Dynamical bifurcation of an eco-epidemiological system

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Abstract. In this paper we have considered a dynamical system which models the evolution of three species, two of them being the susceptible and infected preys, respectively and the other one -the predator population. The system depends on eight parameters. We found a Hopf bifurcation point when one of the parameters was varied and we deduced the presence of a stable limit cycle. Bifurcation diagrams are presented and we established the important types of dynamics of the system. By numerical integration, we obtained the phase portrait for different types of dynamics and plots of time course for the corresponding solutions.

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Key words: predator-prey system; stability; limit cycles; Hopf points.

1 Introduction

In this paper, we study a prey-predator system with three populations, the infected prey, the susceptible prey and the predators on both populations. The system models the combined effect of epidemiological and demographic features on real ecological populations. The dynamical system was studied in [3] and there were analyzed sufficient conditions for the local stability of the equilibrium points of the system and numerical simulations for its dynamical behavior.

After we obtained the non-dimensional form, the system has now eight parameters. Our goal is to find the domain in the parameters space for the existence of the equilibria and for local stability and to proof a Hopf bifurcation point, under one parameter variation. Also, we search the ecological interpretation of this point and we shall establish all the important types of dynamics of the system.

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2 The eco-epidemiological model. Stability and bifurcation analysis

The model considered here is described by the following three-dimensional ODE system:

$$(2.1)\qquad \begin{cases} S'(t) = rS(1-S-I) - bSI - \frac{p_1 SY}{m+S} \\ I'(t) = bSI - d_1 I - \frac{p_2 IY}{m+I} \\ Y'(t) = -d_2 Y + q\frac{p_1 SY}{m+S} + q\frac{p_2 IY}{m+I}, \end{cases}$$

where the prey population density consists of susceptible one- S and the infected prey- I. The predator population density is Y.

There are general assumptions of the model, namely [3]:

1. In the absence of disease, the prey population grows logistically with intrinsic growth rate r.

2. Only the susceptible prey can reproduce. The infected prey is removed with death rate d_1 or by predation. The infected population I contributes with S to population growth towards the carrying capacity.

3. The disease is spread among the prey only. Susceptible prey becomes infected when it comes in contact with the infected prey and this process follows the simple mass action kinetics with b as the rate of conversion.

4. The predation functional response of the predator towards susceptible, as well as infected prey, namely $\frac{p_1 S}{m+S}$ and $\frac{p_2 I}{m+I}$ are of Michaelis-Menten type (see for example [4]) with predation coefficients p_1 and p_2. Here m denotes the half-saturation constant. Consumed prey is converted into predator with efficiency q. The loss of predator population is due to death at a constant rate, d_2.

In [1] we proved that $\mathbb{R}^3_+$ is an invariant set for the system and the existence criteria of the equilibrium points are the following:

Proposition 2.1. *i) The trivial equilibrium* $E_0 = (0,0,0)$ *and the axial equilibrium* $E_1 = (1,0,0)$ *always exist;*

ii) The boundary equilibria $E_{B1} = (\frac{d_1}{b}, \frac{r(b-d_1)}{b(b+r)}, 0)$ *exists iff* $b > d_1$ *and* $E_{B2} = (\widehat{S}, 0, \widehat{Y})$ *exists iff* $qp_1 > d_2(1+m)$*, where* $\widehat{S} = \frac{md_2}{qp_1 - d_2}$, $\widehat{Y} = \frac{r(1-\widehat{S})(m+\widehat{S})}{p_1}$;

iii) The interior equilibrium is $E^* = (S^*, I^*, Y^*)$*, where* $Y^* = \frac{(bS^* - d_1)(m+I^*)}{p_2}$, $S^* = \frac{m[(d_2 - qp_2)I^* + md_2]}{(qp_1 + qp_2 - d_2)I^* + m(qp_1 - d_2)}$ *and* I^* *is the positive root of the equation*

$$(2.2)\qquad g(I^*) := \left[1 - \frac{m((d_2 - qp_2)I^* + md_2)}{(qp_1 + qp_2 - d_2)I^* + m(qp_1 - d_2)} - I^*\right] - \frac{bd_2(m+I^*)}{p_2 q} + \frac{d_1}{p_2 qm}[(qp_1 + qp_2 - d_2)I^* + m(qp_1 - d_2)] = 0.$$

We found, as well, necessary and sufficient conditions for the local stability of the boundary equilibria:

Proposition 2.2. *i)* E_0 *is a saddle point, always stable in the direction of* I *and* Y *and unstable in* S *- direction;*

ii) E_1 *is locally asymptotic stable iff* $b < d_1$ *and* $q < \frac{d_2(1+m)}{p_1} =: q_{\min}$ *;*

iii) E_{B1} *is locally asymptotic stable iff* $b > d_1$ *and* $q < \frac{d_2}{\frac{p_1 d_1}{mb + d_1} + \frac{p_2 r(b-d_1)}{mb(b+r) + r(b-d_1)}} =: q_1$.

For the disease-free equilibrium E_{B2}, the eigenvalues of the Jacobian matrix in this point, are $\lambda_1 = b\,\widehat{S} - d_1 - \frac{p_2}{m}\widehat{Y}$ and $\lambda_{2,3}$, the roots of the equation

$$\lambda^2 + \lambda[r - \frac{p_1\widehat{Y}}{(m+\widehat{S})^2}]\widehat{S} + qm\frac{p_1^2\widehat{S}\widehat{Y}}{(m+\widehat{S})^3} = 0. \tag{2.3}$$

We assume $m < 1$ and the equilibrium E_{B2} is asymptotic stable if $\mathrm{Re}(\lambda_{2,3}) < 0$ and $\lambda_1 < 0$. The first one is equivalent with $q < \frac{d_2(1+m)}{p_1(1-m)} =: q_0$ and the second one, with $\widehat{S} < \widehat{S}_+$, where $\widehat{S}_+$ is the single positive root of the equation $f(x) := p_2rx^2 + (mbp_1 - p_2r + p_2rm)x - m(p_1d_1 + p_2r) = 0$.

The last condition can be written as $q > \frac{d_2}{p_1}(\frac{m}{\widehat{S}_+} + 1) =: \widehat{q}$. So, in order to be in the case of local stability, it is necessary that $\widehat{q} < q_0 \Longleftrightarrow \widehat{S}_+ > \frac{1-m}{2} \Leftrightarrow f(\frac{1-m}{2}) < 0$.

Proposition 2.3. *Let be $m < 1$. i) If $b > d_1$, the equilibrium E_{B2} is locally asymptotic stable iff $\widehat{q} < q < q_0$ and $b < \frac{2d_1}{1-m} + \frac{p_2r(1+m)^2}{2mp_1(1-m)}$.*

ii) When $b < d_1$, E_{B2} is locally asymptotic stable iff $q_{\min} < q < q_0$.

In the present paper, for the interior equilibrium E^*, we search conditions for the uniqueness which is the case with biological relevance.

The components of $E^*(S^*, I^*, Y^*)$ must be positive and we obtain:

Lemma 2.4. *If $qp_1 > d_2$ and $p_1 < p_2$, then E^* exists iff $q < \frac{d_2(bm+d_1)}{d_1p_1}$ and $0 < I^* < \frac{m[d_2(bm+d_1)-d_1qp_1]}{(qp_2-d_2)(bm+d_1)+d_1qp_1} =: I^*_m$.*

Let us consider $q > q_{\min}$, $b \geq d_1$ and the function $\psi(b) := d_2 - q[\frac{p_1d_1}{mb+d_1} + \frac{p_2r(b-d_1)}{mb(b+r)+r(b-d_1)}]$. Since $\psi(d_1) < 0$, the equation $\psi(b) = 0$ is equivalent with a third order equation having only one solution greater then d_1, and this is by definition b_+. So E_{B1} is stable iff $\psi(b) > 0 \Leftrightarrow b > b_+$.

Combining the previous results, we find equivalent conditions for equation $g(I^*) = 0$ to have a unique solution $I^* \in (0, I^*_m)$.

Proposition 2.5. *i) When $p_1 < p_2$, $b > d_1$ and $f(\frac{d_1}{b}) < 0$, there exists only one interior equilibrium iff q is between q_1 and $\widehat{q}$;*

ii) When $p_1 < p_2$ and $q_{\min} < q < q_0$, there is only one interior equilibrium iff b is between b_+ and b_2, where $b_2 = \frac{d_1(qp_1-d_2)+p_2qr}{d_2m} - \frac{rp_2q}{qp_1-d_2}$.

Proof. The equation (2.2) is equivalent with a second order equation, $g_2(I^*) = 0$ and this one has a unique solution $I^* \in (0, I^*_m)$ iff $g_2(0)g_2(I^*_m) < 0$. It can be established by straightforward calculations that $g_2(I^*_m) < 0 \Leftrightarrow q > q_1 \Leftrightarrow \psi(b) < 0 \Leftrightarrow b < b_+$. Also $g_2(0) > 0 \Leftrightarrow b > b_2 \Leftrightarrow f(\widehat{S}) > 0 \Leftrightarrow q < \widehat{q}$. Also note that $f(\frac{d_1}{b}) < 0$ holds iff $\widehat{q} < \frac{d_2(bm+d_1)}{d_1p_1}$. □

Remark 2.1. i) $E_{B1} = E_1$ iff $b = d_1$;

ii) $E_{B2} = E_1$ iff $q = q_{\min} \Leftrightarrow b = b_+$;

iii) $E_{B1} = E^* \Leftrightarrow q = q_1$;

iv) $E_{B2} = E^* \Leftrightarrow b = b_2 \Longleftrightarrow q = \widehat{q}$;

v) $E_{B1} = E_{B2}$ iff $b = d_1$ and $q = q_{\min}$ and in this case, both equilibria coincide with E_1.

We are now investigating whether the system admits a stable limit cycle which represents states of coexistence of all species of the system, as well as the interior equilibrium E^*. When interested in periodic solutions of a dynamical system, Hopf bifurcation points are first to be considered.

Let q be the control parameter. For $q = q_0$ we found such a dynamic bifurcation point:

Theorem 2.6. *Suppose $m < 1$. The point (E_{B2}, q_0) is a supercritical non-degenerate Hopf bifurcation point if, for the other parameters,*

$$b \neq \frac{2d_1}{1-m} + \frac{p_2 r(1+m)^2}{2mp_1(1-m)}. \tag{2.4}$$

The first Lyapunov coefficient is $l_1 = -\frac{\sqrt{r}}{2\sqrt{md_2}(m+1)} < 0$.

Proof. A necessary condition to be a Hopf bifurcation point is that the equilibrium E_{B2} has at the critical parameter value $q = q_0$, a simple pair of purely imaginary eigenvalues and no other with the real part, zero. Only $\lambda_{2,3}$, the roots of equation (2.3) can satisfy this condition iff $\lambda_2 + \lambda_3 = 0 \Longleftrightarrow q = q_0$.

Also we need $\lambda_1 \neq 0 \Leftrightarrow \widehat{S} \neq \widehat{S}_+$. In consequence it is necessary that $q \neq \widehat{q}$ at the bifurcation parameter value, so $q_0 \neq \widehat{q} \Leftrightarrow f(\frac{1-m}{2}) \neq 0$ or in the form (2.4).

As a function of the control parameter, $\lambda_{2,3}(q) = \alpha(q) \pm i\omega(q)$, $\omega(q) > 0$ and it is defined in a neighborhood of $q_0 = \frac{d_2(1+m)}{p_1(1-m)}$. Since $\alpha(q) = \frac{\lambda_2+\lambda_3}{2} = \frac{rd_2}{2qp_1}(1-m-\frac{2md_2}{qp_1-d_2})$, we find that $\alpha'(q_0) = \frac{p_1 r(1-m)^3}{4d_2 m(1+m)} > 0$ (H1) and the first non-degeneracy condition for Hopf bifurcation is satisfied.

Next we shall find the first Lyapunov coefficient and for this we fix $q = q_0$. Using the equation (2.3), we compute $\omega^2(q_0) = qm\frac{p_1^2\widehat{S}\widehat{Y}}{(m+\widehat{S})^3}\Big|_{q=q_0} = rmd_2$ and the Jacobian matrix at E_{B2} for $q = q_0$, $A = \begin{pmatrix} 0 & a_{12} & a_{13} \\ 0 & a_{22} & 0 \\ a_{31} & a_{32} & 0 \end{pmatrix}$ where $a_{12} = \frac{(r+b)(m-1)}{2}$, $a_{13} = \frac{p_1(m-1)}{m+1}$, $a_{22} = \frac{b(1-m)}{2} - \frac{p_2 r(1+m)^2}{4p_1 m} - d_1$; $a_{31} = \frac{rd_2 m(1+m)}{p_1(1-m)}$; $a_{32} = \frac{rd_2 p_2(1+m)^3}{4p_1^2 m(1-m)}$.

We need eigenvectors corresponding to the purely imaginary eigenvalues of A and its transpose A^T. From now on we denote by $\omega = \omega(q_0)$. We compute $u \in \mathbb{C}^3$ an eigenvector corresponding to $i\omega$ and $v \in \mathbb{C}^3$ the adjoint eigenvector, having the properties $Au = i\omega u$, $A^T v = -i\omega v$ and satisfying the normalization $\langle u, v\rangle = 1$ in $\mathbb{C}^3$.

Next, we make a translation of the variables in the system (2.1), so that E_{B2} becomes the origin and we find its coefficients at the critical parameter value. We substitute $(S - \widehat{S}, I, Y - \widehat{Y}) = (x_1, x_2, x_3)$ and the system becomes at $q = q_0$:

$$\begin{cases} \frac{dx_1}{dt} &= r(x_1 + \frac{1-m}{2})(\frac{1+m}{2} - x_1 - x_2) - b(x_1 + \frac{1-m}{2})x_2 \\ & \quad -[p_1 x_3 + \frac{r}{4}(1+m)^2]\frac{2x_1+1-m}{2x_1+1+m} \\ \frac{dx_2}{dt} &= b(x_1 + \frac{1-m}{2})x_2 - d_1 x_2 - p_2\frac{x_2}{x_2+m}[x_3 + \frac{r}{4p_1}(1+m)^2] \\ \frac{dx_3}{dt} &= \frac{d_2(1+m)}{p_1(1-m)}[x_3 + \frac{r}{4p_1}(1+m)^2][p_1\frac{2x_1+1-m}{2x_1+1+m} + p_2\frac{x_2}{x_2+m}] \\ & \quad -d_2[x_3 + \frac{r}{4p_1}(1+m)^2], \end{cases} \tag{2.5}$$

which is in the form $\dot{x}^T = Ax^T + F(x)$, $x \in \mathbb{R}^3$ and $F(x) = \mathcal{O}(\|x\|^2)$, so we express $F(x)$ in terms of the multilinear functions $B(x,y)$, $C(x,y,z)$:

$F(x) = \frac{1}{2}B(x,x) + \frac{1}{6}C(x,x,x) + \mathcal{O}(\|x\|^4)$, $B_i(x,y) = \sum_{j,k=1}^{3} \left.\frac{\partial^2 F_i(\zeta)}{\partial\zeta_j\partial\zeta_k}\right|_{\zeta=0} x_j y_k$,

$C_i(x,y,z) = \sum_{j,k=1}^{3} \left.\frac{\partial^3 F_i(\zeta)}{\partial\zeta_j\partial\zeta_k\partial\zeta_l}\right|_{\zeta=0} x_j y_k z_l$, $i = 1,3$.

From [2], the first Lyapunov coefficient is

$$l_1 = \frac{1}{2\omega}\mathrm{Re}[\langle \mathrm{v}, \mathrm{C}(\mathrm{u},\mathrm{u},\bar{\mathrm{u}})\rangle - 2\left\langle \mathrm{v}, \mathrm{B}(\mathrm{u}, \mathrm{A}^{-1}\mathrm{B}(\mathrm{u},\bar{\mathrm{u}}))\right\rangle + \left\langle \mathrm{v}, \mathrm{B}(\bar{\mathrm{u}}, (2\mathrm{i}\omega\mathrm{I}_3 - \mathrm{A})^{-1}\mathrm{B}(\mathrm{u},\mathrm{u}))\right\rangle].$$

Using MAPLE, we found that $l_1 = \frac{-r}{2\omega(m+1)} \Rightarrow l_1 < 0$ (H2), for every combination of the other parameters. Thus, the Hopf bifurcation is non-degenerate and always supercritical. The conditions (H1) and (H2) determine the sense of bifurcation and the stability of the solutions. In consequence, from a stable branch of equilibrium points corresponding to E_{B2} for $q < q_0$, it bifurcates a branch of periodic solutions (stable limit cycles) for $q > q_0$, while E_{B2} becomes unstable. □

3 The bifurcation diagrams and numerical results

First we use q as a control parameter and the fixed parameters satisfy $p_1 < p_2$, $b > d_1$, $f(\frac{d_1}{b}) < 0$, $f(\frac{1-m}{2}) < 0$ ($\Leftrightarrow \widehat{q} < q_0$), $q_1 < q_{\min}$. We plot the bifurcation diagram for the system (2.1) and make its projection into the plane (q, S). The diagram contains the branches of stationary solutions. Solid and broken lines correspond to stable, respectively unstable equilibrium points (see fig. 1). The static bifurcation parameters are, in order $q_1, q_{\min}$ and $\widehat{q}$. Also we proved that $q = q_0$ is the value of the parameter corresponding to Hopf bifurcation.

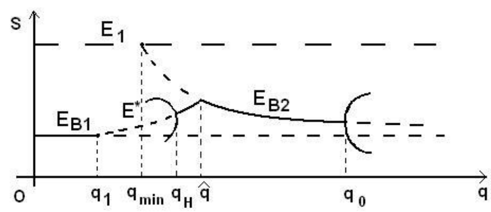

Figure 1: The bifurcation diagram with q as a control parameter which contains static bifurcation points, also Hopf points q_H and q_0. For decreasing values of q, from the stable branch of E^*, a stable limit cycle emerges for $q < q_H$. For increasing q, from the stable branch E_{B2}, a stable limit cycle appears for $q > q_0$.

For the asymptotic stability of E^*, we computed the Jacobian matrix at E^* and the characteristic equation is $\lambda^3 + A_1\lambda^2 + A_2\lambda + A_3 = 0$. Using Routh-Hurwitz criterion, all the eigenvalues λ have negative real part iff $A_1A_2 > A_3$ and $A_1, A_3 > 0$. Otherwise, E^* is unstable.

We took $r = 11.2$, $p_1 = d_1 = 0.4$, $m = 0.016$, $p_2 = 0.6$, $d_2 = 0.08$, $b = 36$ and we found $q_1 \simeq 0.1102$; $q_{\min} \simeq 0.2032$; $\widehat{q} \simeq 0.20331$; $q_0 \simeq 0.2065$.

We detected numerically another Hopf bifurcation point $q_H \in (q_{\min},\ \widehat{q})$, $q_H \simeq 0.203305$ when $A_1A_2 = A_3,\ A_1, A_3 > 0$. We integrated the system using MATLAB and for decreasing values of q, from the stable branch of E^*, a stable limit cycle emerges for $q < q_H$.

Also we illustrated our analytical findings through numerical integration for $q > q_0$, $q = 0.21$ and we depicted one trajectory which tends to a stable limit cycle.(fig. 2) Our simulations revealed that the cycle is a global attractor for the interior of the first octant. In fig. 3 we represented the time evolution of the corresponding solution.

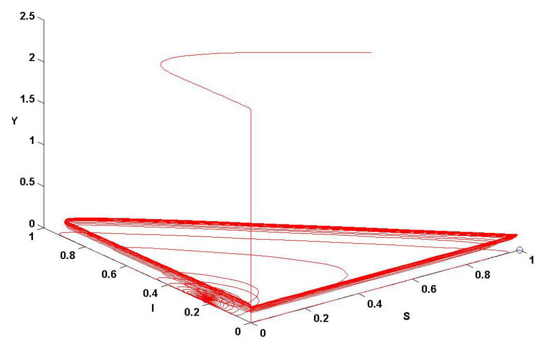

Figure 2: One trajectory from the phase portrait which tends to the limit cycle, when $q > q_0$, $q = 0.21$.

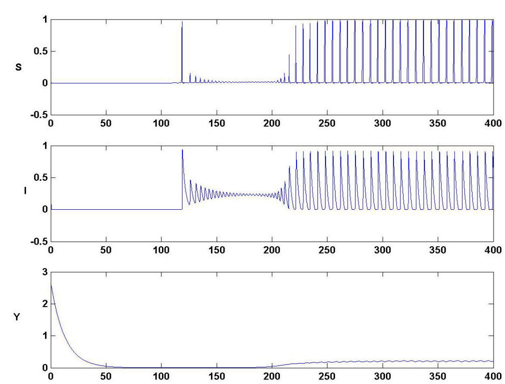

Figure 3: Time evolution of the solution which tends to a periodic behavior, corresponding to the limit cycle.

For $q \in (\widehat{q}, q_0)$, numerical simulations showed that the stability of E_{B2} is of local nature. For q small, $q < q_1$, $q = 0.05$, numerical integration revealed that E_{B1} (the predator free state) is not only locally asymptotic stable, but moreover it has global stability in the interior of $\mathbb{R}^3_+$ (fig. 4 and 5).

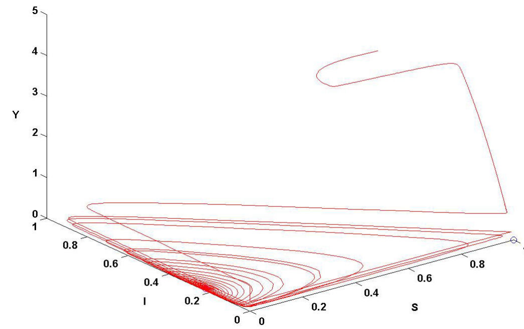

Figure 4: One trajectory for $q < q_1$, $q = 0.05$, which tends to the predator free equilibrium.

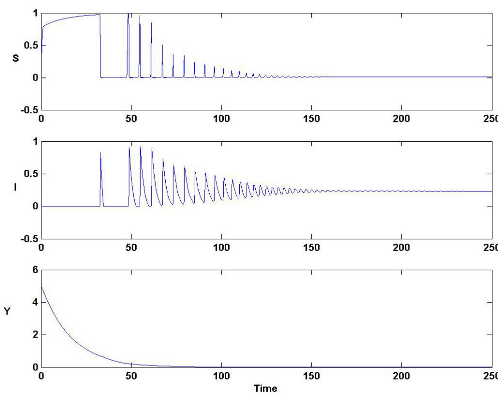

Figure 5: Time evolution of the corresponding solution.

Now we take b as a control parameter and we fix the other ones, satisfying the hypothesis of proposition 2.5 ii): $p_1 < p_2$ and $q_{\min} < q < q_0$ so that E^* is unique for b bettween b_+ and b_2. On the bifurcation diagram (fig. 6), there are three static bifurcation points, in order: $b = d_1$ when $E_{B1} = E_1$; $b = b_+$ when $E_{B1} = E^*$ and $b = b_2$ when E^* meets E_{B2}. For numerical simulations, the fixed parameters are $r = 11.2$, $p_1 = 0.3; d_1 = 0.2$, $m = 0.036$, $p_2 = 0.32$, $d_2 = 0.17$, $q = 0.6$ and we found $b_+ \simeq 62.219$; $b_2 \simeq 136.659$.

For $b \in (b_+, b_2)$, we obtained that E^* is unstable. In consequence, this is an interval for b where two stable branches of solutions coexist (E_{B2} and E_{B1}). So it is an interval of bi-stability. We integrated numerically the system for $b = 63$ and the phase portrait obtained (fig. 7) is in agreement with the analytical result, so there are solutions which start from a small neighborhood of $E_{B2} = (0.612; 0; 9.386)$ and will approach the equilibrium for $t \to \infty$, but other solutions tend to E_{B1}.

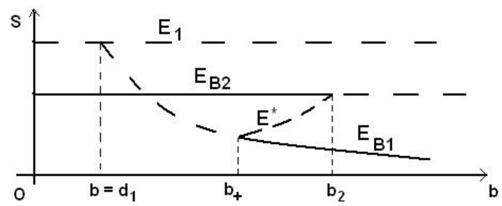

Figure 6: Bifurcation diagram with b as the control parameter, when $p_1 < p_2$ and $q_{\min} < q < q_0$.

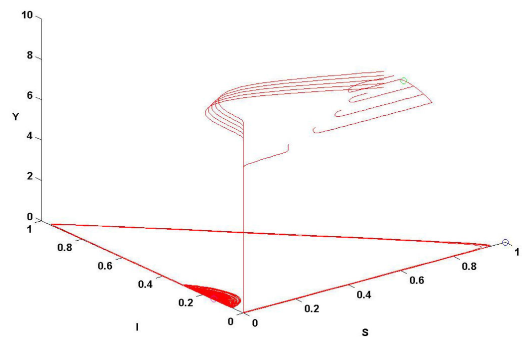

Figure 7: The phase portrait of the system when $b \in (b_+, b_2)$, $b = 63$. Trajectories which start in a neighborhood of $E_{B2} = (0.612; 0; 9.386)$ will approach the equilibrium for $t \to \infty$, others tend to predator free equilibrium.

4 Conclusions

We have examined the behavior of the system (2.1) under the variation of one parameter (q) and then another, (b) in order to establish the important types of dynamics. We discussed the case $p_1 < p_2$ because the predator have a natural tendency to consume a larger number of infected preys [3].

1) For small values of predator conversion efficiency ($q < q_1$) and for average values of b - the rate of conversion of the susceptible prey into infected prey, the system evolves to the free-predator state E_{B1}. (fig. 4) Also this is the evolution for average q (i.e. $q \in (q_{\min}, q_0)$ and large b (i.e. $b > \max(b_+, b_2)$).

2) For average q (i.e. q between $\widehat{q}$ and q_1) or large q, i.e. $q > q_0$, all the three populations coexist in an oscillatory behavior, namely the system tends to a stable limit cycle. (fig. 2)

3) For $q \in (\widehat{q}, q_0)$ and average b or $q \in (q_{\min}, q_0)$ and $b < b_+$, the system can evolve to the free-disease state, if $I(0)$ is small.

We determined several threshold values $\widehat{q}$ and q_0, which are important for disease eradication, as well as for the coexistence (in a stable state or oscillatory stable state) of species.

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