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Stability of Modified Host-Parasitoid Model with Allee Effect

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Abstract

This paper deals with a host-parasitoid model subject to Allee effect and its dynamical behavior. Steady state points of the proposed host-parasitoid model are computed. Stability properties are analyzed with eigen values of Jacobian matrix which are determined at the steady states. Theoretical findings are supported by numerical illustrations and enhanced by pictorial representations such as bifurcation diagrams, phase portraits and local amplifications for different parameter values. Existence of chaotic behavior in the system is established via bifurcation and sensitivity analysis of the system at the initial conditions. Various phase portraits are simulated for a better understanding of the qualitative behavior of the considered model.

Keywords: Discrete-time; Host-parasitoid model; Stability; Steady state point; Maynard-Smith form; Allee effect

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1. Introduction

The behavior of the population can be studied, analyzed and predicted by means of suitable mathematical models. Biological parameters which are introduced in the model influence its stability as seen in Gümüş (2014) and Merdan et al. (2018). Classical prey predator model was formulated by Alfred J. Lotka in 1925 and Vito Volterra in 1926, independently. Volterra predicted oscillations in prey and predator fish populations in the Adriatic Sea. Basic Lotka-Volterra model considered only the growth and death rates of the species. Also, the model assumed that there will be unrestricted growth of prey in the absence of predator. In view of more accurate predictions, many researchers studied the model with a logistic growth term which does not permit infinite growth. Later on, more realistic models were developed by introducing functional responses like Holling Type Functional Responses (I,II,III and IV), Crowley-Martin Response Function and Beddington-DeAngelis Functional Response (Ashok et al. (2018); Lazaar and Mustapha (2019); Moulipriya et al. (2017)).

The Allee factor is one such parameter which is vital to study the stability of an ecological model. Warder Clyde Allee was an American ecologist who explored an effect called Allee Effect (earlier *the Allee principle*) on smaller populations. It defines a relation between population density and the per capita growth rate. To be precise, it means that for smaller populations, the reproduction and individual fitness decrease. When the population grows larger, this effect usually saturates or disappears. Allee effect comes in to play in natural population, when decrease in per capita growth rate of a population at densities less than a critical value leads to limitations in finding mates. Allee effect is useful in studying the dynamics of endangered and rare populations. Thus the models involving allee effect are essential in conservation ecology (Allee (1931); Din (2017); Selvam et al. (2018); Gümüş and Kose (2012); Gümüş (2015); Manoj Kumar and Bhadauria (2019); Merdan and Gümüş (2012)).

Host- Parasitoid model is an example of population model (Allen (2007); Din et al. (2017); Din and Hussain (2019); Nicholson and Bailey (1935)). Wasps, flies, moths and lacewings are some examples of parasitoid species and most of the parasitoids are insects. It is estimated that there are about $800,000$ parasitoid species. Parasites benefit from other organisms, the hosts, which may lose their life at the end of the encounter. Parasitoids are insect species where larvae develops as parasites on the hosts. Parasitoid larvae utilizes the resources from the host and may eventually kill its host whereas adult parasitoids are free-living insects. Parasitoids and their hosts often have synchronized life-cycles, e.g., both have one generation per year. Thus, host-parasitoid models usually prefer to use discrete time steps that corresponds to generations (Gümüş (2017); Gümüş (2018); Huu et al. (2008); May et al. (1981); Schreiber (2006); Tang and Chen (2002)). When a suitable host is found, parasitoid lays only a single egg in it. However, the same host can be found again later and then the parasite will lay another egg in it because parasites do not distinguish between healthy hosts and already parasitized hosts. In Nicholson and Bailey model, the potential fecundity of parasites is not limited. Parasites lay an egg at every encounter with the host even when the number of encounters is very large. Thus, this model may overestimate parasitism rates at high host density.

Motivated by the important role of Allee effect in conservation biology, we propose to study the impact of Allee effect in a host parasitoid system. This work is organized in the following manner. Section 2 describes the model under discussion. In Section 3, we obtain steady state points and stability is analyzed. In Section 4, a special form of Allee effect is introduced for illustrating the dynamical properties of the system with time plots and bifurcation diagrams. Existence of chaos is established and sensitivity of the system to initial conditions is also analyzed. Finally, the paper ends with a section on conclusion.

2. Model Description

This paper aims at investigating the dynamical properties, especially, the stability of the host parasitoid system with Allee effect. In the following sections, we investigate the stability behavior of a host-parasitoid model with the Allee effect (Gümüş (2017)) connected to Maynard-Smith growth (Smith (1974)) of the form:

$$\begin{aligned} x_{n+1} &= \frac{r x_n \alpha(x_n)}{1+(r-1)x_n^p} e^{-a y_n}, \\ y_{n+1} &= c x_n (1 - e^{-a y_n}), \end{aligned} \tag{1}$$

where $r > 1$ and $a, c, p > 0$, x_n is the host population at time n, y_n is the parasitoid population at time n, $\frac{r}{1+(r-1)x_n^p}$ is the growth rate of the host population, c is the number of eggs laid by parasitoid. Here, $\alpha(x_n)$ is the Allee function at n^{th} generation.

The conclusion of the biological facts requires the following assumptions on α :

(1) if $N = 0$, then $\alpha(N) = 0$, i.e., there is no reproduction without partners.
(2) $\alpha'(N) > 0$ for $N \in (0, \infty)$, i.e., the effect of Allee parameter decreases as density increases.
(3) $\lim_{N\to\infty} \alpha(N) = 1$. That is, Allee effect vanishes at high densities.

3. Main Results

This section is devoted to the computation of steady state points of model (1) and the study of local asymptotic stability of these points.

3.1. Steady state points of model (1)

Now, let us determine the steady state points of the model (1) by setting $x_n = x_{n+1} = x_1^*$ and $y_n = y_{n+1} = y_1^*$ where (x_1^*, y_1^*) denote the steady state points. Thus, system (1) is transformed in to

$$\begin{aligned} x_1^* &= \frac{r x_1^* \alpha(x_1^*)}{1+(r-1)x_1^{*p}} e^{-a y_1^*}, \\ y_1^* &= c x_1^* (1 - e^{-a y_1^*}). \end{aligned} \tag{2}$$

Assume that model (1) has positive steady state points. Then, we have the following theorem.

Theorem 3.1.

If $\frac{1+(r-1)x_1^{*p}}{r\alpha(x_1^*)} < 1$ such that $x_1^* \neq 0$, then model (1) has steady states (x_1^*, y_1^*). Otherwise, model (1) has the steady state $(x_1^*, 0)$.

Proof:

Let us consider $x_1^* \neq 0$ and $y_1^* = 0$. Then, we can write

$$x_1^* = \frac{r x_1^* \alpha(x_1^*)}{1+(r-1)x_1^{*p}} e^{-a y_1^*},$$

which implies that,

$$r = \frac{1+(r-1)x_1^{*p}}{\alpha(x_1^*)}\ . \tag{3}$$

Let us define the following function by considering the right hand side of the Equation (3) such that

$$k(x) = \frac{1+(r-1)x^p}{\alpha(x)}, \quad x_1^* \neq 0. \tag{4}$$

From (4), we can see that the presence of an interaction point in Equation (3) can be determined by a simple analysis of function $k(x)$ for the selected function $\alpha(x)$ and values of p.

Now, let us investigate other steady state points (x_1^*, y_1^*) of the model (1) such that $x_1^* \neq 0$ and $y_1^* \neq 0$. By considering the first equality, we can write

$$e^{-a y_1^*} = \frac{1+(r-1)x_1^{*p}}{r\alpha(x_1^*)}, \tag{5}$$

which implies,

$$y_1^* = -\frac{1}{a} \ln\left[\frac{1+(r-1)x_1^{*p}}{r\alpha(x_1^*)}\right]. \tag{6}$$

If the following inequality holds

$$0 < \frac{1+(r-1)x_1^{*p}}{r\alpha(x_1^*)} < 1,$$

then, $y_1^* > 0$ in Equation (6). Since $x_1^* \neq 0$ and $r > 1$, it is clear that $\frac{1+(r-1)x_1^{*p}}{r\alpha(x_1^*)} > 0$. Then, we have

$$\frac{1+(r-1)x_1^{*p}}{r\alpha(x_1^*)} < 1. \tag{7}$$

When Equation (5) is combined with the second equation, we obtain

$$y_1^* = c x_1^* \left(1 - \frac{1+(r-1)x_1^{*p}}{r\alpha(x_1^*)}\right).$$

If y_1^* is used in the first equation, then we obtain

$$x_1^* = \frac{r x_1^* \alpha(x_1^*)}{(1+(r-1)x_1^{*p})} e^{-ac x_1^* \left(1-\frac{1+(r-1)x_1^{*p}}{r\alpha(x_1^*)}\right)}.$$

Therefore,

$$r = \frac{1+(r-1)x_1^{*p}}{\alpha(x_1^*)} e^{acx_1^*\left(1-\frac{1+(r-1)x_1^{*p}}{r\alpha(x_1^*)}\right)}. \tag{8}$$

We shall write the following function $h(x)$ by using the right hand side of Equation (8) for $x_1^* = x$,

$$h(x) = \frac{1+(r-1)x^p}{\alpha(x)} e^{acx\left(1-\frac{1+(r-1)x^p}{r\alpha(x)}\right)}.$$

Similarly, we can see that Equation (8) can have many interaction points. This situation can be determined by a simple analysis of the function $h(x)$ for the selected function $\alpha(x)$ and values p, a, c, r. ■

3.2. Stability analysis of model (1)

This section analyze the local asymptotic stability conditions of steady state points of model (1). If model (1) is considered, we can write

$$\begin{aligned} F(H_t, P_t) &= \frac{rx_n\alpha(x_n)}{1+(r-1)x_n^p} e^{-ay_n}, \\ G(H_t, P_t) &= cx_n(1-e^{-ay_n}). \end{aligned} \tag{9}$$

Then, we state the following theorem.

Theorem 3.2.

For the steady state points of the model (1), the following statements hold:

(a) Assume that inequality (7) is not provided. The steady state $(x_1^*, 0)$ of the model (1) is locally asymptotically stable if $acx_1^* < 1$ and

$$\left| \frac{r\left[(\alpha(x_1^*) + \alpha\prime(x_1^*)x_1^*)(1+(r-1)x_1^{*p}) - p(r-1)x_1^{*p}\alpha(x_1^*)\right]}{(1+(r-1)x_1^{*p})^2} \right| < 1$$

such that $x_1^* \neq 0$.

(b) Assume that inequality (7) is provided. The steady state (x_1^*, y_1^*) of the model (1) is locally asymptotically stable under

$$\begin{aligned} &\left| e^{-ay_1^*}\left(acx_1^* + \frac{r\left[(\alpha(x_1^*) + \alpha\prime(x_1^*)x_1^*)(1+(r-1)x_1^{*p}) - p(r-1)x_1^{*p}\alpha(x_1^*)\right]}{[1+(r-1)x_1^{*p}]^2} \right) \right| \\ &< 1 + e^{-2ay_1^*} \frac{acx_1^* r\left[(\alpha(x_1^*) + \alpha\prime(x_1^*)x_1^*)(1+(r-1)x_1^{*p}) - p(r-1)x_1^{*p}\alpha(x_1^*)\right]}{[1+(r-1)x_1^{*p}]^2} \\ &+ \frac{e^{-ay_1^*}arcx_1^*\alpha(x_1^*)(1-e^{-ay_1^*})}{1+(r-1)x_1^{*p}} < 2. \end{aligned}$$

Proof:

(a) On the assumption, let $(x_1^*, 0)$ be the unique steady state of the model (1). The Jacobian matrix evaluated in the neighborhood of $(x_1^*, 0)$ is then written as follows:

$$J_{(x_1^*,0)} = \begin{bmatrix} \frac{r[(\alpha(x_1^*)+\alpha'(x_1^*)x_1^*)(1+(r-1)x_1^{*p})-p(r-1)x_1^{*p}\alpha(x_1^*)]}{(1+(r-1)x_1^{*p})^2} & -\frac{arx_1^*\alpha(x_1^*)}{1+(r-1)x_1^{*p}} \\ 0 & acx_1^* \end{bmatrix}. \tag{10}$$

The eigenvalues of $J_{(x_1^*,0)}$ are $\lambda_1 = \frac{r[(\alpha(x_1^*)+\alpha'(x_1^*)x_1^*)(1+(r-1)x_1^{*p})-p(r-1)x_1^{*p}\alpha(x_1^*)]}{(1+(r-1)x_1^{*p})^2}$ and $\lambda_2 = acx_1^*$. Consequently, $(x_1^*, 0)$ is locally asymptotically stable if

$$\left|\frac{r\left[(\alpha(x_1^*)+\alpha'(x_1^*)x_1^*)(1+(r-1)x_1^{*p})-p(r-1)x_1^{*p}\alpha(x_1^*)\right]}{(1+(r-1)x_1^{*p})^2}\right| < 1 \text{ and } acx_1^* < 1. \tag{11}$$

(b) On the assumption, we consider that condition (7) is provided. The Jacobian matrix evaluated in the neighborhood of (x_1^*, y_1^*) is written as follows:

$$J_{(x_1^*,y_1^*)} = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix}. \tag{12}$$

Here,
$a_{11} = \frac{re^{-ay_1^*}[(\alpha(x_1^*)+\alpha'(x_1^*)x_1^*)(1+(r-1)x_1^{*p})-p(r-1)x_1^{*p}\alpha(x_1^*)]}{[1+(r-1)x_1^{*p}]^2}$, $a_{12} = \frac{-e^{-ay_1^*}arx_1^*\alpha(x_1^*)}{1+(r-1)x_1^{*p}}$, $a_{21} = c(1-e^{-ay_1^*})$ and $a_{22} = acx_1^*e^{-ay_1^*}$.

From the definition of the determinant and the trace of the matrix $J_{(x_1^*,y_1^*)}$, we can write

$$\begin{aligned} trJ_{(x_1^*,y_1^*)} &= e^{-ay_1^*}\left(acx_1^* + \frac{r\left[(\alpha(x_1^*)+\alpha'(x_1^*)x_1^*)(1+(r-1)x_1^{*p})-p(r-1)x_1^{*p}\alpha(x_1^*)\right]}{[1+(r-1)x_1^{*p}]^2}\right), \\ \det J_{(x_1^*,y_1^*)} &= \frac{e^{-2ay_1^*}acx_1^*}{[1+(r-1)x_1^{*p}]^2} r\left[(\alpha(x_1^*)+\alpha'(x_1^*)x_1^*)(1+(r-1)x_1^{*p})-p(r-1)x_1^{*p}\alpha(x_1^*)\right] \\ &+ \frac{e^{-ay_1^*}arcx_1^*\alpha(x_1^*)(1-e^{-ay_1^*})}{1+(r-1)x_1^{*p}}, \end{aligned} \tag{13}$$

respectively. If the following inequality (see Allen (2007))

$$|trJ| < 1 + \det J < 2 \tag{14}$$

is provided, then (x_1^*, y_1^*) is locally asymptotically stable. ■

Corollary 3.1.

The model (1) possess the positive steady states $(x_1^*, 0)$ and (x_1^*, y_1^*). When inequality (7) is not provided, $(x_1^*, 0)$ is the steady state of model (1) and is locally asymptotically stable under (11). When inequality (7) is provided, then the steady state (x_1^*, y_1^*) is locally asymptotically stable under (14).

Proof:

Note that the steady state $(x_1^*, 0)$ is a solution of the Equation (3) when $x_1^* \neq 0$ and $y_1^* = 0$. If $\frac{\alpha(x)}{\alpha'(x)} > \frac{1}{p(r-1)x^{p-1}} + \frac{x}{p}$, then $k(x)$ is an increasing function in $(0, \infty)$. So, Equation (3) has only one interaction point x_1^*. Consequently, this steady state $(x_1^*, 0)$ is local asymptoticaly stable under the conditions (11). Otherwise, Equation (3) can have many interaction points.

When $x_1^* \neq 0$ and $y_1^* \neq 0$, if inequality (7) is provided, then y_1^* will be a positive value. Equation (8) can have many interaction points for the selected function $\alpha(x)$ and p, r, a, c. If $h'(x) > 0$, then Equation (8) has only one solution. Consequently, (x_1^*, y_1^*) is locally asymptotically stable under the conditions (14). ■

4. Numerical Simulations

As a special case, we consider the function $\alpha\left(x_n\right)$ in the form

$$\alpha\left(x_n\right) = \frac{x_n}{b + x_n},$$

where b is the positive Allee constant. Model (1) is transformed into

$$\begin{aligned} x_{n+1} &= \frac{r x_n^2}{\left(b + x_n\right)\left(1 + (r-1)x_n^p\right)} e^{-a y_n}, \\ y_{n+1} &= c x_n (1 - e^{-a y_n}). \end{aligned} \tag{15}$$

The Jacobian matrix of the model (15) is

$$J\left(x_1^*, y_1^*\right) = \begin{bmatrix} b_{11} \; b_{12} \\ b_{21} \; b_{22} \end{bmatrix}. \tag{16}$$

Here,
$b_{11} = \frac{r x_1^* e^{-a y_1^*}\left[2(b+x_1^*)(1+(r-1)x_1^{*p}) - bp(r-1)x_1^{*p} - x_1^* - (p+1)(r-1)x_1^{*(p+1)}\right]}{[(b+x_1^*)(1+(r-1)x_1^{*p})]^2}$, $b_{12} = -\frac{a r x_1^{*2} e^{-a y_1^*}}{(b+x_1^*)(1+(r-1)x_1^{*p})}$,
$b_{21} = c\left(1 - e^{-a y_1^*}\right)$ and $b_{22} = acxe^{-a y_1^*}$.

Numerical experiments of model (15) supplement the analytical results attained in the previous section exhibit interesting dynamics of the model. Mainly, we present the trajectories of the solutions x and y with corresponding phase plane diagrams (like sinks and limit cycles) for the host-parasitoid model (15). Dynamic nature of system (15) about the steady states under various different sets of parameter values are revealed in the following numerical examples.

Example 4.1.

This example considers $r = 1.99; a = 1.25; b = 0.01; c = 2.6; p = 0.95;$ and the initial condition $(0.65, 0.45)$. Computation yields $(x_1^*, y_1^*) = (0.363, 0.2722)$. The Jacobian matrix of (15) is $J(0.363, 0.2722) = \begin{bmatrix} 0.7661 & -0.4537 \\ 0.7499 & 0.8395 \end{bmatrix}$. Here, Trace $= 1.6056$ and Det $= 0.9834$. Hence, the stability condition Trace $< 1 +$ Det < 2 is satisfied as Trace $= 1.6056 < 1.9834(1 +$ Det$) < 2$. Also the eigen values are $\lambda_{1,2} = 0.8028 \pm i5821$ such that $|\lambda_{1,2}| = 0.9917 < 1$. The criteria for stability are satisfied. Hence, the system (15) is stable. The phase portrait in Figure 1 displays a sink and the trajectory spiraling inwards towards the steady state (x_1^*, y_1^*).

Example 4.2.

Taking $r = 1.99; a = 1.25; b = 0.005; c = 2.9; p = 0.9;$ and the initial condition $(0.65, 0.45)$ results in the steady state $(x_1^*, y_1^*) = (0.3289, 0.2902)$. The Jacobian matrix of (15) is $J(0.3289, 0.2902) = \begin{bmatrix} 0.7779 & -0.4111 \\ 0.8822 & 0.8296 \end{bmatrix}$. Here, Trace $= 1.6075$ but Det $= 1.0080$. Hence, the stability condition Trace $< 1 +$ Det < 2 is not satisfied as Trace $= 1.6075 < 2.0080(1 +$ Det$)$ and $2.0080(1+$Det$) > 2$. Also the eigenvalues are $\lambda_{1,2} = 0.8037 \pm i6017$ such that $|\lambda_{1,2}| = 1.0040 > 1$. Thus, the criteria for stability are not satisfied. Hence, the system (15) is unstable. The trajectory spirals inwards but does not approach a single point. The trajectory finally settles down as a limit cycle, see the phase portrait in Figure 2.

The qualitative nature of a system can change as certain parameters are varied. In particular, stability nature of the steady states can change suddenly. These qualitative changes in the dynamics are often termed as bifurcation. In short, qualitative changes are tied with bifurcation. The parametric values at which they occur are called bifurcation points. Five cases are considered for the parameters (bifurcation) r, a, b, c and d.

Case I: Parameters are assigned the values $a = 1.5; b = 0.01; c = 2.4; p = 0.95$ with the initial value $(0.65, 0.45)$. Bifurcation is plotted for the growth parameter r in the range $1.2 - 4$. Reverse bifurcation of host-parasitoid population is produced in Figure 3. The system moves from chaotic behavior to order and finally tends to a stable steady state.

Case II: Take the parameter values $r = 1.99; b = 0.01; c = 2.6; p = 0.95$ with the initial value $(0.65, 0.45)$, bifurcation diagram is plotted for a in the range $1 - 2.05$. Host-parasitoid population tends to the stable steady state and its stability is lost and leading to chaos (see Figure 4).

Case III: Considering the parameter values $r = 1.99; a = 1.25; c = 2.6; p = 0.95$ along with the initial value $(0.65, 0.45)$, bifurcation parameter is chosen as b and the bifurcation is obtained for the parameter b in the range $0 - 0.065$, see Figure 5.

Case IV: Consider the values $r = 1.99; a = 1.25; b = 0.01; p = 0.95$ with the initial value $(0.65, 0.45)$. By taking c as the bifurcation parameter, bifurcation diagram is plotted for in the range $2 - 4.2$ (see Figure 6).

Case V: Choosing the parameter values $r = 1.95; a = 1.5; b = 0.05; c = 1.9$ with the initial value $(0.65, 0.35)$, bifurcation diagrams of (15) are exhibited in Figure 7 with p as the bifurcation parameter in the range $0.5 - 12$. Unique bifurcation diagrams for both host and parasitoid population appear and it is observed that the system is initially stable and loss its stability, then becomes unstable and finally exhibits chaos.

Figure 8 and 9 are local amplifications of Figure 7, showing periodic window appearing in the chaotic region. In periodic window, emerges periodic orbits. In addition, each window proceeds a sub periodic doubling cascade and leads to chaos.

Phase plane portraits are also presented for the system with various values of p in Figure 10. For $p = 1$ and $p = 1.3$, the solution curves spiral inwards and converges to a point indicating stability and for $p = 1.4$ though curve spirals inwards, it settles down as limit cycle. For $p = 1.7 - 5.66$, the solution curve spirals inwards, but does not converge to a point and circles are formed with different radii. Finally, for $p = 6 - 11$, chaotic attractors appear. Comparing the bifurcation and phase plane diagrams, we justify our conclusions.

A characteristic of chaos is its dependency on initial conditions. In order to analyze the sensitivity of the system (15) to initial values, two paths are calculated with initial conditions (x_0, y_0), $(x_0 + 0.00001, y_0)$ as well as $(x_0, y_0 + 0.00001)$ respectively. The result is displayed in Figure 11. Initially, the two trajectories are impossible to distinguish; however there is a separation between them after a certain number of iterations, which builds up rapidly.

5. Conclusion

This paper includes the qualitative nature of a discrete host-parasitoid model by involving Allee effect. Biologically meaningful positive steady states are computed. Stability conditions are discussed with Jacobian matrices calculated at the steady state points. Jury conditions are used in the investigation of dynamical behavior of the model especially the local stability analysis of the steady states. Moreover, the system undergoes bifurcation when the chosen parameter passes through a critical value, and closed invariant curves arise from a stable equilibrium state. The analytical results are strengthened with appropriate simulations and the system demonstrates chaotic behavior over a wide range of parameters.

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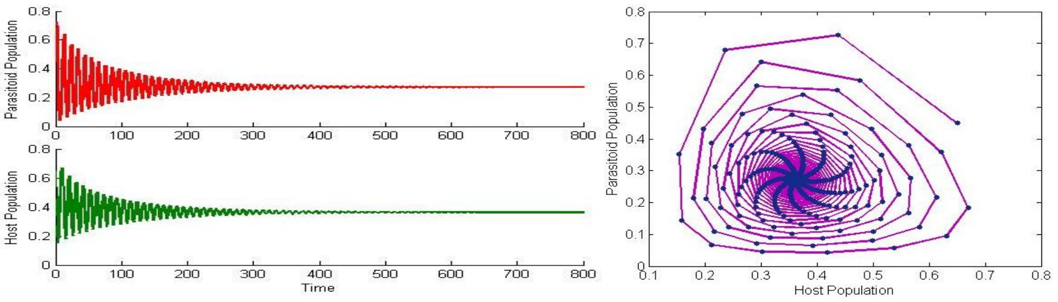

Figure 1. Stability of the model (15)

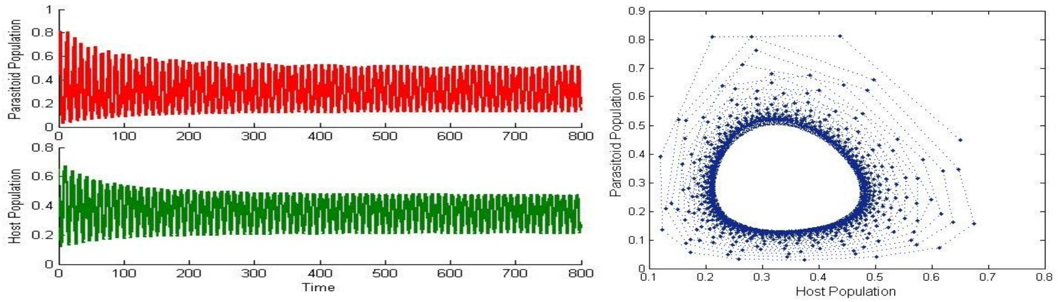

Figure 2. Unstability of the model (15)

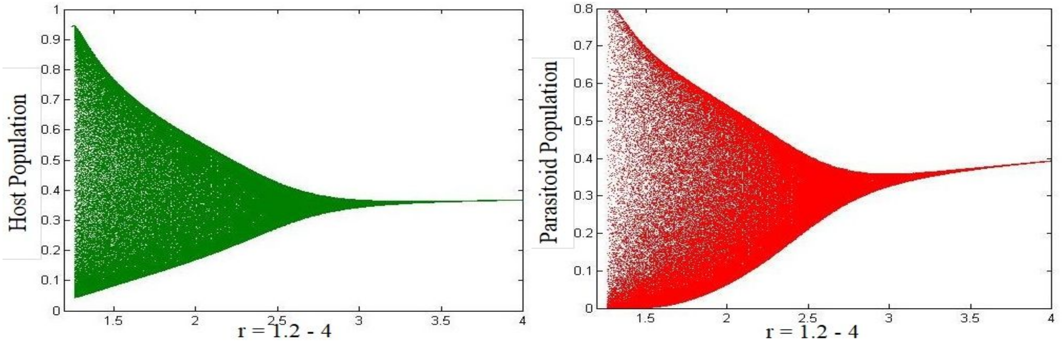

Figure 3. Bifurcation structure of host-parasitoid population model (15) corresponding to r

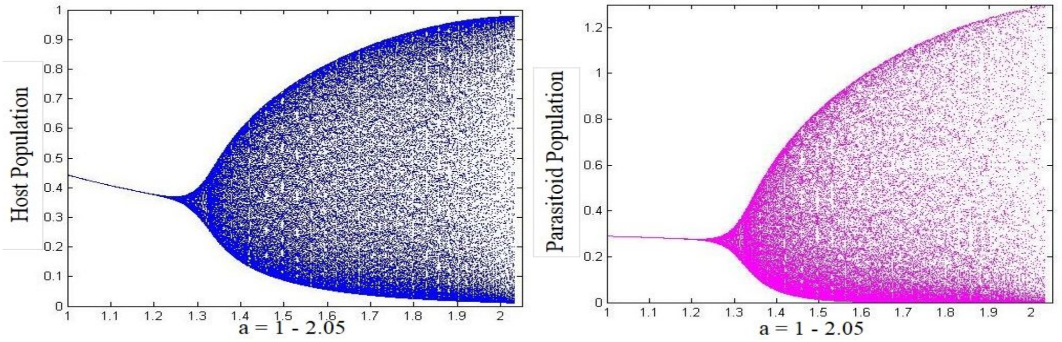

Figure 4. Bifurcation structure of host-parasitoid population model (15) corresponding to a

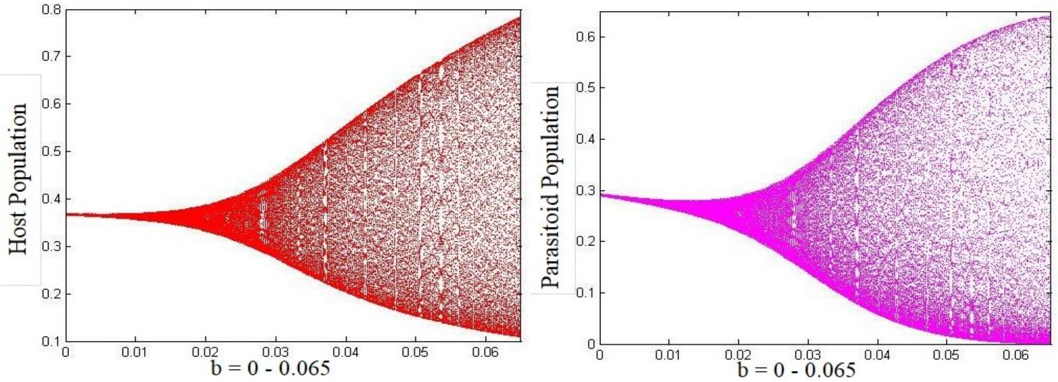

Figure 5. Bifurcation structure of host-parasitoid population model (15) corresponding to b

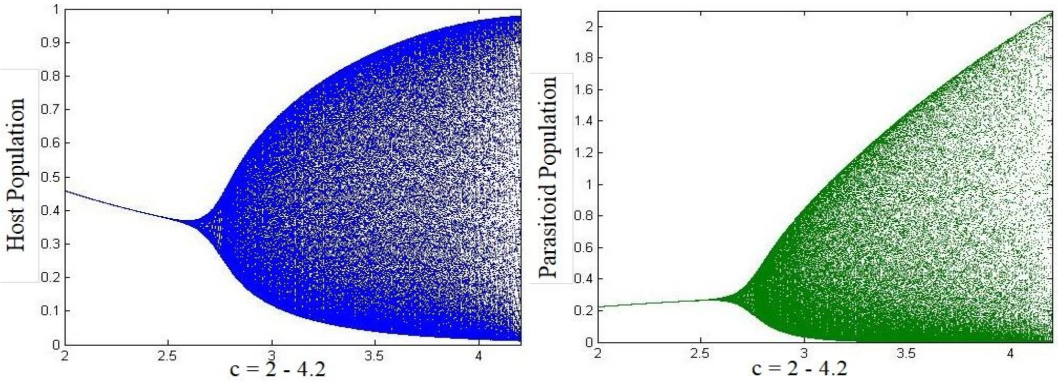

Figure 6. Bifurcation structure of host-parasitoid population model (15) corresponding to c

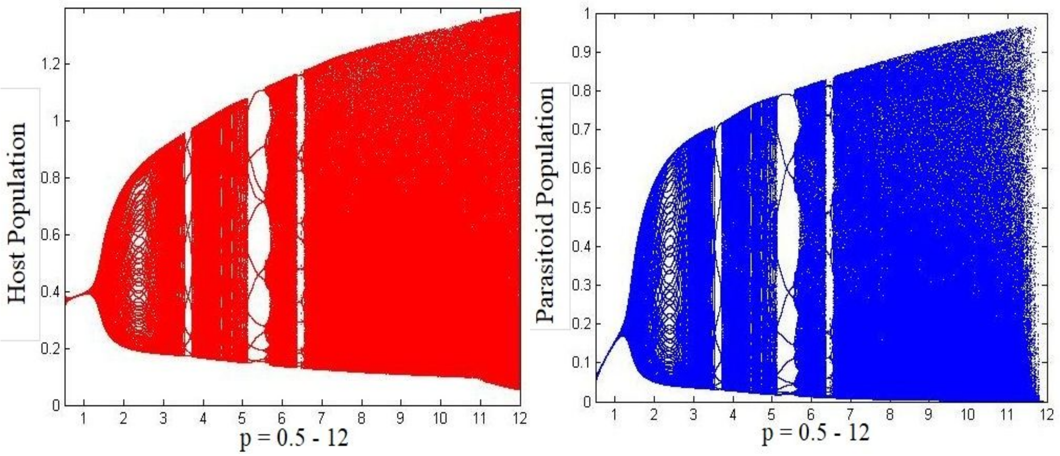

Figure 7. Bifurcation structure of host-parasitoid population model (15) corresponding to p

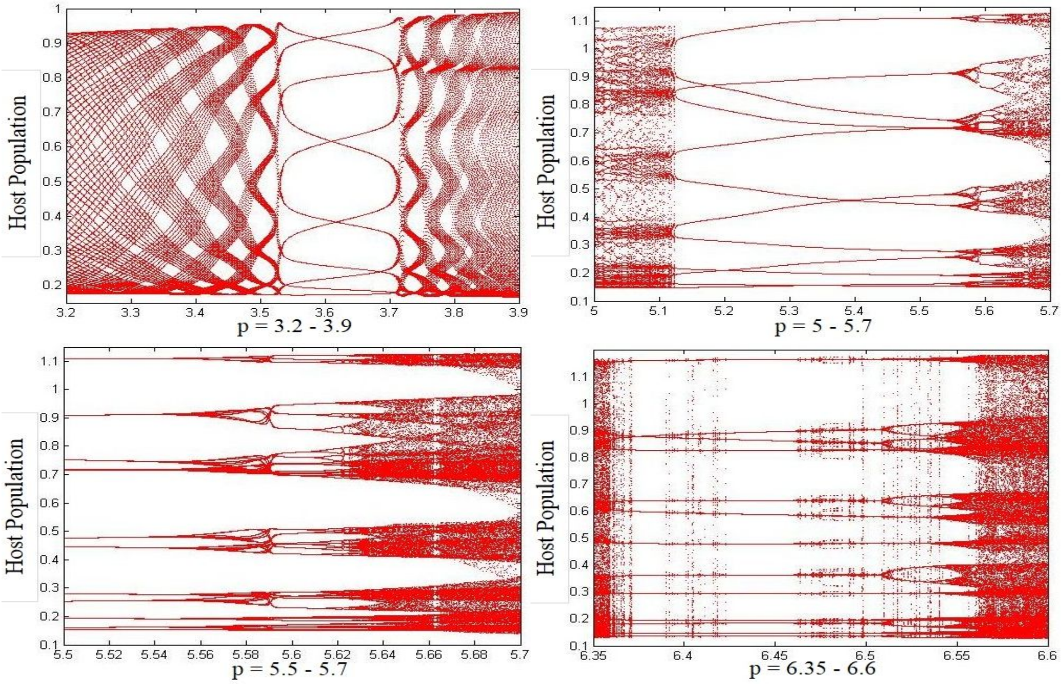

Figure 8. Local amplification of Host population model (15) corresponding to p

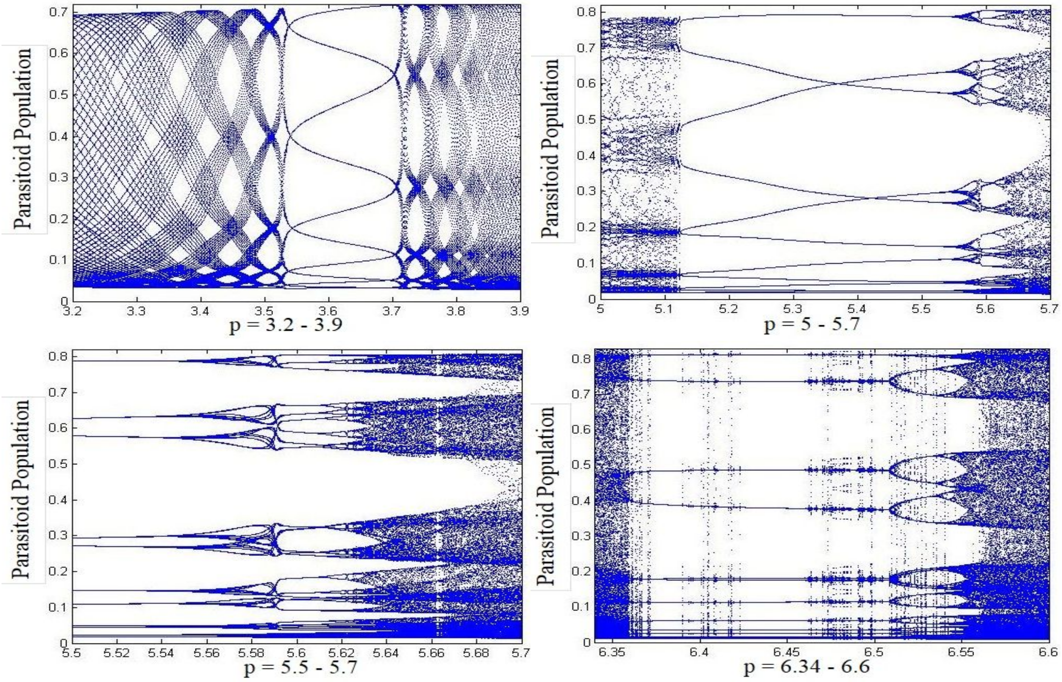

Figure 9. Local amplification of parasitoid population model (15) corresponding to p

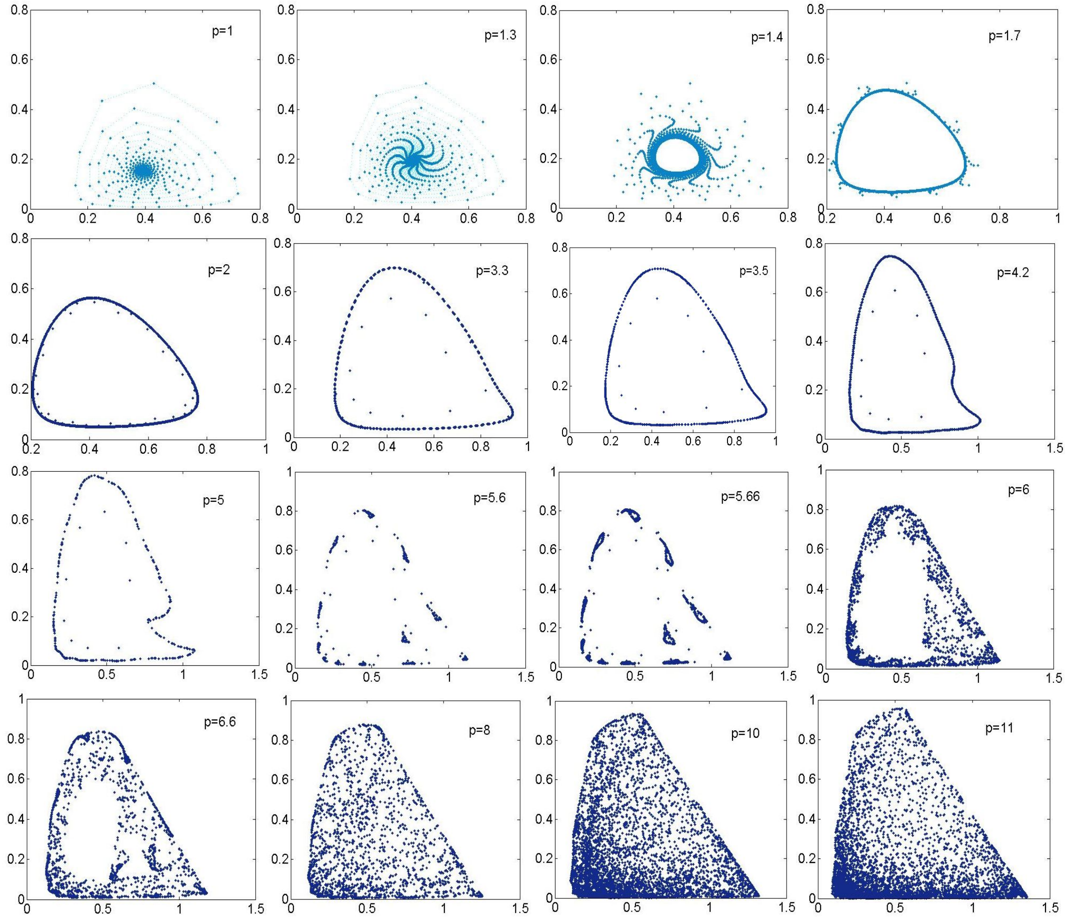

Figure 10. Phase portraits of the host-parasitoid population model (15) for different values of p

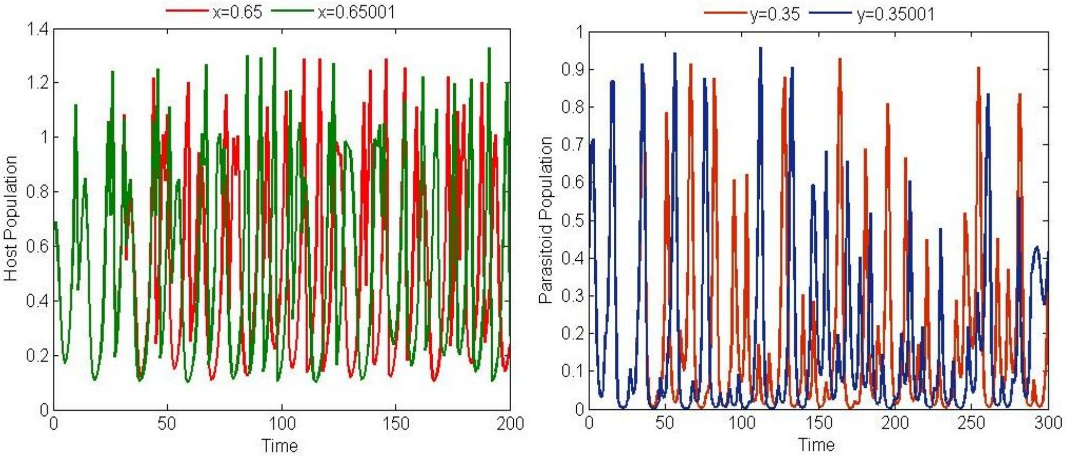

Figure 11. Sensitive analysis for the host-parasitoid population model (15)