

# The sterile insect release technique in a predator–prey system with monotone functional response

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**Abstract.** In this paper, we focus on the sterile insect release technique (SIRT) in a predator–prey system with monotone functional response. Unlike most of the existing modeling studies in this field that mainly deal with the pest population only, we have incorporated the predation population as a distinct dynamical equation together with the wild and sterile insect pests. The aim is to investigate the influence of the predation on the SIRT. We use both the continuous model and the impulsive model to carry out a theoretical study, discuss the dynamical behaviour of the model, and compute the critical conditions for eradication of wild insects. We get that both kinds of the predator–prey system with the most popular functional responses Holling type II and III and some other monotone response functions always have the wild insects eradication solution under the certain conditions. Our analytical findings are verified through computer simulation.

**Keywords:** sterile insect release technique, saddle–node bifurcation, Hopf bifurcation, impulsive differential equations, global stability.

**2010 Mathematics Subject Classification:** 92D25, 34C25.

## 1 Introduction

People want to control insect populations, not only because some insects disseminate vector-borne diseases but simply because some insects cause huge economic losses in global food production. Several kinds of methods and tools, e.g. pesticide, predators and pathogens, are used to manage or eradicate insects. One commonly used method is the sterile insect release technique (SIRT) which was introduced by Knippling [8]. Compared with other methods, SIRT is friendly to the environment and is easily operated for the practitioners.

Mathematical models have been used to answer important questions about SIRT since the 1950s [3,5,19]. In 1955, Knippling [8] defined a pest population in a single equation as a discrete time difference equation and Barclay [2,4] in 1980 modeled it as a continuous time differential equation and they found the insects could be eradicated by SIRT. In their models, sterile insects were released at a constant level to reduce the pest population and they calculated the

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minimum rate of sterile releases required to eradicate the insects' population. Esteva et al. [6] in 2005 reported that *Aedes aegypti* mosquitoes had been controlled by using SIRT. Meats et al. [11] proved that Queensland fruit fly *Bactrocera tryoni* has been controlled in South Australia. In fact, all the developed countries increasingly realized the potential of SIRT in the control of exotic insects [10,20].

In this paper we use two models to investigate the influence of the predation on the SIRT. The first one is under the framework of Murray's model in [12]. In his work, the population of sterile insects is kept as a constant. We extend Murray's model to a general predator-prey model and carry out a theoretical study, discuss the dynamical behaviour of the model, and compute the critical conditions for eradication of wild insects. In order to account for the release of sterile insects, we introduce the second model, a periodic or pulsed release method, which is fairly well modelled by an impulsive system of ordinary differential equations. The impulsive model is widely used in the area of epidemiology and population dynamics. Compared with the continuous system, the pulsed SIRT is easily operated for the practitioners. We calculate a critical condition for eradication of wild insects and get the global stability of the trivial solution of the impulsive SIRT model. We also show that the impulsive SIRT model may have a semi-trivial periodic solution.

This paper is organized as follows. In Section 2, we recall a special continuous release of sterile insect model which was introduced by Murray in [12]. In Section 3, we consider a continuous predator-prey model with SIRT. We discuss the dynamical behaviour of the system, and get the critical conditions for eradication of wild insects. In Section 4, we introduce a impulsive model with SIRT. We get the trivial solution and semi-trivial solution of the system, and give the release strategy for wild insects eradication. We compare the two different models and summarize our major results in Section 5.

## 2 A basic SIRT Model

The sterile insect release technique use the following equation to depict wild insects population:

$$\frac{dx}{dt} = \left( a \frac{x}{x+y} - b \right) x - kx(x+y), \quad (2.1)$$

where  $x, y$  are the wild insects and sterile insects, respectively;  $a, b$  represent the birth rate, the density-independent death rate of wild insects, respectively;  $k$  represents the density-dependent death rate of wild insects and  $-kx(x+n)$  summarizes the competition between wild insects and sterile insects. We assume that  $K$  denotes the carrying capacity of wild insects and it is given by  $K = \frac{a-b}{k}$ .

We now study a special continuous release of sterile insects model which was introduced by Murray in [12]. He kept the sterile insects  $y$  as a constant  $y = n$ , then equation (2.1) becomes

$$\frac{dx}{dt} = \left( a \frac{x}{x+n} - b \right) x - kx(x+n) = x * f(x). \quad (2.2)$$

The number of equilibria of equation (2.2) is determined by the discriminant  $\Delta$  of  $f(x) = 0$ , which is given by

$$\Delta = (a-b)^2 - 4kna.$$

Notice the null line  $(a \frac{x}{x+n} - b)x - kx(x+n) = x * f(x) = 0$  in the  $x-n$  plane in (3.1). The

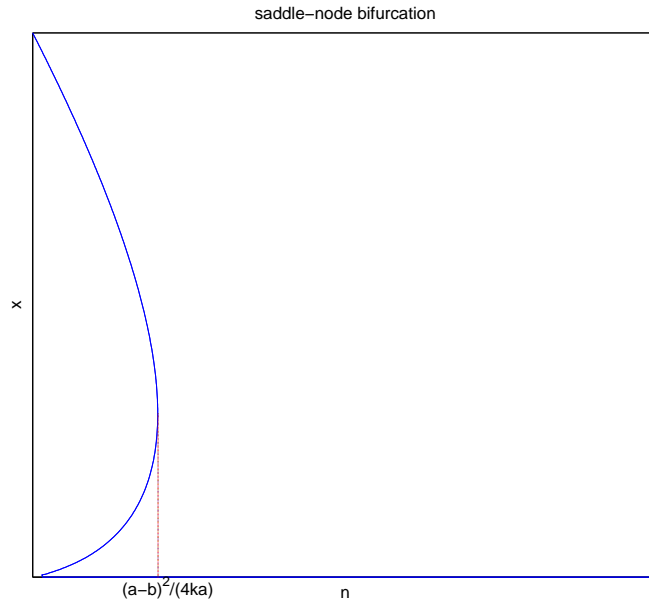


Figure 2.1: The saddle-node bifurcation of the system (2) with respect to  $n$ .

system (2.2) has three equilibria,  $x_0 = 0$ ,  $x_+$ ,  $x_-$  given by

$$x_+ = \frac{a - b - 2kn + \sqrt{\Delta}}{2k}, \quad x_- = \frac{a - b - 2kn - \sqrt{\Delta}}{2k},$$

where necessarily, we must have  $\Delta \geq 0$ . So the features of the dynamics of system (2.2) can be summarized in the following results.

**Lemma 2.1.** *The equilibria of system (2.2) satisfy the following.*

1. When  $n < \frac{(a-b)^2}{4ka}$ , the system has three equilibria,  $x_0$ ,  $x_+$ ,  $x_-$  and  $x_0$  is locally asymptotically stable,  $x_-$  always unstable,  $x_+$  is locally asymptotically stable.
2. When  $n > \frac{(a-b)^2}{4ka}$ , the system has only one equilibrium,  $x_0$  and it is globally stable.
3. When  $n = \frac{(a-b)^2}{4ka}$ , the system has two equilibria  $x_0$ ,  $x_+ = x_-$  and  $x_0$  is locally asymptotically stable,  $x_+ = x_-$  is a saddle.

**Theorem 2.2.** *Model (2.2) has a globally stable trivial solution  $x = 0$  that corresponds to wild insects eradication if  $n > \frac{(a-b)^2}{4ka}$ .*

It is important to compare this threshold with realistic size of populations (i.e. the carrying capacity  $K$ ):

$$\frac{\frac{(a-b)^2}{4ka}}{K} = \frac{1}{4} \left( 1 - \frac{b}{a} \right).$$

So if the density-independent death rate  $b$  is close to the birth rate  $a$ , the release of the sterile insects has a high efficiency.

### 3 A general SIRT Model with predator

The predator–prey system with the sterile insect technique is given by the following nonlinear differential equations system:

$$\begin{cases} \dot{x} = \left(\frac{ax}{x+n} - b\right)x - kx(x+n) - g(x,n)xz, \\ \dot{z} = h(x,n)z - dz, \end{cases} \quad (3.1)$$

where  $x, n, z$  are the wild insects, sterile insects and their nature enemy (predator), respectively. Here, the population of the sterile insects  $n$  is also a constant.  $g(x, n)$ ,  $h(x, n)$  and  $d$  denotes the predators' functional response, numerical response and mortality rate. Here we assume the predator cannot distinguish between wild insects and sterile insects. Since biological processes are always different, we only assume general hypotheses on the functions  $g(\cdot)$  and  $h(\cdot)$ . And this approach guarantees that our analyses can be applied to a wide range of biological systems.

**Hypotheses.** Let  $g(x, n)$  and  $h(x, n)$  be locally Lipschitz function on  $R^+ \times R^+$  such that:

$$(H-1)) \forall x > 0 \text{ or } n > 0, g(x, n) > 0 \text{ and } \frac{\partial g(x, n)}{\partial x} > 0, \frac{\partial g(x, n)}{\partial n} > 0, g(0, 0) = 0$$

$$(H-2)) h(0, 0) = 0, \frac{\partial h(x, n)}{\partial x} > 0, \frac{\partial h(x, n)}{\partial n} > 0$$

**Remark 3.1.** (H-1)) means our model is well-defined and if the prey is present, the predators are able to find and consume them. (H-2)) is made because our argumentation is mainly based on the fact that  $g(x, n)$  (and  $h(x, n)$ ) are monotone functions with respect to  $x$  and  $n$ . According to the monotonicity, we can get following conditions:

- (1) for two fixed number  $m$  and  $n$ , there exists only one  $x$  satisfying  $h(x, n) = m$ , i.e, there exists a inverse function  $h_x^{-1}(m, n) = x$ ;
- (2) for two fixed number  $m$  and  $x$ , there exists only one  $n$  satisfying  $h(x, n) = m$ , i.e, there exists a inverse function  $h_n^{-1}(x, m) = n$ .

A large part of the predator-prey functions encountered in the literature fit these hypotheses, such as Holling type I, II and III, sigmoidal, Ivlev and some other monotone response functions.

#### 3.1 Stability of equilibria and possible bifurcations

In this section we analyze conditions for existence and stability of the equilibrium points. For this, we first rewrite (3.1) as

$$\begin{cases} \dot{x} = x[f(x) - g(x, n)z], \\ \dot{z} = z[h(x, n) - d], \end{cases} \quad (3.2)$$

here  $f(x) = \frac{ax}{x+n} - b - k(x+n)$ . And we calculate the eigenvalues regarded to the Jacobian matrix of system (3.2), given by

$$J = \begin{pmatrix} f(x) - g(x, n)z + x\left(\frac{\partial f(x)}{\partial x} - \frac{\partial g(x, n)}{\partial x}z\right) & -g(x, n)x \\ \frac{\partial h(x, n)}{\partial x}z & h(x, n) - d \end{pmatrix}. \quad (3.3)$$

**Theorem 3.2.** *The system (3.1) has a trivial equilibrium  $(0, 0)$ , which is locally asymptotically stable (LAS) when  $h(0, n) < d$ .*

*Proof.* System (3.1) has a trivial equilibrium  $P_0 = (0, 0)$ , corresponding to the state where the wild insects and their predators are all absent. Then,

$$J_{(0,0)} = \begin{pmatrix} -b - kn & 0 \\ 0 & h(0, n) - d \end{pmatrix}, \quad (3.4)$$

so  $P_0$  is a locally asymptotically stable node if and only if  $h(0, n) < d$ .  $\square$

**Theorem 3.3.** *The system (3.1) has two feasible  $x$ -axial equilibria  $P_+ = (x_+, 0)$  and  $P_- = (x_-, 0)$  when  $n \leq \frac{(a-b)^2}{4ka}$ . In this case,  $P_-$  is always unstable and  $P_+ = (x_+, 0)$  is locally asymptotically stable (LAS) when  $n < h_n^{-1}(x_+, d)$  and  $n \neq \frac{(a-b)^2}{4ka}$ .*

*Proof.*  $x_+/x_-$  is the solution of  $f(x) = 0$ , and  $x_+/x_- = \frac{a-b-2kn \pm \sqrt{(a-b)^2 - 4kan}}{2k}$ , which are positive if and only if  $n \leq \frac{(a-b)^2}{4ka}$ . And

$$J_{(x_+/x_-, 0)} = \begin{pmatrix} \frac{\partial f(x_{\pm})}{\partial x} x_{\pm} & -g(x_{\pm}, n) x_{\pm} \\ 0 & h(x_{\pm}, n) - d \end{pmatrix}. \quad (3.5)$$

So,  $P_+/P_-$  is stable if and only if

$$\frac{\partial f(x_{\pm})}{\partial x} < 0, h(x_{\pm}, n) - d < 0.$$

And after calculation, we get  $\frac{\partial f(x_-)}{\partial x} > 0$  when  $n < \frac{(a-b)^2}{4ka}$ , so  $P_-$  is always unstable. If  $h(x_-, n) < d$ ,  $P_-$  is a saddle; if  $h(x_-, n) > d$ ,  $P_-$  is an unstable node.

When  $n < \frac{(a-b)^2}{4ka}$ , we have  $\frac{\partial f(x_+)}{\partial x} < 0$ . So if  $h(x_+, n) < d$ ,  $P_+$  is a locally asymptotically stable node; if  $h(x_+, n) > d$ ,  $P_+$  is a saddle.

So  $h(x_-, n) < d$  and  $h(x_+, n) > d$ , there exists a heteroclinic orbit between  $P_-$  and  $P_+$ .  $\square$

**Theorem 3.4.** *The interior equilibrium  $P^* = (x^*, z^*)$  of system (3.1) is feasible when  $x^* = h_x^{-1}(d, n) > 0$  and  $\frac{f(x^*)}{g(x^*, n)} > 0$ . Furthermore, it is locally asymptotically stable when  $(\frac{f(x)}{g(x, n)})'_x|_{x^*} < 0$ .*

*Proof.* The interior equilibrium of system (3.1) is  $(x^*, z^*) = (h_x^{-1}(d, n), \frac{f(x^*)}{g(x^*, n)})$ , here we need  $x^*, z^*$  is positive. And we know if  $h(0, n) < d$  and  $h(x^*, n) = d$ , then we have  $x^* > 0$ ; if  $h(0, n) > d$  and  $h(x^*, n) = d$ , then we have  $x^* < 0$ . By calculation, we get if  $n > \frac{(a-b)^2}{4ka}$ , we have  $z^* = \frac{f(x^*)}{g(x^*, n)} < 0$ .

The Jacobian matrix is

$$\begin{aligned} J &= \begin{pmatrix} f(x) - g(x, n)z + x(\frac{\partial f(x)}{\partial x} - \frac{\partial g(x, n)}{\partial x}z) & -g(x, n)x \\ \frac{\partial h(x, n)}{\partial x}z & h(x, n) - d \end{pmatrix} \Big|_{(x^*, z^*)} \\ &= \begin{pmatrix} x^*(\frac{\partial f(x^*)}{\partial x} - \frac{\partial g(x^*, n)}{\partial x}z^*) & -g(x^*, n)x^* \\ \frac{\partial h(x^*, n)}{\partial x}z^* & 0 \end{pmatrix} \doteq \begin{pmatrix} A & -B \\ C & 0 \end{pmatrix}. \end{aligned}$$

The stability of  $P^*$  is given by the sign of  $\frac{\partial f(x^*)}{\partial x} - \frac{\partial g(x^*, n)}{\partial x}z^*$ . So it is stable if and only if  $\frac{\partial f(x^*)}{\partial x} - \frac{\partial g(x^*, n)}{\partial x} \frac{f(x^*)}{g(x^*, n)} < 0$ , which is equal to  $(\frac{f(x)}{g(x, n)})'_x|_{x^*} < 0$ .

Furthermore, if  $A^2 - 4BC > 0$ ,  $P^*$  is a node. If  $A = 0$ ,  $P^*$  is a center. And if  $A^2 - 4BC < 0$ ,  $P^*$  is a focus. According to the Hopf bifurcation theory, there may exist a Hopf bifurcation when  $A^2 - 4BC = [x^*(\frac{\partial f(x^*)}{\partial x} - \frac{\partial g(x^*, n)}{\partial x}z^*)]^2 - 4 * [g(x^*, n)x^*][\frac{\partial h(x^*, n)}{\partial x}z^*] \leq 0$ . By choosing the value of the parameters, we could conclude the stability of the bifurcating periodic orbit by using [7, Theorem 3.4.2].  $\square$

**Theorem 3.5.** All the points on the  $z$ -axis  $P_z = (0, z_+)$  are the equilibrium when  $n = h_n^{-1}(0, d)$ .

*Proof.* In this case, the  $z$ -axis is an invariable region of the system. For any  $P_z = (0, z_+)$  on the  $z$ -axis, the Jacobian is

$$J_{(0,0)} = \begin{pmatrix} -b - g(0, n)z^* & 0 \\ \frac{\partial h(x, n)}{\partial x} z^* & 0 \end{pmatrix}.$$

According to the inequality  $f(0, n) = -b - kn < 0$  and the continuity of  $f(x, n)$ , there exist a region  $(x, z) \in (0, \epsilon) \times \mathbb{R}^+$  in which the stable manifold  $(x, z^*)$  move to  $(0, z^*)$  and the centre manifold  $(0, z)$  always stay its initial position. For this we could say this invariable region is local attracting.  $\square$

### 3.2 Global dynamics and condition for wild insects eradication

The analysis given above can be applied in the context of wild insects eradication. According to the Theorems 3.2–3.5, the system may have one or two or even more locally stable equilibria.

**Case 1.** When  $n > \frac{(a-b)^2}{4ka}$

According to Theorem 3.3 and 3.4, we know  $P_{\pm}$  does not exist. For the interior equilibrium  $P^*$ ,  $z^* < 0$  means that  $P^*$  does not exist in the first quadrant.

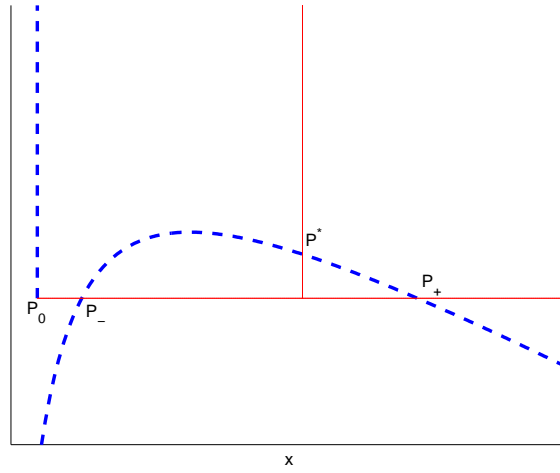
- (1) If  $h(0, n) < d$ , there is only one globally stable equilibrium  $P_0$ .
- (2) If  $h(0, n) = d$ , the manifold  $(x, 0)$  moves to  $(0, 0)$  along the  $x$ -axis, the center manifold  $(0, z)$  will stay in its initial position, and the other manifold  $(x, z)$  moves to the  $z$ -axis and finally stays on the  $z$ -axis (at the point  $P_z$  on the invariable region).
- (3) If  $h(0, n) > d$ , the system (3.1) admits the trivial equilibrium  $P_0$  which is a saddle. We can observe the stable manifold  $(x, 0)$  moves to  $(0, 0)$  along the  $x$ -axis. The unstable manifold  $(0, z)$  will move towards  $(0, +\infty)$  along the  $z$ -axis. The other manifold  $(x, z)$  moves to the  $z$ -axis first, and then moves towards  $(0, +\infty)$  along the  $z$ -axis.

**Case 2.** When  $n < \frac{(a-b)^2}{4ka}$

- (1) If  $h(0, n) < d$ , the system has four equilibria:  $P_0$  is a locally stable node; the stability of  $P_+$ ,  $P_-$ ,  $P^*$  is decided by Theorem 3.3 and 3.4. And there may exist a limit cycle in the first quadrant. In this case, whether SIRT can kill the wild insects depends on the basins of attraction of the equilibria and the initial position of the system. In this case, if the initial position of the system (3.1) is in the nontrivial invariable regions (interior equilibrium, limit cycle), we cannot achieve our goal to eradicate the wild insects.
- (2) If  $h(0, n) = d$ , the system has two kinds of equilibria:  $P_0$  and  $P_z$  in the  $z$ -axis;  $P_+$  which is a saddle and  $P_-$  which is an unstable node. If the initial value  $(x_0, z_0)$  is under the null line  $f(x, n) - g(x, n)z = 0$ , the manifold  $(x, z)$  will cross the null line  $f(x, n) - g(x, n)z = 0$ , and move to the  $z$ -axis; after it touches  $z$ -axis, it will stay at the  $P_z$  point (on the invariable region). If the initial value  $(x_0, z_0)$  is above the null line  $f(x, n) - g(x, n)z = 0$ , it will move to the point  $P_z$  directly.
- (3) If  $h(0, n) > d$ , the system has three equilibria:  $P_0$  is unstable,  $P_+$  is a saddle and  $P_-$  is an unstable node. And if the initial value is under the null line  $f(x, n) - g(x, n)z = 0$ , the manifold  $(x, z)$  will cross the null line  $f(x, n) - g(x, n)z = 0$ , and move to the  $z$ -axis heading towards  $+\infty$ . If the initial value is above the null line  $f(x, n) - g(x, n)z = 0$ , the manifold will move to  $(0, +\infty)$  along the  $z$ -axis.

		Behavior of trajectories
$n > \frac{(a-b)^2}{4ka}$	$h(0, n) < d$	Approach $P_0$
	$h(0, n) = d$	Approach $P_z$ on the z-axis
	$h(0, n) > d$	Move towards $(0, +\infty)$ along the z-axis
$n < \frac{(a-b)^2}{4ka}$	$h(0, n) < d$	-
	$h(0, n) = d$	Approach $P_z$ on the z-axis
	$h(0, n) > d$	Move towards $(0, +\infty)$ along the z-axis

Table 3.1: Summary of results in 3.2


 Figure 3.1: The equilibria of the system (3.6) when  $n < \frac{(a-b)^2}{4ka}$  and  $P^* > 0$ .

The analysis offers a few options for control strategy depending on the objective. If the objective of the SIRT is just to eliminate the wild insects, then the strategy is to make every trajectory to meet the predator axis. We just need  $n \in \mathbf{N} = \{n | h(0, n) \geq d \text{ or } n > \frac{(a-b)^2}{4ka}\}$ .

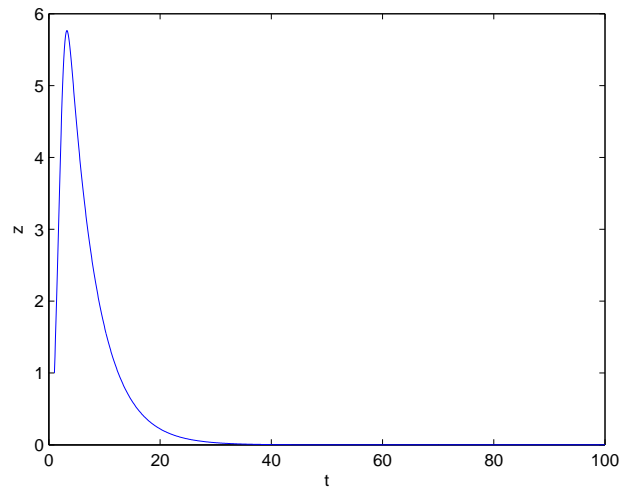
Here we can call the threshold  $\frac{(a-b)^2}{4ka}$  as the SIRT threshold, and call the threshold  $n = h_n^{-1}(0, d)$  as the predation threshold. Compared to the Theory 2.2, we find if the predation threshold is smaller than the SIRT threshold, predation has a positive effort on SIRT.

### 3.3 One example and numerical simulation

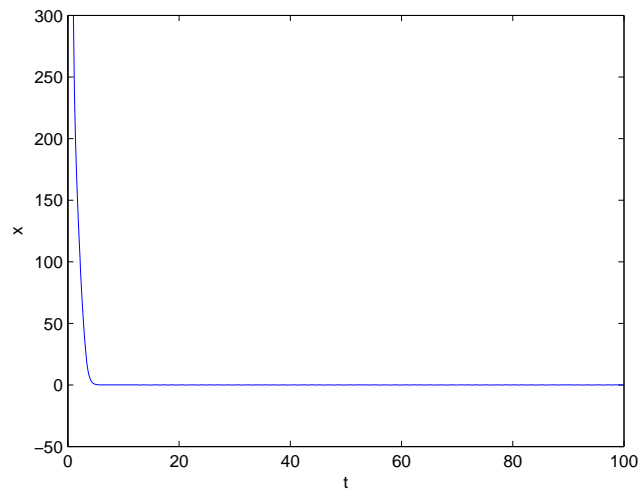
We use the Holling type I model:

$$\begin{cases} \dot{x} = \left( \frac{ax}{x+n} - b \right) x - kx(x+n) - exz, \\ \dot{z} = \lambda e(x+n)z - dz, \end{cases} \quad (3.6)$$

Note the null line  $\left( \frac{ax}{x+n} \right) x - kx(x+n) - exz = 0$  and  $\lambda e(x+n)z - dz = 0$  and the signs of them decide the local dynamics of the equilibrium. The points when the red line and the dashed blue line meet in Figure 3.1 are the equilibria of the system (3.6). According to the above analysis, we can kill the wild insects if  $n > \frac{(a-b)^2}{4ka}$  or  $n \geq \frac{d}{\lambda e}$ . Furthermore, if  $\frac{d}{\lambda e} < \frac{(a-b)^2}{4ka}$ , the predation have a positive effect on the SIRT.



(a)



(b)

Figure 3.2: The figure shows the dynamics of the model (3.6) states as time changes for the sterile insects population  $n = 80$ : (a) the predator population  $z$  (b) the wild insects  $x$ . The parameter values  $a = 5$ ,  $b = 1$ ,  $k = 0.01$ ,  $e = 0.2$ ,  $d = 1$ ,  $\lambda = 0.1$ .



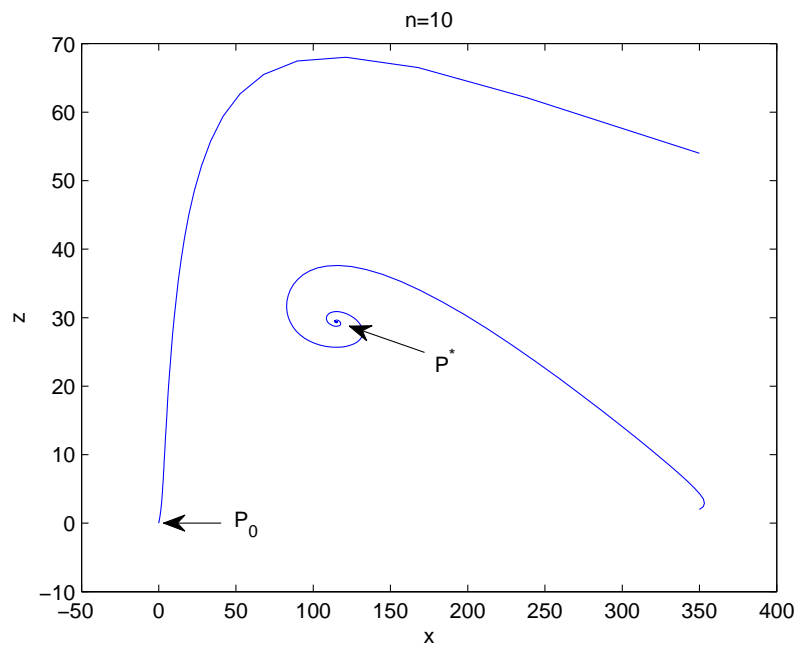


Figure 3.3: Phase portrait of system (3.6) with different initial position when  $n = 10$ . The parameter values  $a = 5, b = 1, k = 0.01, e = 0.2, d = 1, \lambda = 0.1$ .

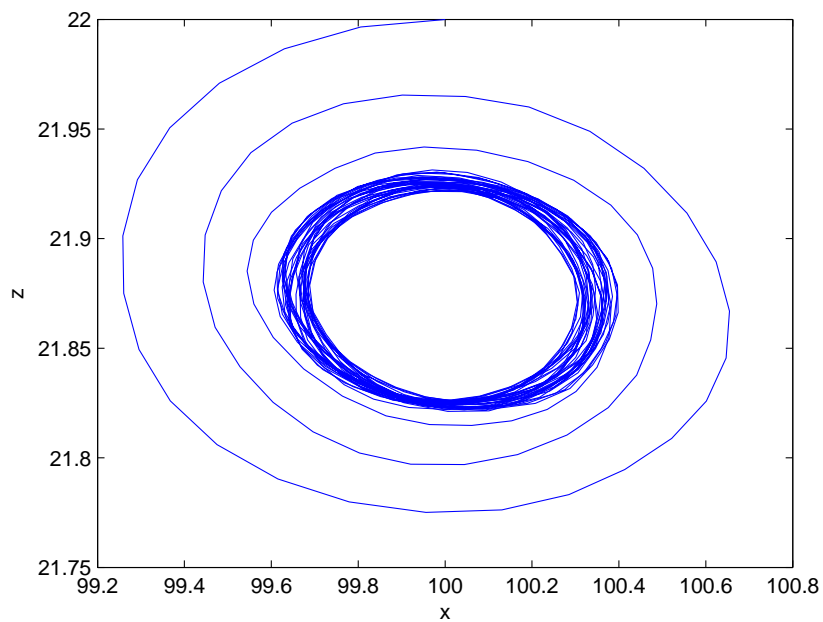


Figure 3.4: Limit cycle of system (3.6) when  $n = 25$ , initial value  $(100, 22)$ . The parameter values  $a = 5, b = 1, k = 0.01, e = 0.2, d = 1, \lambda = 0.1$ .

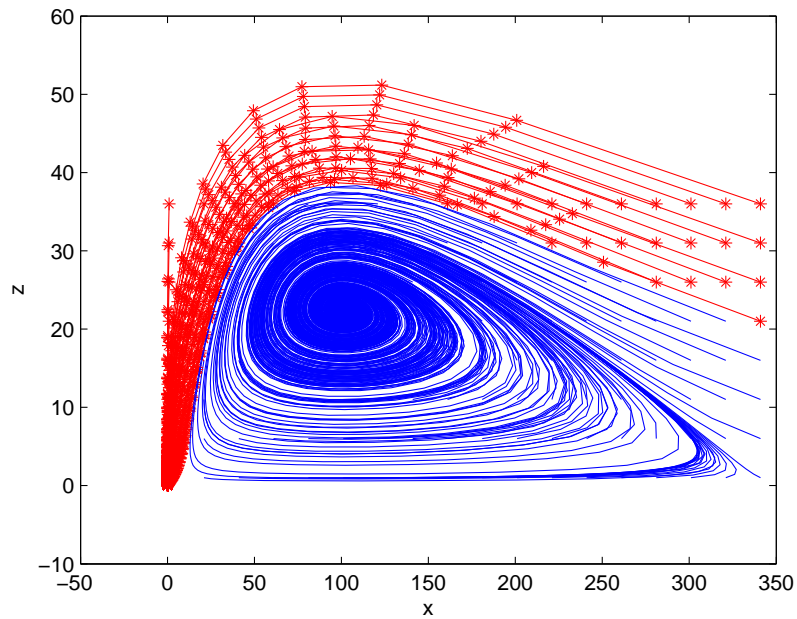


Figure 3.5: Phase portrait of system (3.6) with different initial position when  $n = 25$ . The dotted red line show the manifold go to  $(0,0)$  at last and the blue show the manifold go to limit cycle of system (3.6) around the equilibrium  $P^*$ . The parameter values  $a = 5, b = 1, k = 0.01, e = 0.2, d = 1, \lambda = 0.1$ .

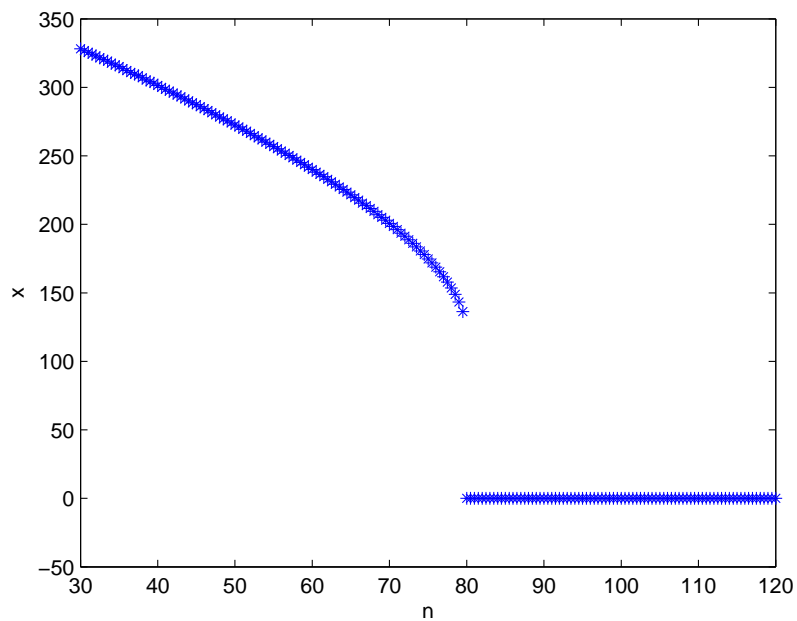
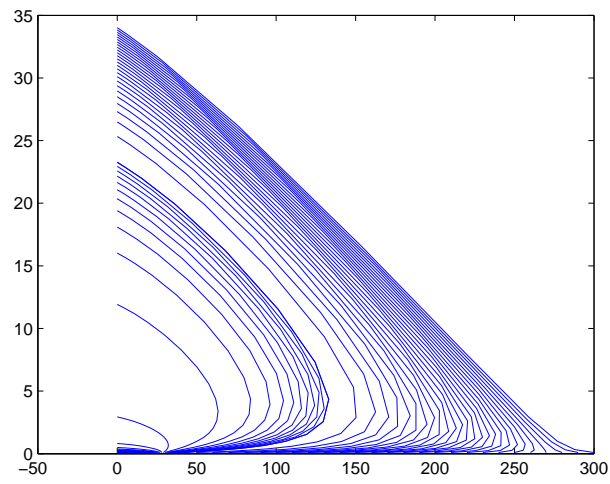
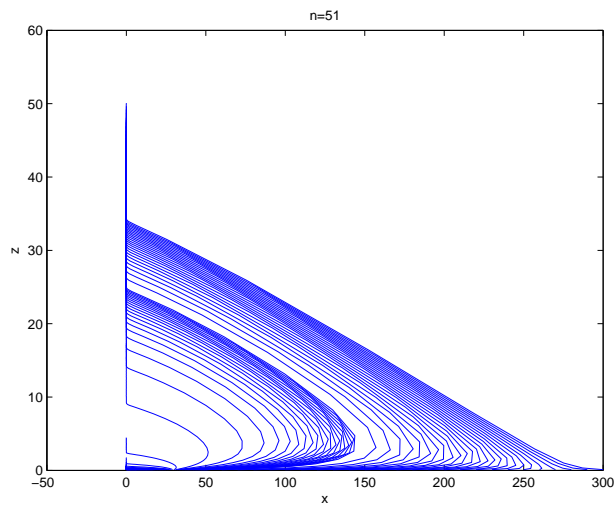


Figure 3.6: Bifurcation diagram of system (3.6) with respect to  $n$ . In this case, we choose the parameter values  $a = 5, b = 1, k = 0.01, e = 0.2, d = 1, \lambda = 0.01$ , the initial position  $(300,2)$ . The critical value  $\frac{(a-b)^2}{4ka} = 80, \frac{d}{\lambda e} = 500$ .



(a)



(b)

Figure 3.7: The phase portrait of system (3.6) with different initial position from  $(1, 0.1)$  to  $(300, 0.1)$  when (a)  $n = 50$  (b)  $n = 51$ . The parameter values  $a = 5$ ,  $b = 1$ ,  $k = 0.01$ ,  $e = 0.2$ ,  $d = 1$ ,  $\lambda = 0.1$ .

In Figures 3.2–3.5, we choose the parameter values  $a = 5$ ,  $b = 1$ ,  $k = 0.01$ ,  $e = 0.08$ ,  $d = 1$ ,  $\lambda = 0.1$  and initial position of the state in  $(300,1)$ . In Figure 3.3 the sterile insects population  $n$  is 10; if the initial position of the state is in  $(350,54)$ , the trajectory reach to the interior equilibrium  $P^*$ ; and if the initial position of the state is in  $(350,2)$ , the trajectory will reach to the trivial equilibrium  $P_0$ . In Figure 3.4, the sterile insects population  $n$  is 25; we get the locally stable limit cycle of system (3.6). In Figure 3.5, we get the phase portrait of system (3.6) with 200 different initial positions from  $(1,1)$  to  $(350,36)$ , and this figure shows the basins of attraction of the equilibria.

In Figure 3.6, we choose the parameter values  $a = 5$ ,  $b = 1$ ,  $k = 0.01$ ,  $e = 0.2$ ,  $d = 1$ ,  $\lambda = 0.01$  and we get the bifurcation diagram of system (3.6) with respect to  $n$ . Here the SIRT threshold  $\frac{(a-b)^2}{4ka} = 80$  and the predation threshold  $\frac{d}{\lambda e} = 500$ . So we just need  $n > 80$  to kill the wild insects.

In Figure 3.7, we choose the parameter values  $a = 5$ ,  $b = 1$ ,  $k = 0.01$ ,  $e = 0.2$ ,  $d = 1$ ,  $\lambda = 0.1$  and we get the phase portrait of system (3.6) with 300 different initial positions from  $(1,0.1)$  to  $(300,0.1)$ . In this case, the SIRT threshold  $\frac{(a-b)^2}{4ka} = 80$ , and the predation threshold  $\frac{d}{\lambda e} = 50$ . When  $n \geq 50$ , there is no nontrivial invariable regions(interior equilibrium, limit cycle). And the position of the  $x$ -axial equilibrium  $P_+ = (272.5, 0)$ ,  $P_- = (27.5, 0)$  when  $n = 50$ . The manifold in Figure 3.7 goes to the  $z$ -axial equilibrium  $P_z$  when  $n = 50$ , and moves to  $z$ -axis heading towards  $+\infty$ . So we just need  $n \geq 50$  to achieve our goal.

## 4 The impulsive SIRT model

We extend the previous model in order to account for the release of sterile insects. There are various ways to account for the release of sterile insects. In this contribution we focus on a periodic or pulsed release method, which is fairly well modelled by an impulsive system of ordinary differential equations [1,9,13–16,18,20]:

$$\left. \begin{cases} \dot{x} = \left(a \frac{x}{x+y} - b\right)x - kx(x+y) - g(x,y)xz, \\ \dot{y} = -by - g(x,y)yz, \\ \dot{z} = h(x,y)z - dz, \\ y(nT^+) = y(nT) + c, \end{cases} \right\} \begin{array}{l} t \neq nT, \\ t = nT. \end{array} \quad (4.1)$$

where  $x, y, z$  represent the wild insects, sterile insects and their nature enemy, respectively. Here  $d$  death rate of the predator,  $c$  population of sterile insects release every period,  $T$  release period.

### 4.1 Trivial periodic solution

We first focus on the trivial solution that corresponds to both wild insects and predator eradication.

**Theorem 4.1.** *Model (4.1) has a trivial solution that corresponds to both wild insects and predator eradication*

$$(\bar{x}(t), \bar{y}(t), \bar{z}(t)) = (0, y^* \exp\{-b(t \bmod T)\}, 0)$$

where

$$y^* = \frac{c}{1 - \exp\{-bT\}}$$

which is locally asymptotically stable (LAS) if and only if

$$\int_0^T h(0, \bar{y}(\tau)) d\tau < dT,$$

and is globally asymptotically stable (GAS) if

$$c > (\exp\{bT\} - 1) \frac{(a - b)^2}{4ka},$$

and

$$\int_0^T h(0, \bar{y}(\tau)) d\tau < dT.$$

We consider the establishment of the periodic solution in the set  $\{(x, y, z) \mid x = 0, z = 0\}$ . From the second and fourth equation in (4.1), we get

$$y((n + 1)T^+) = y(nT^+) \exp\{-bT\} + c$$

This is exponentially stable discrete dynamical system that converges to

$$y^* = \frac{c}{1 - \exp\{-bT\}}$$

as  $n \rightarrow \infty$ . By this we get the trivial solution of the system (4.1).

To prove LAS, we define small amplitude perturbations  $\tilde{x} = x - \bar{x} = x$ ,  $\tilde{y} = y - \bar{y}$ ,  $\tilde{z} = z - \bar{z} = z$ . This result in the equivalent system

$$\begin{cases} \dot{\tilde{x}} = \left( \frac{a\tilde{x}}{\tilde{x} + \bar{y} + \tilde{y}} - b \right) \tilde{x} - k\tilde{x}(\tilde{x} + \bar{y} + \tilde{y}) - g(\tilde{x}, \bar{y} + \tilde{y})\tilde{x}\tilde{z}, \\ \dot{\tilde{y}} = -b\tilde{y} - g(\tilde{x}, \bar{y} + \tilde{y})(\bar{y} + \tilde{y})\tilde{z}, \\ \dot{\tilde{z}} = h(\tilde{x}, \bar{y} + \tilde{y})\tilde{z} - d\tilde{z} \end{cases} \quad (4.2)$$

where the impulsive component disappears since

$$\tilde{y}(nT^+) = y(nT) + c - \bar{y}(nT) - c = \tilde{y}(nT).$$

This gives the following matrix equation:

$$\begin{pmatrix} \tilde{x}(nT) \\ \tilde{y}(nT) \\ \tilde{z}(nT) \end{pmatrix} = \Phi(t) \begin{pmatrix} \tilde{x}(0) \\ \tilde{y}(0) \\ \tilde{z}(0) \end{pmatrix}, \quad (4.3)$$

and

$$\frac{d\Phi(t)}{dt} = A(t)\Phi(t) \quad (4.4)$$

where

$$A(t) = \begin{pmatrix} -b - k\bar{y} & 0 & 0 \\ 0 & -b & 0 \\ 0 & 0 & h(0, \bar{y}) - d \end{pmatrix},$$

$$\begin{pmatrix} \tilde{x}(nT^+) \\ \tilde{y}(nT^+) \\ \tilde{z}(nT^+) \end{pmatrix} = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{pmatrix} \begin{pmatrix} \tilde{x}(nT) \\ \tilde{y}(nT) \\ \tilde{y}(nT) \end{pmatrix}. \quad (4.5)$$

The monodromy matrix is

$$\Gamma = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{pmatrix} \Phi(T) = \Phi(T). \quad (4.6)$$

We have  $\Phi(T) = \Phi(0) \exp\{A(t)\}$ .  $\Phi(0)$  is the identify matrix. Let  $\lambda_1, \lambda_2, \lambda_3$  be eigenvalues of  $\exp\{A(t)\}$ . Then  $\lambda_1 = \exp\{\int_0^T (-b - k\bar{y})dt\}$ ,  $\lambda_2 = \exp\{-\int_0^T bdt\}$ ,  $\lambda_3 = \exp\{\int_0^T (h(0, \bar{y}) - d)dt\}$ . Using Floquet's theorem [1], the conditions for local stability of  $(\bar{x}(t), \bar{y}(t), \bar{z}(t)) = (0, y^* \exp\{-m(t \bmod T)\}, 0)$  are  $\lambda_1 = \exp\{\int_0^T (-b - k\bar{y})dt\} < 1$ ,  $\lambda_2 = \exp\{-\int_0^T bdt\} < 1$ ,  $\lambda_3 = \exp\{\int_0^T (h(0, \bar{y}) - d)dt\} < 1$ . The first and second conditions are both trivial, the third solution is equal to

$$\int_0^T h(0, \bar{y})dt < dT.$$

For GAS, we focus on the second equation in (4.2). Obviously, we know  $\dot{\tilde{y}} < -b\tilde{y}$ , so  $\lim_{t \rightarrow +\infty} \tilde{y}(t) = 0$ . And for the first equation in (4.2), we have  $\dot{\tilde{x}} \leq \dot{\tilde{x}}_1 = (\frac{a\tilde{x}_1}{\tilde{x}_1 + \bar{y} + \tilde{y}} - b)\tilde{x}_1 - k\tilde{x}_1(\tilde{x}_1 + \bar{y} + \tilde{y})$ . For the subsystem

$$\begin{cases} \dot{\tilde{x}}_1 = \left( \frac{a\tilde{x}_1}{\tilde{x}_1 + \bar{y} + \tilde{y}} - b \right) \tilde{x}_1 - k\tilde{x}_1(\tilde{x}_1 + \bar{y} + \tilde{y}), \\ \dot{\tilde{y}} = -b\tilde{y} - g(\tilde{x}_1, \bar{y} + \tilde{y})(\bar{y} + \tilde{y})\tilde{z} \end{cases} \quad (4.7)$$

we introduce another system

$$\begin{cases} \dot{\tilde{x}}_2 = \left( \frac{a\tilde{x}_2}{\tilde{x}_2 + \bar{y} + \tilde{y}} - b \right) \tilde{x}_2 - k\tilde{x}_2(\tilde{x}_2 + \bar{y} + \tilde{y}), \\ \dot{\tilde{y}} = -b\tilde{y} - g(K, \bar{y} + \tilde{y})(\bar{y} + \tilde{y})\tilde{z}. \end{cases} \quad (4.8)$$

Using comparison theorem, we have  $\tilde{x} \leq \tilde{x}_1 \leq \tilde{x}_2$ .

**Lemma 4.2** ([17]). *Consider the following  $C^1$  system*

$$\begin{cases} \frac{dx}{dt} = f(x), \\ \frac{dy}{dt} = g(x, y), \end{cases} \quad (4.9)$$

with  $(x, y) \in R^n \times R^m$ . Let  $(x^*, y^*)$  be an equilibrium point.

If  $x^*$  is GAS in  $R^n$  for system  $\frac{dx}{dt} = f(x)$ , and if  $y^*$  is GAS in  $R^m$  for the system  $\frac{dy}{dt} = g(x^*, y)$ , then  $(x^*, y^*)$  is asymptotically stable for system (4.9). Moreover, if all trajectories of (4.9) are forward bounded, then  $(x^*, y^*)$  is GAS for (4.9).

In fact, 0 is GAS for  $\frac{d\tilde{y}}{dt} = -b\tilde{y} - g(K, \bar{y} + \tilde{y})(\bar{y} + \tilde{y})\tilde{z}$ , where  $K$  is the carrying capacity of  $x$ . We just need prove 0 is GAS for the system  $\frac{d\tilde{x}}{dt} = (\frac{a\tilde{x}}{\tilde{x} + \bar{y}} - b)\tilde{x} - k\tilde{x}(\tilde{x} + \bar{y})$ .

From computation we have

$$y^* e^{-bT} \leq \bar{y} \leq y^*$$

Let us consider the following systems

$$\frac{d\tilde{x}_{\min}}{dt} = \left( \frac{a\tilde{x}_{\min}}{\tilde{x}_{\min} + y^*} - b \right) \tilde{x}_{\min} - k\tilde{x}_{\min}(\tilde{x}_{\min} + y^*) \quad (4.10)$$

and

$$\frac{d\tilde{x}_{\max}}{dt} = \left( \frac{a\tilde{x}_{\max}}{\tilde{x}_{\max} + y^*e^{-bT}} - b \right) \tilde{x}_{\max} - k\tilde{x}_{\max}(\tilde{x}_{\max} + y^*e^{-bT}) \quad (4.11)$$

with  $\tilde{x}_{\min}(0) = \tilde{x}(0) = \tilde{x}_{\max}(0) = x(0)$ . Using comparison theorem, we have

$$0 \leq \tilde{x}_{\min}(t) \leq \tilde{x}(t) \leq \tilde{x}_{\max}(t).$$

Using Theorem 2.2, we know (4.10) and (4.11) have GAS trivial solution if  $y^* > \frac{(a-b)^2}{4ka}$  and  $y^* \exp\{-bT\} > \frac{(a-b)^2}{4ka}$ , respectively. Using comparison theorem, 0 is GAS for the system  $\frac{d\tilde{x}}{dt} = \left( \frac{a\tilde{x}}{\tilde{x} + \bar{y}} - b \right) \tilde{x} - k\tilde{x}(\tilde{x} + \bar{y})$  if  $y^* \exp\{-bT\} > \frac{(a-b)^2}{4ka}$ . Using Lemma 4.2, (0,0) is GAS for model (4.8) if  $c > (\exp\{bT\} - 1) \frac{(a-b)^2}{4ka}$ .

Then using comparison theorem, we can get  $\lim_{t \rightarrow +\infty} \tilde{x}(t) = 0$  if  $c > (\exp\{bT\} - 1) \frac{(a-b)^2}{4ka}$ .

Now we shall show how  $\tilde{z}$  converges to zero. Since if  $c > (\exp\{bT\} - 1) \frac{(a-b)^2}{4ka}$ , we know for  $\forall \varepsilon > 0$ , we can find a  $t_1$  and  $t_2$  so that  $\forall t > t_{\max} = \max\{t_1, t_2\}$ ,  $\tilde{x} < \varepsilon$ ,  $\tilde{y} < \varepsilon$ . Then if we want  $\tilde{z}$  converges to zero, we just need to make  $\int_{t_{\max}}^t \frac{\tilde{z}}{\tilde{z}} d\tau \rightarrow -\infty$  as  $t \rightarrow +\infty$ .

$$\begin{aligned} \int_{t_{\max}}^t \frac{\tilde{z}}{\tilde{z}} d\tau &\leq \int_{t_{\max}}^t (h(\varepsilon, \varepsilon + \bar{y}(\tau)) - d) d\tau \\ &= \int_{t_{\max}}^{(\lfloor \frac{t}{T} \rfloor + 1)T} (h(\varepsilon, \varepsilon + \bar{y}(\tau)) - d) d\tau + \left( \left\lfloor \frac{t}{T} \right\rfloor - \left\lfloor \frac{t_{\max}}{T} \right\rfloor - 1 \right) \\ &\quad \times \int_0^T (h(\varepsilon, \varepsilon + \bar{y}(\tau)) - d) d\tau + \int_{\lfloor \frac{t}{T} \rfloor T}^t (h(\varepsilon, \varepsilon + \bar{y}(\tau)) - d) d\tau \end{aligned}$$

Notice that the first and third terms are bounded, so we just need

$$\int_0^T (h(\varepsilon, \varepsilon + \bar{y}(\tau)) - d) d\tau < 0,$$

which is equal to

$$\int_0^T h(\varepsilon, \varepsilon + \bar{y}(\tau)) d\tau < dT.$$

For any  $\varepsilon > 0$  is suitable, we conclude  $\tilde{z}$  converges to zero if  $\int_0^T h(0, \bar{y}(\tau)) d\tau < dT$ . We have shown that (0,0,0) is globally attractive for system (4.2), so  $(\bar{x}(t), \bar{y}(t), \bar{z}(t))$  is globally attractive for system (4.1) if

$$\int_0^T h(0, \bar{y}(\tau)) d\tau < dT, \quad c > (\exp\{bT\} - 1) \frac{(a-b)^2}{4ka}.$$

## 4.2 Semi-trivial periodic solution

In fact, the system (4.1) may have a semi-trivial periodic solution that corresponds to wild insects eradication  $(0, y^+, z^+)$ .

We consider the establishment of the semi-trivial periodic solution in the set  $\{(x, y, z) \mid x = 0\}$ . Then we get

$$\begin{cases} \dot{y} = -by - g(0, y)yz, \\ \dot{z} = h(0, y)z - dz, \end{cases} t \neq nT, \quad (4.12)$$

$$y(nT^+) = y(nT) + c, \quad t = nT.$$

The system (4.1) has a semi-trivial periodic solution that corresponds to wild insects eradication  $(0, y^+, z^+)$  if the system (4.12) has a nontrivial periodic solution  $(y^+, z^+)$ . To prove the existence of nontrivial-trivial periodic solution of system (4.12), we followed the technique used by A. Lakmeche and O. Arino in [9]. And we have got the nontrivial periodic solution of a Beddington–DeAngelis interference model in [18]. Here we just introduced some notations and stated some results. Let us consider the following impulsive system given below

$$\begin{cases} \dot{y} = -by - g(0, y)yz = F_1(y, z), \\ \dot{z} = h(0, y)z - dz = F_2(y, z), \end{cases} t \neq nT, \\ \begin{cases} y(nT^+) = y(nT) + c = \Theta_1(y, z), \\ z(nT^+) = z(nT) = \Theta_2(y, z), \end{cases} t = nT. \end{cases} \quad (4.13)$$

According to the proof of Theorem 4.1, we can get that the system (4.13) has a trivial periodic solution  $(y^* \exp\{t \bmod T\}, 0)$ . Denote this trivial periodic solution of system (4.13) by  $\pi = (U, 0)$ . Letting  $\Phi$  be the flow associated to system (4.13), we have  $U(t) = \Phi(t, y_0, z_0)$ ,  $0 < t \leq T$ , where  $U_0 = U(y_0, z_0)$ . The flow  $\Phi$  applies to time T. So,  $U(T) = \Phi(T, U_0)$ . The following notations of [9] will be used:

$$\begin{aligned} d'_0 &= 1 - \left( \frac{\partial \Theta_2}{\partial z} \frac{\partial \Phi_2}{\partial z} \right) (\tau_0, U_0), \\ a'_0 &= 1 - \left( \frac{\partial \Theta_1}{\partial y} \frac{\partial \Phi_1}{\partial y} \right) (\tau_0, U_0), \\ b'_0 &= - \left( \frac{\partial \Theta_1}{\partial y} \frac{\partial \Phi_1}{\partial z} \right) (\tau_0, U_0), \\ B &= - \frac{\partial^2 \Theta_2}{\partial y \partial z} \left( \frac{\partial \Phi_1(\tau_0, U_0)}{\partial \tau} + \frac{\Phi_1(\tau_0, U_0)}{\partial y} \frac{1}{a'_0} \frac{\partial \Theta_1}{\partial y} \frac{\partial \Phi_1(\tau_0, U_0)}{\partial \tau} \right) \frac{\partial \Phi_2(\tau_0, U_0)}{\partial z} \\ &\quad - \frac{\partial \Theta_2}{\partial z} \left( \frac{\partial^2 \Phi_2(\tau_0, U_0)}{\partial y \partial z} \frac{1}{a'_0} \frac{\partial \Theta_1}{\partial y} \frac{\partial \Phi_1(\tau_0, U_0)}{\partial \tau} \right) \\ C &= -2 \frac{\partial^2 \Theta_2}{\partial y \partial z} \left( - \frac{b'_0}{a'_0} \frac{\partial \Phi_1(\tau_0, U_0)}{\partial y} \frac{\Phi_1(\tau_0, U_0)}{\partial z} \right) \frac{\Phi_2(\tau_0, U_0)}{\partial z} - \frac{\partial^2 \Theta_2}{\partial z^2} \left( \frac{\partial \Phi_2(\tau_0, U_0)}{\partial z} \right)^2 \\ &\quad + \frac{\partial \Theta_2}{\partial z} \frac{b'_0}{a'_0} \frac{\partial^2 \Phi_2(\tau_0, U_0)}{\partial y \partial z} - \frac{\partial \Theta_2}{\partial I} \frac{\partial^2 \Phi_2(\tau_0, U_0)}{\partial z^2}. \end{aligned}$$

where  $\tau_0$  is the root of  $d'_0 = 0$ , then we get the following theorem

**Theorem 4.3.** *If  $|1 - a'_0| < 1$  and  $d'_0 = 0$ , then we get if  $BC \neq 0$ , then we have a bifurcation. Moreover, we have a bifurcation of a nontrivial periodic solution of system (4.13) if  $BC < 0$ .*

According to Theorem 4.3, the system (4.1) has a semi-trivial periodic solution that corresponds to wild insects eradication  $(0, y^+, z^+)$  if the system (4.13) has a bifurcation of a nontrivial periodic solution.

### 4.3 Control strategy and numerical simulation

The impulsive model (4.1) leads to complex dynamics, but if the objective of the SIRT is just to eliminate the wild insects, we just need  $\lim_{t \rightarrow +\infty} \tilde{x}(t) = 0$ . It is easy to get  $\lim_{t \rightarrow +\infty} \tilde{x}(t) = 0$  if  $c > (\exp\{bT\} - 1) \frac{(a-b)^2}{4ka}$  from the proof of Theorem 4.1.



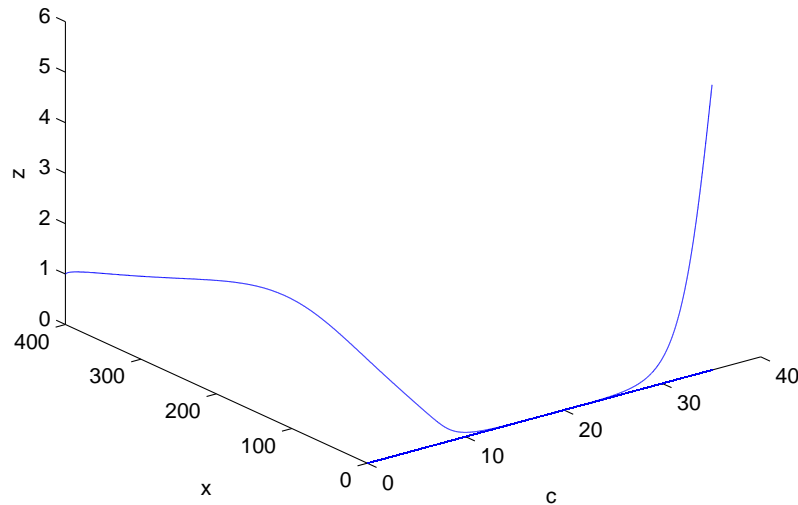


Figure 4.1: Bifurcation diagram of Holling type I model with respect to  $c$ . We choose the parameter values  $a = 5$ ,  $b = 1$ ,  $k = 0.01$ ,  $T = 0.05$ ,  $d = 1$ ,  $e = 0.01$ ,  $\lambda = 0.08$ . When  $13 < c < 25$ , we get the both wild insects and predation eradication solution. When  $c > 25$ , we get the wild insects eradication solution. This two critical value is achieved by  $t = 100$  and our analytical results is got by  $t = +\infty$ .

We have shown the system may have a trivial solution and a semi-trivial periodic solution. The results in Holling type I model are verified through computer simulation in Figure 4.1. We got the bifurcation diagram of Holling type I model with respect to  $c$ . We choose the parameter values  $a = 5$ ,  $b = 1$ ,  $k = 0.01$ ,  $T = 0.05$ ,  $d = 1$ ,  $e = 0.01$ ,  $\lambda = 0.08$ . When  $13 < c < 25$ , we get the trivial periodic solution that corresponds to both wild insects and predation eradication. When  $c > 25$ , we get the semi-trivial solution that corresponds to wild insects eradication.

## 5 Conclusion

In this paper we are concerned with both the continuous and impulsive dynamical aspects of stability of two mathematical models to investigate the influence of the predation on the SIRT. We use one simple example Holling type I model to verify our result by numerical simulation.

These features in the context of a SIRT model with predation lead to rich, interesting, and complex dynamics. We summarize and compare the continuous model and the impulsive model in the following.

### 5.1 The fixed SIRT threshold

In the continuous model (3.1), the stability analysis indicates that the critical value  $\frac{(a-b)^2}{4ka}$  has an important effect on the release of SIRT in the predator-prey model. If the population of

sterile insects  $n$  is larger than this SIRT threshold, wild insects will be killed. The predators' functional response  $g(\cdot)$  has no influence on this threshold. Furthermore, by comparing this threshold with the realistic size of populations, we find if the density-independent death rate  $b$  is close to the birth rate  $a$ , the SIRT has a high efficiency.

In the impulsive model (4.1), the critical value is  $(\exp\{bT\} - 1) \frac{(a-b)^2}{4ka}$  and if the population of sterile insects every period  $c$  is larger than this threshold, wild insects also can be killed. We calculate the population of sterile insects release per unit time and get

$$\frac{c}{T} > \frac{\exp\{bT\} - 1}{T} \frac{(a-b)^2}{4ka}.$$

And it is shown the smaller the release period is, the smaller the population of sterile insects release per unit time could be. But the threshold per unit time has a lower bound because  $\lim_{T \rightarrow 0} \frac{\exp\{bT\} - 1}{T} = b$ .

If we do not consider the predation threshold, we compare condition  $n > \frac{(a-b)^2}{4ka}$  in the continuous model with condition  $\frac{c}{T} > \frac{\exp\{bT\} - 1}{T} \frac{(a-b)^2}{4ka}$  for some finite  $T$  in the impulsive model. Both release strategies will succeed if  $n$  or  $c$  is large enough. But if the density-independent death rate  $b > 1$ , there are some intermediate values of the sterile insects release rate with a release strategy based on impulsive model would fail, but the continuous counterpart would succeed. If  $b < 1$  and  $\frac{\exp(bT) - 1}{T} < 1$ , a release strategy may more easily succeed if the release is impulsive rather than continuous.

## 5.2 The predation threshold

In the continuous model (3.1), the effect of predation on the efficiency of SIRT depend on the predators' numerical response  $h(0, n)$  and death rate of the predator. If the predation threshold  $h_n^{-1}(0, d) < \frac{(a-b)^2}{4ka}$ , predation has a positive effort and we just need  $n > h_n^{-1}(0, d)$  to kill wild insects; if not, predation has no influence on the efficiency of SIRT.

In the impulsive model (4.1), the predation threshold condition is  $\int_0^T h(0, \bar{y}(\tau)) d\tau < dT$ . And this condition decides the globally asymptotical stability of the trivial periodic solution, but it does not change our control strategy.

If we consider the predation threshold, we compare condition  $n > h_n^{-1}(0, d)$  in the continuous model with condition  $\frac{c}{T} > \frac{\exp\{bT\} - 1}{T} \frac{(a-b)^2}{4ka}$  in the impulsive model. If  $h_n^{-1}(0, d) < \frac{\exp\{bT\} - 1}{T} \frac{(a-b)^2}{4ka}$ , the best strategy is the continuous one; if not, the result is same to the case without predation.

## 5.3 Hysteresis

In the continuous model (3.1), Theorems 3.2–3.5 show that it can support one, two, three even four equilibria when  $n < \frac{(a-b)^2}{4ka}$  and  $h(0, n) < d$ . And all the points on the  $z$ -axis  $P_z = (0, z_+)$  are the equilibrium when  $n = h_n^{-1}(0, d)$ . And the system also may have saddle–node bifurcation, Hopf bifurcation, heteroclinic orbit and so on. In the impulsive model (4.1), it is shown the system may have a trivial solution and a semi-trivial periodic solution and some other undetermined case.

This paper gives a theoretical foundation for the SIRT technique in the predator–prey model. All these results give biological control practitioners two kinds of control strategies of

wild insects management in the biological model. And we believe the method could be used in other systems such as epidemiology or immunology.

The model presented here, and hence the above conclusions, are based on the assumption that when the insect pest population declines the predators either die or emigrate. Frequently predators have several important alternative food sources and the model would need corresponding modification.

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