

THE DYNAMICS OF AN ECO-EPIDEMIOLOGICAL SYSTEM

Cristina BER CIA¹

In acest articol se prezintă un sistem de ecuații diferențiale care modelează evoluția a trei specii, două dintre ele sunt populația susceptibilă, respectiv cea infectată, iar a treia este cea a prădătorilor. Am realizat un studiu de stabilitate locală a acestui model. La variația unuia dintre parametri, am gasit un punct de bifurcație Hopf care reprezintă o limită între controlul eradicării bolii, pe de o parte și coexistența celor trei specii pe de altă parte. Apoi am ilustrat rezultatele analitice prin simulări numerice.

In this paper we present an ODE system which models the evolution of three species, two of them are susceptible, respectively infected preys, and the third is the predator population. We performed a local stability study of the model. We found a Hopf bifurcation point by varying one of the parameters, point which represents a threshold between the control disease eradication and the three species coexistence. We illustrated the analytical results through numerical simulations.

Keywords: Predator-prey system, Stability, Limit cycles.

1. Introduction

It is worthwhile to study the combined effect of epidemiological and demographic features on real ecological populations.

The classical prey-predator system which is a two trophic level food chain model often takes the general form

$$\begin{cases} x'(t) = xr(1 - \frac{x}{k}) - cyp(x) \\ y'(t) = (p(x) - d)y \end{cases} \quad (1)$$

where x, y stand for prey and predator density, respectively and $p(x)$ is so called predator functional response. If $p(x) = \frac{mx}{a+x}$, then (1) becomes the predator-prey model with Michaelis-Menten (or Holling type II) functional response.

In this paper we study a prey-predator system with three populations, infected prey, susceptible prey and predators on both populations. Here the Michaelis-Menten type predation functional response is also used. The model has 9 parameters and was studied in [1], regarding sufficient conditions for the local

¹ Lecturer, Dept. of Mathematics II, University POLITEHNICA of Bucharest, Romania, e-mail: cristina_bercia@yahoo.co.uk

stability of the equilibrium points of the system and numerical simulations for its dynamical behavior. In the present article our goal is to find the domain of the parameters for the existence and local stability of the equilibrium points and to proof the existence of a Hopf bifurcation point, when one parameter is varied. This point will represent a threshold between the control disease eradication and the coexistence of the three populations.

2. The eco-epidemiological model

The three-dimensional ODE system is described by the following three-differential equations:

$$\begin{cases} S'(t) = rS\left(1 - \frac{S+I}{k}\right) - bSI - \frac{p_1SY}{m+S} \\ I'(t) = bSI - d_1I - \frac{p_2IY}{m+Y} \\ Y'(t) = -d_2Y + q\frac{p_1SY}{m+S} + q\frac{p_2IY}{m+Y} \end{cases} \quad (2)$$

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:

1. In the absence of disease, the prey population grows logistically with intrinsic growth rate r and environmental carrying capacity k .
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 and the infected ones do not recover. 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.

The predation functional response of the predator towards susceptible as well as infected prey are following Michaelis-Menten kinetics 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 .

So all the parameters are strictly positive and $q \in (0,1]$. We introduce scaling variables, $\frac{S}{k} = \tilde{S}$, $\frac{I}{k} = \tilde{I}$, $\frac{Y}{k} = \tilde{Y}$, $bk = b'$, $\frac{m}{k} = m'$, and then still using old variables for simplicity in notations, we obtain

$$\begin{cases} S'(t) = rS(1 - S - I) - bSI - \frac{p_1 SY}{m + S} \\ I'(t) = bSI - d_1 I - \frac{p_2 IY}{m + Y} \\ Y'(t) = -d_2 Y + q \frac{p_1 SY}{m + S} + q \frac{p_2 IY}{m + Y} \end{cases} \quad (3)$$

and the system will remain with 8 parameters.

Proposition 1 The first octant \mathbf{R}_+^3 is an invariant set for the system (3).

Proof Let be (v_1, v_2, v_3) the vector-field which defines the differential system (3). In I - Y plane, $v_1(0, I, Y) = 0$, therefore all trajectories which initiate in this plane, remain in it, $\forall t \geq 0$, so the plane $S=0$ is an invariant set for the system. With similar arguments, $S=0$, $Y=0$ are also invariant sets and the three coordinate planes separate the interior of \mathbf{R}_+^3 which will be also an invariant set.

In consequence, all solutions with $S(0), I(0), Y(0) > 0$ remain in the first octant. From [1] we know that, with positive initial conditions and $S(0) < k$, the system (2) has only bounded solutions.

The existence criteria of the equilibrium points of the system (3) are the following:

Proposition 2 i) The trivial equilibrium $E_0 = (0, 0, 0)$ and the axial equilibrium $E_1 = (1, 0, 0)$ always exist;

ii) The boundary equilibrium $E_{B1} = \left(\frac{d_1}{b}, \frac{r(b-d_1)}{b(b+r)}, 0 \right)$ exists iff $b > d_1$ and

$$E_{B2} = (\hat{S}, 0, \hat{Y}) \quad \text{exists iff} \quad qp_1 > d_2(1+m), \quad \text{where} \quad \hat{S} = \frac{md_2}{qp_1 - d_2},$$

$$\hat{Y} = \frac{r(1-\hat{S})(m+\hat{S})}{p_1};$$

iii) The interior equilibrium is $E^* = (S^*, I^*, Y^*)$, where $Y^* = \frac{(bS^* - d_1)(m + I^*)}{p_2}$,

$$S^* = \frac{m[md_2 - (qp_2 - d_2)I^*]}{(qp_1 + qp_2 - d_2)I^* + m(qp_1 - d_2)} \quad \text{and} \quad I^* \quad \text{is the positive root of the}$$

$$\text{equation} \quad r \left[1 - \frac{m[md_2 - (qp_2 - d_2)I^*]}{(qp_1 + qp_2 - d_2)I^* + m(qp_1 - d_2)} \right] - \frac{b}{p_2 q} [md_2 - (qp_2 - d_2)I^*] - (r + b)I^* + \frac{d_1}{p_2 q m} [(qp_1 + qp_2 - d_2)I^* + m(qp_1 - d_2)] = 0.$$

3. Stability analysis and a bifurcation study from an equilibrium point

We discuss the local stability of the equilibria of the system (3). We evaluate the Jacobian matrix at every equilibrium point and the sign of the real part of each eigenvalue will give us information about local stability.

Proposition 3 i) $E_0 = (0,0,0)$ is a saddle-point, always stable in the directions of I and Y and unstable in S direction;

ii) $E_1 = (1,0,0)$ is local asymptotic stable iff $b < d_1$ and $qp_1 > d_2(1+m)$, stable in the direction of S ;

iii) E_{B1} is local asymptotic stable iff $b > d_1$ and

$$d_2 > q \left(\frac{p_1 d_1}{mb + d_1} + \frac{p_2 r(b - d_1)}{mb(b + r) + r(b - d_1)} \right). \quad (4)$$

Proof The eigenvalues corresponding to E_0 are $r, -d_1, -d_2$. For the Jacobian matrix in E_1 , we find the eigenvalues $-r, b - d_1, \frac{qp_1}{1+m} - d_2$. An eigenvector corresponding to $(-r)$ is $(1,0,0)$, so OS is the invariant stable manifold if the two conditions for E_1 don't hold.

The Jacobian matrix evaluated in E_{B1} gives one eigenvalue $\lambda_1 \in \mathbf{R}$ and the condition (4) is equivalent with $\lambda_1 < 0$. The others verify the equation $b\lambda^2 + rd_1\lambda + rd_1(b - d_1) = 0$. So, if E_{B1} exists, $b > d_1$, then $\text{Re } \lambda_{2,3} < 0$. If (4) doesn't hold, the plain $Y=0$ is a stable manifold for it.

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

$$\lambda^2 + \lambda \left(r - \frac{p_1 \hat{Y}}{(m + \hat{S})^2} \right) \hat{S} + \frac{qp_1^2 m \hat{Y}}{(m + \hat{S})^3} = 0. \quad (5)$$

We assume $qp_1 > d_2$, $m < 1$ and the equilibrium point E_{B2} is stable in the plane $I = 0$ iff the coefficient of λ is strictly positive, equivalent with

$$q < \frac{d_2(1+m)}{p_1(1-m)} =: q_0. \quad (6)$$

$\lambda_1 < 0 \Leftrightarrow \hat{S} < \hat{S}_+$, where \hat{S}_+ is the positive root of the equation

$$f(x) := p_2 rx^2 + (mbp_1 - p_2 r + p_2 rm)x - m(p_1 d_1 + p_2 r) = 0. \quad (7)$$

The last condition can be written as $q > \frac{d_2}{p_1} \left(\frac{m}{\hat{S}_+} + 1 \right) =: \hat{q}$ and we can

establish the following result:

Proposition 4 i) Let $m < 1$, $b > d_1$. Then E_{B2} is local asymptotic stable iff $\hat{q} < q < q_0$ and for the other parameters, $f\left(\frac{1-m}{2}\right) < 0$;

ii) When $b < d_1$, E_{B2} is local asymptotic stable iff $\frac{d_2(1+m)}{p_1} < q < q_0$.

We are investigating now whether the system admits a stable limit cycle which also represents states of coexistence for the biological system. When interested in periodic or quasiperiodic solutions of a dynamical system, Hopf bifurcation points are first to be considered.

Suppose we have an autonomous system of ODE, $v' = F(v, p)$ where $v \in \mathbf{R}^n$ is the vector of variables and $p \in \mathbf{R}^m$ is the vector of parameters. We say that $(v_0, p_0) \in \mathbf{R}^n \times \mathbf{R}^m$ is a Hopf point, provided there exists $a > 0$ such that there is a smooth function $\varphi: [-a, a] \rightarrow \mathbf{R}^{n+m}$, $\varphi(\zeta) = (v(\zeta), p(\zeta))$ such that

i) $\varphi(0) = (v_0, p_0)$;

ii) $F(v(\zeta)) = 0, \forall \zeta \in [-a, a]$;

iii) The Jacobian matrix $\frac{DF}{Dv}(v(\zeta), p(\zeta))$ has at least one pair of conjugated complex eigenvalues $\alpha(\zeta) \pm i\beta(\zeta)$, $\forall \zeta \in [-a, a]$ with $\alpha(0) = 0, \alpha'(0) \neq 0, \beta(0) \neq 0$;

iv) All other eigenvalues of the Jacobian matrix except $\pm i\beta(0)$ have nonzero real parts.

In our case we consider q as a control parameter.

Theorem 1 Suppose $m < 1$. The point (E_{B2}, q_0) is a supercritical Hopf bifurcation point, for every value of the other parameters, for the system (3).

Proof A necessary condition for Hopf bifurcation is that the Jacobian matrix evaluated at E_{B2} has one pair of pure imaginary eigenvalues. Only $\lambda_{2,3}$

which verify equation (5) can satisfy this condition iff $\lambda_2 + \lambda_3 = 0 \Leftrightarrow q = q_0$. As a function of the control parameter q , $\lambda_{2,3}(q) = \alpha(q) \pm i\beta(q)$ defined in a neighborhood of $q_0 = \frac{d_2(1+m)}{p_1(1-m)}$. Since $\alpha(q) = \frac{\lambda_2 + \lambda_3}{2}$, we find

$$\alpha'(q) = \frac{rd_2(1+m)}{2q^2mp_1} > 0. \text{ In consequence, from a stable branch of equilibrium}$$

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. This is the case of supercritical Hopf bifurcation.

4. Numerical simulations

In this section we expect some numerical simulations to illustrate our analytical findings. Since we took q as a control parameter, we fixed the others: $r = 11.2, b = 36, p_1 = d_1 = 0.4, m = 0.016, p_2 = 0.6, d_2 = 0.08$. We found

$$q_0 = 0.206, \hat{q} = 0.2034, q_{\min} = \frac{d_2(1+m)}{p_1} = 0.2033.$$

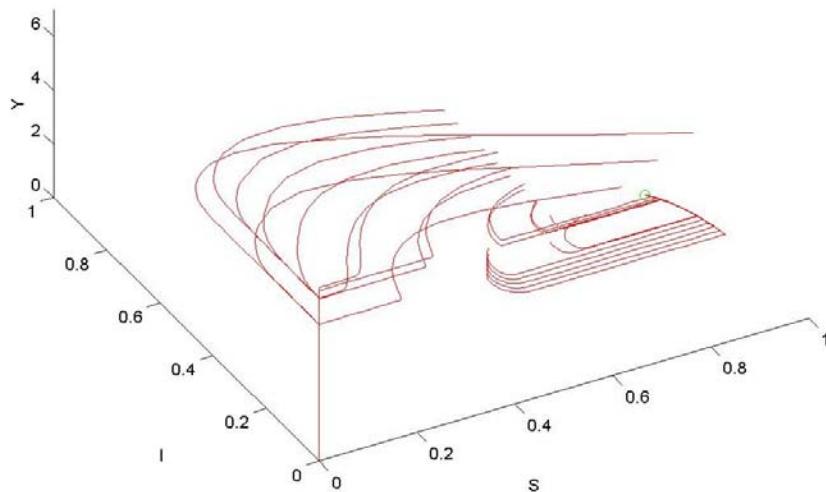


Fig. 1. The phase portrait of the system (2) for $q \in (\hat{q}, q_0)$ around the disease free steady state $(0.66; 0; 6.37)$ when $q = 0.205$.

For $q \in (\hat{q}, q_0)$, $q = 0.205$, we integrated numerically the system using MATLAB. Solutions which start only from a neighborhood of $E_{B2} = (0.66; 0; 6, 37)$ will approach the equilibrium point for $t \rightarrow \infty$ (figure 1), so the stability of E_{B2} is of local nature.

For $q > q_0$, $q = 0.25$, we depicted one trajectory which tends to a stable limit cycle (Fig. 2-left). Our simulations revealed that the cycle is a global attractor for the interior of the first octant. In Fig. 2-right we represented the time evolution of the correspondent solution.

Now for q very small, satisfying the condition (4), $q = 0.02$, the boundary equilibrium E_{B1} is stable. A solution with initial condition $Y(0) > 0$ will end at E_{B1} where $Y = 0$ (see figure 3).

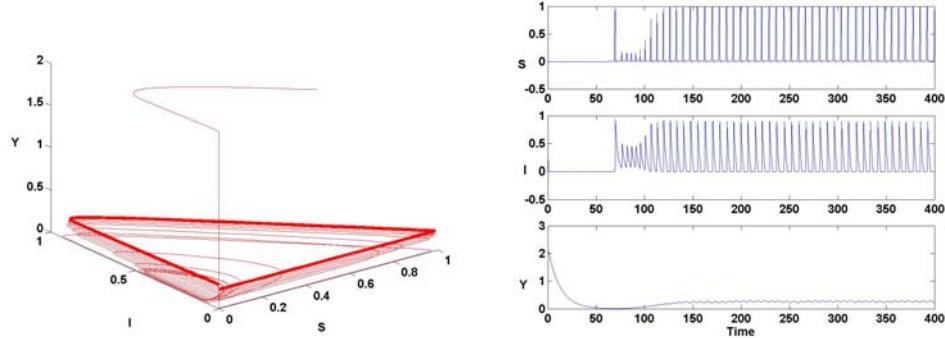


Fig. 2-left. One trajectory which tends to the stable limit cycle, when $q > q_0$, $q = 0.25$. Fig. 2-right. Time evolution of the solution which tends to a periodic behavior, corresponding to the limit cycle

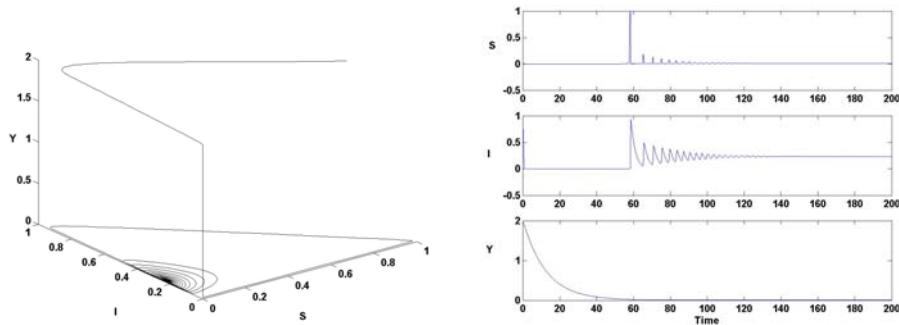


Fig. 3-left. For $q = 0.02$, a trajectory which starts at $(0.9; 0.3; 2)$ tends to the predator free equilibrium for $t \rightarrow \infty$. Fig. 3-right. Time evolution of the correspondent solution.

5. Conclusions

Using the predator conversion efficiency (q) as a control parameter, we showed that for small values of q , the system evolves to the free-predator state (condition (4)). Then, for medium q , we have obtained a threshold value q_0 , such that for $q < q_0$, the system exhibits stable characteristics around the uninfected steady state and for $q > q_0$, this state is replaced by a limit cycle, so all the three populations coexist in an oscillatory behavior with no possibility of disease eradication. Since $q_0 = \frac{d_2(1+m)}{p_1(1-m)}$, the predator conversion efficiency (q),

together with the half saturation constant (m), the predator mortality (d_2) and the consuming capacity of the predator on the susceptible prey (p_1) are important parameters that control global stability aspects.

A further study should be a two-parameter bifurcation analysis which could bring us new information about the periodic behavior of the dynamical system. A simultaneous variation of parameters such as q and b could raise the question whether a generalized Hopf bifurcation can take place. This codimension 2 bifurcation type from equilibria could demonstrate the appearance of limit cycle bifurcation.

R E F E R E N C E S

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