2 . Therefore at time t the total prey population is

$$x(t) = x_1(t) + x_2(t).$$

- We assume that both susceptible and infected prey are capable of reproducing and contribute with carrying capacity of the system.

Based on the above assumptions the generalized Gause model can be written as:

$$\begin{aligned} \frac{dx_1}{dt} &= xg(x) - yp_1(x_1) - r(x_2), \\ \frac{dx_2}{dt} &= r(x_2) - yp_2(x_2), \\ \frac{dy}{dt} &= y\{-\gamma + q(x)\}, \end{aligned} \quad (2.3)$$

where, $g(x)$ is the growth rate of the prey in the absence of any predators and $p_i(x_i)$, $i = 1, 2$ is the predator response functions for the predator with respect to that particular prey x_1 and x_2 respectively. $r(x_2)$ is the growth rate of the infected prey population such that $r(x_2)$ is continuously differentiable for $x \geq 0$, $r_x(x_2) \leq 0$. $q(x)$ follows the same properties of $g(x)$ and $p_i(x_i)$, $i = 1, 2$. In addition to that we also consider a function (a linear transform) $p(x)$, following the same properties of $p_i(x_i)$ such that

$$p(x) = p_1(x_1) + p_2(x_2). \quad (2.4)$$

System (2.3) has an interior equilibrium (x_1^*, x_2^*, y^*) iff

$$\begin{aligned} x^*g(x^*) - y^*p_1(x_1^*) + r(x^*) &= 0, \\ r(x^*) - y^*p_2(x_2^*) &= 0, \\ q(x^*) - \gamma &= 0, \end{aligned} \quad (2.5)$$

have a unique solution.

2.2. Local Asymptotic Stability (LAS) analysis

Adopting the same notation those were used in Freedman [5], we compute the real parts of the eigenvalues of the Jacobian matrix evaluated at the interior equilibrium as

$$J(x_1^*, x_2^*, y^*) = \begin{pmatrix} H(x^*) + y^* p_{2x}(x_2^*) & H(x^*) + y^* p_x(x^*) - r_x(x_2^*) & -p_1(x_1^*) \\ 0 & r_x(x_2^*) - y^* p_{2x}(x_2^*) & -p_2(x_2^*) \\ y^* q_x(x^*) & y^* q_x(x^*) & 0 \end{pmatrix}, \quad (2.6)$$

where $H(x^*)$ is given in (2.2).

The characteristic equation of the linearized system of (2.3) is given by

$$\Delta(\lambda) \equiv \lambda^3 + \alpha_2 \lambda^2 + \alpha_1 \lambda + \alpha_0 = 0, \quad (2.7)$$

where

$$\begin{aligned} \alpha_2 &= -(H(x^*) + r_x(x_2^*)), \\ \alpha_1 &= y^* p(x^*) q_x(x^*) + (H(x^*) + y^* p_{2x}(x_2^*))(r_x(x_2^*) - y^* p_{2x}(x_2^*)) \\ \alpha_0 &= y^* q_x(x^*) (y^* (p_1(x_1^*) p_2(x_2^*))_x - p(x^*) r_x(x_2^*)). \end{aligned} \quad (2.8)$$

Following Routh–Hurwitz conditions, system (2.3) is LAS iff

- (i) $\alpha_2 > 0$, i.e., $H(x^*) + r_x(x_2^*) < 0$,
- (ii) $\alpha_0 > 0$, i.e. $y^* (p_1(x_1^*) p_2(x_2^*))_x > p(x^*) r_x(x_2^*)$,
- (iii) $\alpha_1 \alpha_2 - \alpha_0 > 0$ i.e., $H^2 + aH + b < 0$, where, (we use H instead of $H(x^*)$)

$$\begin{aligned} a &= \frac{y^* p(x^*) q_x(x^*)}{r_x(x_2^*) - y^* p_{2x}(x_2^*)} + r_x(x_2^*) + y^* p_{2x}(x_2^*), \\ b &= y^* p_{2x}(x_2^*) r_x(x_2^*) + \frac{y^{*2} q_x(x^*) (p_1(x_1^*) p_2(x_2^*))_x}{r_x(x_2^*) - y^* p_{2x}(x_2^*)}. \end{aligned} \quad (2.9b)$$

The following two cases which are arising from (2.9b) are to be useful to determine the range of stability of the systems around the positive equilibrium.

- (i) $r_x(x_2^*) - y^* p_{2x}(x_2^*) > 0$ then, $H(x^*) < \min(H_1, H_2) < 0$,
- (ii) $r_x(x_2^*) - y^* p_{2x}(x_2^*) < 0$ then, $\max(H_1, H_2) < H(x^*) < 0$,

where, H_1, H_2 are the roots of $H^2 + aH + b = 0$.

Now we are in position to compare the Gause model (2.1) and the modified Gause model (2.3):

- a. If $H(x^*) < 0$ then the system (2.1) is LAS at (x^*, y^*) . From Eq. (2.8), it is clear that if $H(x^*) + r_x(x_2^*) > 0$, then $\alpha_2 > 0$, hence the system (2.3) is unstable. Thus there exists a threshold level of infection below which the dynamics of the interior steady state becomes stable and above which unstable.

- b. If $H(x^*) < 0$ and the conditions given in (2.9) hold, then the system (2.3) at (x_1^*, x_2^*, y^*) is LAS. This observation shows that infection on prey population decreases stability region (see Eq. (2.9c)).
- c. If $H(x^*) > 0$ both systems are unstable.

To substantiate analytical findings, model (2.1) and model (2.3) have been integrated using fourth order Runge Kutta method with the following hypothetical set of parameter values and functional forms. Let us consider $g(x) = R(1 - \frac{x}{K})$, $p_i(x_i) = b_i x_i$, $i = 1, 2$, $p(x) = \sum_{i=1}^2 p_i(x_i)$, $r(x_2) = \frac{\beta_1 x_2}{1 + \beta_2 x_2}$, $q(x) = \rho x$.

For Gause model we consider $R = 1.5$, $b_1 = 0.8$, $\gamma = 0.25$, $\rho = 0.78$ and $K = 5$. We observe that the system settles down to steady state solutions, depicting stable solution (Fig. 1). Now keeping all other parameters fixed and assuming $b_2 = 0.3$, $\beta_1 = 1.45$, $\beta_2 = 0.15$, we observe that one of the population (susceptible prey) of system (2.3) becomes extinct, an unstable situation (Fig. 2). This result shows that infection on prey population has a destabilizing effect.

In predator-prey models the carrying capacity of the environment and half saturation constant are two important factors. Murdoch and Oaten [10] showed that half saturation constant, which is proportional to β_2^{-1} is a key parameter in determining the stability of predator-prey system. To observe the role of these factors in this modified system we have just changed the value of $K = 5$ to $K = 250$ (other parameters have unchanged) and have observed that the system undergoes limit cycle oscillation (see Fig. 3.) Increasing β_2 from $\beta_2 = 0.15$ to $\beta_2 = 0.2$, we have

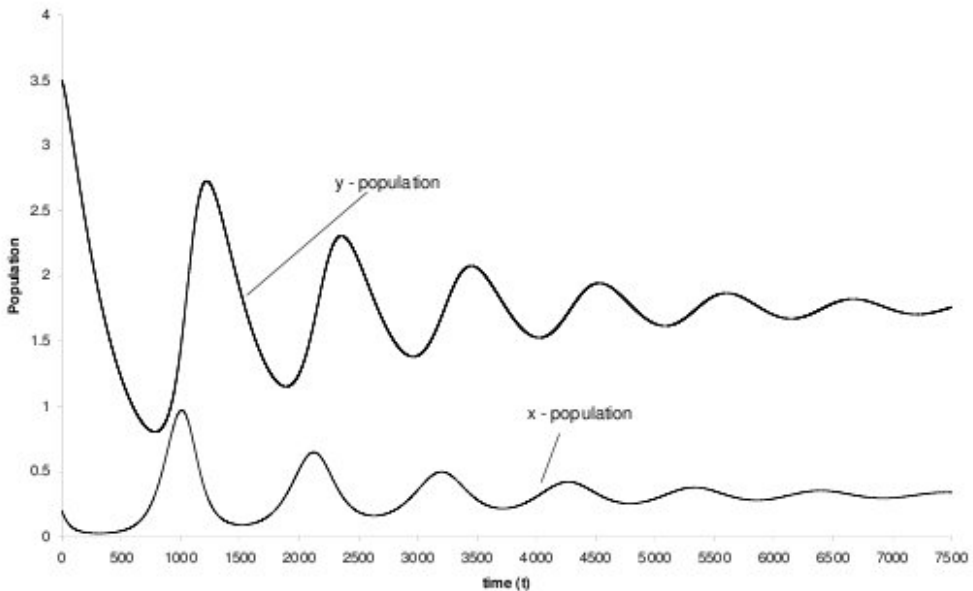


Fig. 1. Stable solution of Gause model.

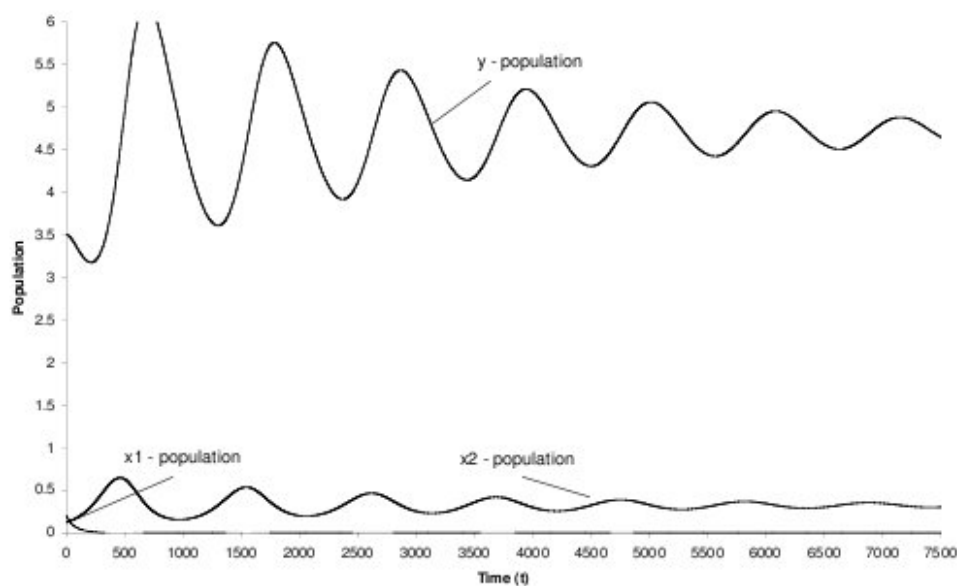


Fig. 2. Unstable situation of system 2.3.

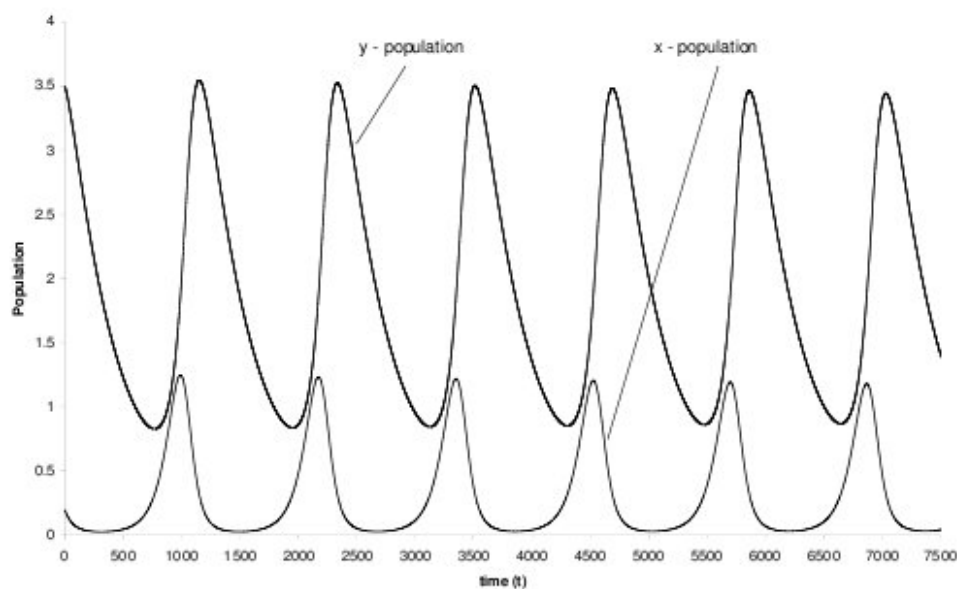


Fig. 3. Limit cycle solution for Gause model.

observed that limit cycle oscillations in Gause model settles down to a steady state solutions (see Fig. 4). This observation indicates that infection in prey population has a stabilizing effect.

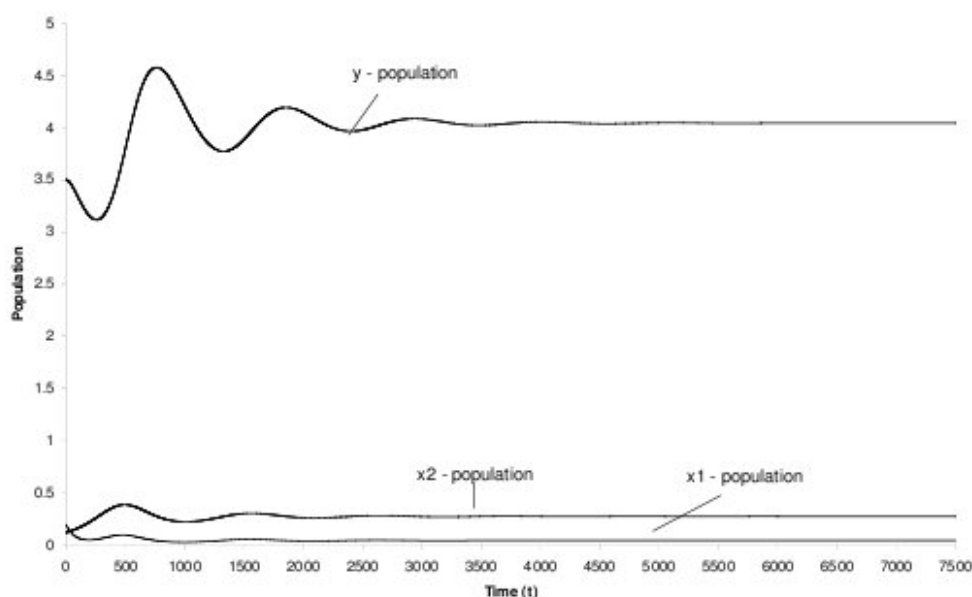


Fig. 4. Stable situation of system 2.3.

3. Conclusion

The dynamics of predator-prey systems are well known but the role of infection in these systems can not be ignored. In this paper we attempted to see the role of infection in the generalized Gause predator prey model and arrived at the conclusion that level of infection plays an important role in determining the dynamics of the system around the positive interior equilibrium. Moreover the disease on prey population may act as a biological control for the persistence of the species.

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