

Dynamics of an eco-epidemic model with stage structure for predator

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Abstract. The predator-prey model with stage structure for predator is generalized in the context of ecoepidemiology, where the prey population is infected by a microparasite and the predator completely avoids consuming the infected prey. The intraspecific competition of infected prey is considered. All the equilibria are characterized and the existence of a Hopf bifurcation at the coexistence equilibrium is shown. Numerical simulations are carried out to illustrate the obtained results.

Keywords: prey-predator model; stage structure; stability; Hopf bifurcation.

AMS Subject Classification: 92D25, 92D30, 34D20, 34D23, 93D20.

1 Introduction

The most celebrated work of Kermack and McKendrick [12] on epidemic models creates major interest to scientists. Much work has been done in this area [1, 3, 6, 11]. Most of the studies deal with the spread of the disease assuming the considered species are not related with the other species.

In the real world, it is seen that when species spreads the disease, it also competes with the other species for space or food, or it is predated by the other species. Thus it is realistic to consider the effect of interacting species when we study epidemiological models. Effect of disease in ecological interactions are investigated in [2, 7, 10, 16–20, 24, 25].

Most of the previous studies on eco-epidemic model showed that predator preferentially selects infected prey and several experimental studies have

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shown that parasite mediated mortality increases vulnerability to predation. However there are situations where predator consumes healthy prey only because it risks incidental infection from infected prey, as many occur with anthrax or bovine tuberculosis. In nature it is observed that predator can discriminate the infected prey and non-infected prey. For example, Bullfrog (*Rana catesbeiana*) tadpoles avoid conspecifics carrying infectious yeast, *Candida humicola*, by detecting chemical cues producing from infected individuals at a distance [13]. Levri [14] pointed out that fish predators avoid infected snails (*Potamopyrgus antipodarum*). Further, Pfennig [21] has done experiment on spadefoot tadpoles (*Spea bombifrons*, *Spea multiplicata*, and *Scaphiopus couchii*), by feeding them either conspecific tadpoles or an equal mass of three different species of heterospecific prey, all of which contained in naturally occurring bacteria. Now if the predator can identify and avoid infected prey, then this selection of the predator may accrue the enhanced nutritional benefits of eating phylogenetically close prey while limiting risks of disease. More biological situations can be found in [9]. Above biological examples in prey-predator interaction with prey infection suggest that disease-selective predation can prevent the predators being affected from the infected prey. But this type of behavior of predator can cause prey extinction. Therefore a natural question arises that, will the prey population always go to extinction if the predator consume susceptible prey only? This question will be answered by analyzing a mathematical model where predator avoid infected prey.

Here we propose and analyze a predator-prey model with stage structure for predator in the context of ecoepidemiology. Further we incorporate intraspecific competition, due also to the infected prey. Predator functional response is taken as Holling type II. Predator consumes susceptible prey only. In our model, predator has two stages. In the first stage, predator can neither attack prey nor reproduce, being raised by their mature parents.

In the next section, we briefly review the starting population model, and in Section 3 introduce the ecoepidemic one with some basic properties and its equilibria. Bifurcation and global stability are presented in Section 4.

2 The original population model

Georgescu and Hsiesh [8] studied the following predator-prey model with stage structure for predator:

$$\begin{aligned}\frac{dx}{dt} &= x(r - ax) - \frac{bx}{1 + mx}z, \\ \frac{dy}{dt} &= q\frac{bx}{1 + mx}z - (D + d_1)y, \\ \frac{dz}{dt} &= Dy - d_2z.\end{aligned}\tag{1}$$

Here, $x(t), y(t), z(t)$ are the densities of prey, immature and mature predators respectively at time t . The growth of prey population follows logistic law. The functional response of the mature predator is taken Holling type II. The positive parameters r, a, b, m, k, D, d_1 and d_2 are interpreted as follows :

- r represents the intrinsic growth rate of the prey population,
- a represents intraspecies competition among the prey,
- b represents the search rate of the mature predators,
- m represents the search rate multiplied by the handling time of the mature predators,
- q represents the conversion coefficient of the mature predators,
- D represents the rate at which immature predators become the mature predators,
- d_1 represents the death rate of the immature predators,
- d_2 represents the death rate of the mature predators.

In [8], the authors defined the basic reproduction number of the predator by

$$R_0 = q\frac{br}{amr}\frac{1}{d_2}\frac{D}{D + d_1},$$

and showed that if $R_0 > 1$ and $\lim_{t \rightarrow \infty} x(t) > \frac{r}{2a}$ then the unique positive steady state of system (1) is globally asymptotically stable on $(0, \infty)^3$. When $R_0 \leq 1$ then the prey only equilibrium $(\frac{r}{a}, 0, 0)$ is globally asymptotically stable. Moreover, if $R_0 > 1$ but the condition $\lim_{t \rightarrow \infty} x(t) > \frac{r}{2a}$ does not necessarily hold, then the prey only equilibrium $(\frac{r}{a}, 0, 0)$ is unstable, there exists a unique positive equilibrium and the system becomes uniformly persistent. In staged model, global stability of the positive steady state requires persistence type condition which is difficult to check analytically. When there is an infection in the prey population, global stability

condition can be achieved by controlling the intrinsic growth rate of the prey population. Further, presence of intraspecific competition of sound prey can give rise to oscillation.

3 The ecoepidemic model

Suppose the prey population in the model (1) is infected by a microparasite. The total prey population x is thus divided into two classes, namely susceptible prey denoted by $S(t)$ and the infected prey denoted by $I(t)$. Thus $x(t) = S(t) + I(t)$. The disease spreads horizontally with mass action incidence rate βSI . The infected prey population cannot recover from the disease nor reproduce but it contributes to intra- and interspecific competition, although at a lower rate c_2 than the susceptible prey, i.e., $c_1 > c_2$. The population density of immature and mature predator are denoted by $Y(t)$ and $Z(t)$ respectively. The predator eats only the susceptible prey with Holling type II response function. The model (1) is then extended to the following one :

$$\begin{aligned}\frac{dS}{dt} &= rS - c_1S(S + I) - \beta SI - \frac{bSZ}{1+mS}, \\ \frac{dI}{dt} &= \beta SI - \mu I - c_2I(S + I), \\ \frac{dY}{dt} &= q \frac{bSZ}{1+mS} - (D + d_1)Y, \\ \frac{dZ}{dt} &= DY - d_2Z,\end{aligned}\tag{2}$$

where r is the growth rate of the susceptible prey, μ is the mortality rate of infected prey including disease related death, b represents the search rate of the mature predators, m denotes the search rate multiplied by the handling time of the mature predators, q is the conversion coefficient of the mature predators, D represents the rate at which immature predators become the mature predators, d_1 is the death rate of the immature predators and d_2 represents the death rate of the mature predators.

3.1 Boundedness

We show that, all the solutions of system (2) are bounded in a positive orthant R_+^4 . The boundedness of system (2) is given by the following lemma.

Lemma 1. *All the solutions of system (2) will be in the region $B = \{(S, I, Y, Z) \in \mathbb{R}_+^4 : 0 \leq S + I + Y + Z \leq \frac{(r+\lambda)^2}{4c_1\lambda}\}$ as $t \rightarrow \infty$ for all positive initial values $(S(0), I(0), Y(0), Z(0)) \in \mathbb{R}_+^4$ where $\lambda = \min\{\mu, d_1, d_2\}$.*

Proof. Define the function $W(t) = S(t) + I(t) + Y(t) + Z(t)$. From equation (2) and if $\lambda = \min\{\mu, d_1, d_2\}$,

$$\frac{dW(t)}{dt} + \lambda W \leq S(r + \lambda) - c_1 S^2 \leq \frac{(r + \lambda)^2}{4c_1}.$$

Then by usual comparison theorem [4], we get the following expression as $t \rightarrow \infty$: $W(t) \leq \frac{(r+\lambda)^2}{4c_1\lambda}$. \square

3.2 Equilibria

The system (2) has the following boundary equilibrium points: $E_0(0, 0, 0, 0)$, $E_1(\frac{r}{c_1}, 0, 0, 0)$, $E_{12}(\bar{S}, \bar{I}, 0, 0)$ where

$$\bar{S} = \frac{(c_1 + \beta)\mu + rc_2}{c_1c_2 + (\beta + c_1)(\beta - c_2)}, \quad \bar{I} = \frac{r(\beta - c_2) - c_1\mu}{c_1c_2 + (\beta + c_1)(\beta - c_2)}.$$

Clearly E_1 and E_2 always exist and E_{12} is feasible if $\beta > \frac{c_1\mu}{r} + c_2$.

Theorem 1.

- i) E_0 is always unstable.*
- ii) E_1 is stable if $\beta r < \mu c_1 + rc_2$ and $(D + d_1)d_2 > \frac{qbr}{c_1 + mr}$ and unstable otherwise.*
- iii) E_{12} is stable if $(D + d_1)d_2 > \frac{qb\bar{S}D}{1 + m\bar{S}}$ and unstable otherwise.*

Proof. It follows immediately by linearizing around the equilibria. \square

It is to be noted here that if E_{12} is feasible then E_1 is unstable. Next we are interested about the existence of the interior equilibrium point of system (2) which is given by $E^*(S^*, I^*, Y^*, Z^*)$ where

$$S^* = \frac{(D+d_1)d_2}{qbd - m(D+d_1)d_2}, \quad I^* = \frac{(\beta - c_2)S^* - \mu}{c_2},$$

$$Y^* = \frac{d_2(1+mS^*)\{r - c_1S^* - (\beta + c_1)I^*\}}{bD}, \quad Z^* = \frac{DY^*}{d_2}.$$

Clearly, the interior equilibrium point E^* is feasible if

- (i) $qbD > m(D + d_1)d_2$,*
 - (ii) $r > (c_1 + \beta)I^* + c_1S^*$,*
 - (iii) $(\beta - c_2)S^* > \mu$.*
- (3)

The condition (iii) indicates that $\beta > c_2$.

Theorem 2. *Suppose (3) holds. Then E^* is locally asymptotically stable provided the following conditions are satisfied: $c_1 - \frac{bZ^*m}{(1+mS^*)^2} > 0$ and $A_3(A_1A_2 - A_3) - A_1^2A_4 > 0$ where*

$$A_1 = c_2I^* + S^*(c_1 - \frac{bZ^*m}{(1+mS^*)^2}) + D + d_1 + d_2,$$

$$A_2 = S^*I^*\{c_2(c_1 - \frac{bZ^*m}{(1+mS^*)^2}) + (\beta + c_1)(\beta - c_2)\}$$

$$+ (D + d_1 + d_2)\{S^*(c_1 - \frac{bZ^*m}{(1+mS^*)^2}) + c_2I^*\},$$

$$A_3 = S^*I^*\{(\beta + c_1)(\beta - c_2) + c_2(c_1 - \frac{bZ^*m}{(1+mS^*)^2})\}(D + d_1 + d_2)$$

$$+ \frac{qb^2S^*Z^*D}{(1+mS^*)^3},$$

$$A_4 = \frac{c_2S^*qb^2I^*Z^*D}{(1+mS^*)^3}.$$

Proof. The characteristic equation about E^* is given by

$$\lambda^4 + A_1\lambda^3 + A_2\lambda^2 + A_3\lambda + A_4 = 0 \quad (4)$$

The result follows by the application of the Routh-Hurwitz criterion. \square

4 Global stability and bifurcation

Let us define $F(S) = \frac{bS}{1+mS}$ and $G(S, I) = S\{r - c_1(S + I) - \beta I\}$.

Theorem 3. *The interior equilibrium point E^* of system (2) is globally asymptotically stable if $\frac{c_1\mu}{\beta - c_2} + c_1S^* + \beta I^* > r$.*

Proof. Consider the following positive definite function about E^*

$$V(t) = \int_{S^*}^S \frac{F(\theta) - F(S^*)}{F(\theta)} d\theta + \frac{\beta}{(1+mS^*)(\beta - c_2)} (I - I^* - I^* \ln \frac{I}{I^*})$$

$$+ \frac{1}{q} \int_{Y^*}^Y \frac{\theta - Y^*}{\theta} d\theta + \frac{D + d_1}{qD} \int_{Z^*}^Z \frac{\theta - Z^*}{\theta} d\theta.$$

Differentiating V with respect to t along the solution of system (2), we get

$$\begin{aligned}
 \frac{dV}{dt} &= \frac{F(S) - F(S^*)}{F(S)} [G(S, I) - F(S)Z] + \frac{\beta(I - I^*)(\beta S - c_2(S + I) - \mu)}{(1 + mS^*)(\beta - c_2)} \\
 &\quad + \frac{1}{q} \frac{Y - Y^*}{Y} [qF(S)Z - (D + d_1)Y] + \frac{D + d_1}{qD} \frac{Z - Z^*}{Z} (DY - d_2Z) \\
 &= G(S, I) \frac{F(S) - F(S^*)}{F(S)} + ZF(S^*) - \frac{(D + d_1)Y^*}{q} \left[\frac{F(S)ZY^*}{F(S^*)Z^*Y} + \frac{Z^*Y}{ZY^*} + \frac{F(S^*)}{F(S)} \right. \\
 &\quad \left. - 3 \right] + \frac{(D + d_1)Y^*}{q} \frac{F(S)}{F(S)} - \frac{(D + d_1)Y^*}{q} - \frac{(D + d_1)d_2Z}{qD} - 3 \frac{(D + d_1)Y^*}{q} \\
 &\quad + \frac{\beta(I - I^*)\{(\beta - c_2)(S - S^*) - c_2(I - I^*)\}}{(1 + mS^*)(\beta - c_2)}.
 \end{aligned}$$

Since $F(S^*) = \frac{(D + d_1)d_2}{qD}$, this yields

$$\begin{aligned}
 \frac{dV}{dt} &= \{G(S, I) - G(S^*, I^*)\} \frac{F(S) - F(S^*)}{F(S)} - \frac{(D + d_1)Y^*}{q} \left[\frac{F(S)ZY^*}{F(S^*)Z^*Y} + \frac{Z^*Y}{ZY^*} \right. \\
 &\quad \left. + \frac{F(S^*)}{F(S)} - 3 \right] + \frac{\beta(S - S^*)(I - I^*)}{1 + mS^*} - \frac{\beta c_2(I - I^*)^2}{(1 + mS^*)(\beta - c_2)} \\
 &= [\{r - c_1(S + S^*) - \beta I^*\}(S - S^*) - \beta S(I - I^*)] \frac{S - S^*}{S(1 + mS^*)} \\
 &\quad - \frac{(D + d_1)Y^*}{q} \left[\frac{F(S)ZY^*}{F(S^*)Z^*Y} + \frac{Z^*Y}{ZY^*} + \frac{F(S^*)}{F(S)} - 3 \right] \\
 &\quad + \frac{\beta(S - S^*)(I - I^*)}{1 + mS^*} - \frac{\beta c_2(I - I^*)^2}{(1 + mS^*)(\beta - c_2)} \\
 &= \frac{\{r - c_1(S + S^*) - \beta I^*\}(S - S^*)^2}{S(1 + mS^*)} - \frac{\beta c_2(I - I^*)^2}{(1 + mS^*)(\beta - c_2)} \\
 &\quad - \frac{(D + d_1)Y^*}{q} \left[\frac{F(S)ZY^*}{F(S^*)Z^*Y} + \frac{Z^*Y}{ZY^*} + \frac{F(S^*)}{F(S)} \right].
 \end{aligned}$$

Using the arithmetic mean is greater than or equal to the geometric mean, it is clear that,

$$\frac{F(S)ZY^*}{F(S^*)Z^*Y} + \frac{Z^*Y}{ZY^*} + \frac{F(S^*)}{F(S)} \geq 3,$$

and the equality holds only for $S = S^*, Y = Y^*, Z = Z^*$. Further, we note that from second equation of system (2), $S > \frac{\mu}{\beta - c_2}$. If $S \leq \frac{\mu}{\beta - c_2}$ then $\frac{dI}{dt}$ will be negative. Thus if $\frac{c_1\mu}{\beta - c_2} + c_1S^* + \beta I^* \geq r$ then $\frac{dV}{dt}$ is negative definite. Hence V is a Lyapunov function with respect to E^* whose domain of attraction is B , proving the theorem. \square

Set $f(c_1) = A_1(c_1)A_2(c_1)A_3(c_1) - A_1^2(c_1)A_4(c_1) - A_3^2(c_1)$.

Theorem 4. *If there exists $c_1 = c_1^*$ such that*

$$i) A_3(c_1^*) > 0,$$

$$ii) f(c_1^*) = 0, f'(c_1^*) > 0,$$

then the positive equilibrium point E^ is locally stable if $c_1 > c_1^*$ but it is unstable for $c_1 < c_1^*$ and a Hopf bifurcation of periodic solution occurs at $c_1 = c_1^*$.*

Proof. Proceeding along the lines in [22], we observe that $f(c_1)$ is monotonic increasing function in the neighbourhood of $c_1 = c_1^*$. As $A_3(c_1^*) > 0$, $f(c_1) > 0$ for $c_1 > c_1^*$, thus local stability of E^* follows from Theorem 2. Again, it is obvious that $f(c_1) < 0$ for $c_1 < c_1^*$ and hence E^* is unstable. Therefore Hopf bifurcation follows from a result in [15]. \square

5 Numerical simulations

In the following section we will present some examples to verify our results obtained earlier. Numerical simulations are performed for a hypothetical set of data.

Example 1. Suppose $r = 8, c_1 = 2, \beta = 1, b = 9, m = 2, \mu = 1, c_2 = 0.5, q = 1, D = 3, d_1 = 0.75, d_2 = 3$. Clearly system (2) has an equilibrium point (2.5, 0.5, 1, 1). Condition of Theorem 3 is satisfied and hence it is globally asymptotically stable. By applying Matlab 7.0.1 to simulate system (2), we obtain Figure 1.

Example 2. Suppose $r = 9, \beta = 3, b = 4, m = 1, \mu = 1, c_2 = 1, q = 1, D = 1, d_1 = 1, d_2 = 1$. Set $c_1 \approx 1.1493$, it is easy to see that system (2) has an equilibrium point (1, 1, 1.8507, 1.8507) and $A_3(c_1^*) \approx 26.493 > 0$, $f(c_1^*) \approx 0$, $f'(c_1^*) = 523.56104 > 0$. Then it follows from Theorem 4 that a Hopf bifurcation of periodic solution occurs at $c_1^* \approx 1.1493$. Choose c_1 to be 1.18, 1 respectively. When $c_1 = 1.18$, the positive equilibrium (1, 1, 1.82, 1.82) is locally asymptotically stable (see Figure 2). When $c_1 = 1.01$, the positive equilibrium (1, 1, 1.99, 1.99) is unstable (see Figure 3).

Example 3. Suppose $r = 9, \beta = 3, b = 4, m = 0, \mu = 1, c_2 = .6, q = 2, D = 2, d_1 = 2, d_2 = 2$. Set $c_1 \approx 2.0127$. It follows from Theorem 4 that a Hopf bifurcation of periodic solution occurs at $c_1^* \approx 2.1$. Choose c_1 to be 2.2, 2 respectively. When $c_1 = 2.2$, the positive equilibrium (.5, .33, 1.541, 1.541) is locally asymptotically stable (see Figure 4). When $c_1 = 2$, the positive equilibrium (.5, .33, 1.583, 1.583) is unstable (see Figure 5).

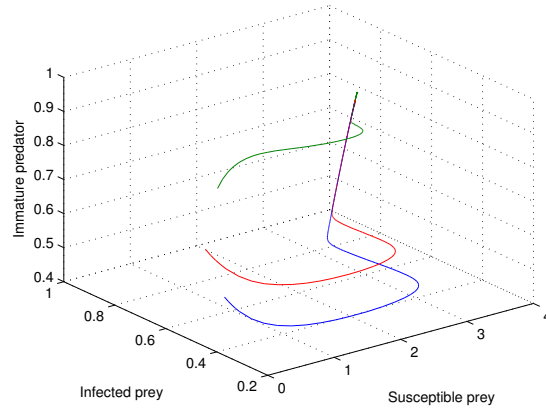


Figure 1: The interior equilibrium point $(2.5, 0.5, 1, 1)$ of system (2) is globally asymptotically stable.

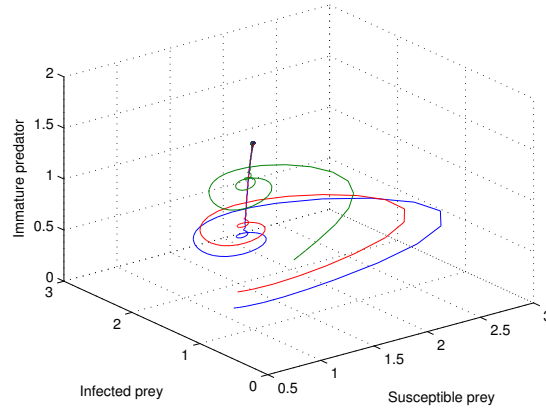


Figure 2: Phase portrait of system (2) when $c_1 = 1.18$ indicates that the equilibrium point $(1, 1, 1.82, 1.82)$ is locally asymptotically stable.

6 Discussion

In this paper, we have proposed and analyzed a four-dimensional three-species eco-epidemiological system with stage structure for predator. We have considered Holling type II predator functional response. It is assumed here that mature predator consumes susceptible prey only. Results ob-

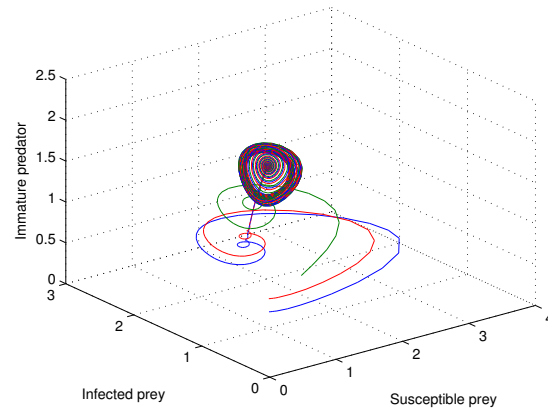


Figure 3: Stability property of system (2) is lost when $c_1 = 1.01$. The interior equilibrium point $(1, 1, 1.99, 1.99)$ is unstable.

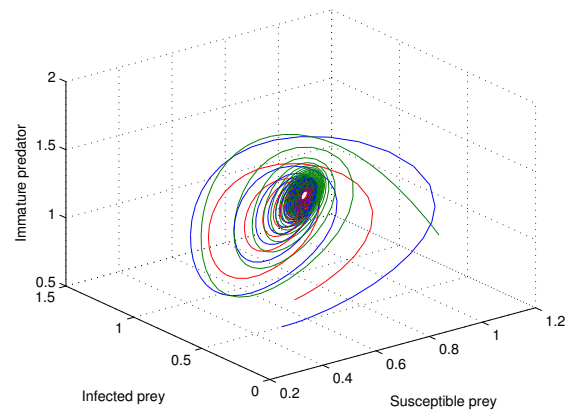


Figure 4: The interior equilibrium point $(0.5, 0.33, 1.541, 1.541)$ of system (2) is locally asymptotically stable when predation follows Holling type I response function.

tained in this paper indicate that intraspecific competition makes possible coexistence of all species. We got four equilibria. The trivial equilibrium point E_0 is always unstable. The equilibrium point E_1 where only susceptible prey population can survive. The equilibrium point E_{12} where both

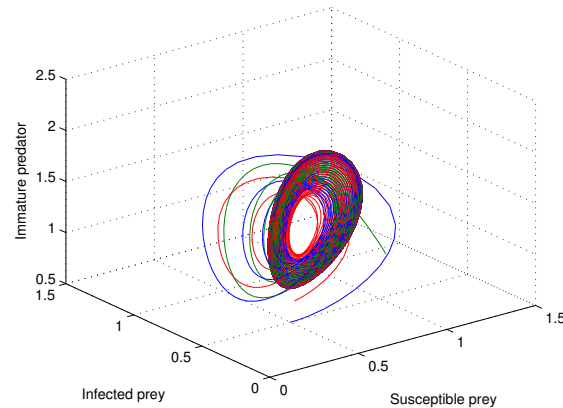


Figure 5: Stability of system (2) is lost when $c_1 = 2$ and $m = 0$. The interior equilibrium point $(0.5, 0.33, 1.583, 1.583)$ is unstable.

types of prey exist but no predators. The equilibrium E_1 becomes unstable when E_{12} exists. The positive equilibrium is that where four type of individuals are present and for some parametric values it is stable for others it is unstable. The global stability condition indicates that the intrinsic growth rate of prey population must be below certain threshold value. This result ensures the coexistence of all the populations in future time. If the global stability condition is not satisfied then there is a possibility of Hopf bifurcation when intraspecific competition c_1 crosses a critical value. Lastly we note that from numerical simulation that limit cycle can arise by Hopf bifurcation in case of Holling type I predator functional response (see Figure 5). Recently some works have been done in eco-epidemic model where predator consumes sound prey with alternative food source [5, 23]. But the model with intraspecific competition and stage structure for predator in eco-epidemic context is not addressed earlier.

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