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Analysis of a Three Species Eco-Epidemiological Model[1]

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This paper formulates and analyzes a predator–prey model with disease in the prey. Mathematical analyses of the model equations with regard to invariance of nonnegativity, boundedness of solutions, nature of equilibria, permanence, and global stability are analyzed. It is also shown that for some parameter values, the positive equilibrium is asymptotically stable, but for other parameter values, it is unstable and a surrounding periodic solution appears by Hopf bifurcation. A concluding discussion with numerical simulation is then presented. © 2001 Academic Press

Key Words: predator–prey model; global stability; permanence; Hopf bifurcation.

1. INTRODUCTION

After the pioneering work of Kermack–McKendrick on susceptible–infective–removal–susceptible (SIRS), epidemiological models have received much attention from scientists. Relevant references in this context are also vast and we shall mention here a survey paper [1] and some books (see [2–4], to mention a few). Assuming that the species has no relation with other species (that is to say, these epidemic models were formulated to describe only the spread of the disease), they obtained some threshold results.

In the natural world, however, species do not exist alone, it is of more biological significance to study the persistence-extinction threshold of each population in systems of two or more interacting species subjected to parasitism. But little attention has been paid so far to merge these two

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areas of research [5–7]. In order to study the influence of disease on an environment where two or more interacting species are present.

We consider a three species, eco-epidemological system, namely, sound prey (susceptible), infected prey (infective), and predator. We consider the case where the predator mainly eats the infected prey. This is in accordance with the fact that the infected individuals are less active and can be caught more easily, or the behavior of the prey is modified such that they live in parts of the habitat which are accessible to the predator (fish and aquatic snails staying close to water surface, snails staying on the top of the vegetation rather than under the plant cover) [8]. Peterson and Page [9] have indicated wolf attacks on moose are more often successful if the moose is heavily infected by "Echinococcus granulosus."

We have two populations:

1. The prey, whose total population density is denoted by N.
2. The predator, whose population density is denoted by Y.

We make the following assumptions:

(H_1) In the absence of disease the prey population density grows according to a logistic curve with carrying capacity $K(K > 0)$, with an intrinsic birth rate constant $r(r > 0)$.

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right). \tag{1.1}$$

(H_2) In the presence of disease we assume that the total prey population N is composed of two population classes: one is the class of susceptible prey, denoted by S, and the other is the class of infected prey, denoted by I. Therefore, at any time t, the total density of prey population is

$$N(t) = S(t) + I(t). \tag{1.2}$$

(Note: In the following we are always referring to population densities; we may omit the word "density" for the sake of simplicity.)

(H_3) We assume that only susceptible prey S are capable of reproducing with logistic law (Eq. (1.1)); i.e., the infected prey I are removed by death (say its death rate is a positive constant c) or by predation before having the possibility of reproducing. However, the infective population I still contributes with S to population growth toward the carrying capacity.

(H_4) We assume that the disease is spread among the prey population only and the disease is not genetically inherited. The infected populations do not recover or become immune. The incidence is assumed to be the simple mass action incidence βSI, where $\beta > 0$ is called the transmission coefficient.

(H_5) We assume that the predator eats only the infected prey with predator response function $\overline{\eta}(I)$. The predator has a death rate constant $d(d > 0)$. The coefficient in conversing prey into predator is constant $k(0 < k \leq 1)$. It is assumed that $\overline{\eta}(I)$ is a positive, increasing, and bounded function of I, and $\overline{\eta}(0) = 0$ (see [6, 10]).

From the above assumptions, the model equations are

$$\begin{aligned} \frac{dS}{dt} &= rS\left(1 - \frac{S+I}{K}\right) - \beta SI \\ \frac{dI}{dt} &= \beta SI - cI - \overline{\eta}(I)Y \\ \frac{dY}{dt} &= Y(-d + k\overline{\eta}(I)). \end{aligned} \tag{1.3}$$

Chattopadhyay and Arino [6] have considered a predator–prey model with disease in the prey. They assumed that the sound prey population grows according to a logistic law involving the whole prey population; i.e.,

$$\frac{dS}{dt} = r(S+I)\left(1 - \frac{S+I}{K}\right) - \beta SI - \gamma(S)Y,$$

where $\gamma(S)$ is the predator response function. They further assumed that the intrinsic growth rate r large enough such that $S + I$ approaches the environment carrying capacity K, and using $S + I = K$, they reduced the three-dimensional system to a two-dimensional system. Hence they studied the local stability, extinction, and Hopf-bifurcation in a two-dimensional system. By applying a Poincaré map they observed the connection between the reduced and the original system. System (1.3) is also similar to the one studied by Venturino [7]. However, there are two differences: (i) Venturino does not allow for density dependence in the host regulation except for the disease. (ii) In our model we consider the effect of the predator response function. So we believe that this is the first time that eco-epidemiology model has been formulated and analyzed.

In analogy to the threshold result of epidemic theory (see, for example, [11]), we obtain the threshold parameters which govern the development of the disease or the growth of the predator population. Furthermore, we discuss the permanence of the system and determine conditions for which the system enters a Hopf-type bifurcation.

For the sake of simplicity, we put in dimensionless form the model equations (1.3) by rescaling the variables on the carrying capacity value K; i.e.,

$$s = \frac{S}{K}, \qquad i = \frac{I}{K}, \qquad y = \frac{Y}{K} \tag{1.4}$$

and then using as dimensionless time, $\omega = \beta K t$. This leads to the dimensionless equations

$$\begin{aligned} \frac{ds}{d\omega} &= as(1-(s+i)) - si \\ \frac{di}{d\omega} &= si - b_2 i - \eta(i) y \\ \frac{dy}{d\omega} &= y(-b_1 + k\eta(i)), \end{aligned} \tag{1.5}$$

where

$$a = \frac{r}{\beta K}, \qquad b_1 = \frac{d}{\beta K}, \qquad b_2 = \frac{c}{\beta K}, \qquad \frac{\overline{\eta}(iK)}{\beta K} = \eta(i) \tag{1.6}$$

are the dimensionless parameters. The initial condition for Eq. (1.5) may be any point in the nonnegative orthant of R^3_+ of R^3, where by R^3_+ we mean

$$R^3_+ = \{(s, i, y) \in R^3 \colon s \geq 0,\ i \geq 0,\ y \geq 0\}.$$

For convenience, in the following we replace ω by t for the dimensionless time.

2. PRELIMINARIES

Positive Invariance

Let us put Eq. (1.5) in a vector form by setting

$$X = \mathrm{col}(s, i, y) \in R^3 \tag{2.1}$$

$$F(X) = \begin{pmatrix} F_1(X) \\ F_2(X) \\ F_3(X) \end{pmatrix} = \begin{pmatrix} as(1-(s+i)) - si \\ si - b_2 i - \eta(i) y \\ -b_1 y + k\eta(i) y \end{pmatrix}, \tag{2.2}$$

where $F\colon R^3 \to R^3$ and $F \in C^\infty(R^3)$. Then Eq. (1.5) becomes

$$\dot{X} = F(X), \tag{2.3}$$

where $\cdot = \frac{d}{dt}$ and with $X(0) = X_0 \in R^3_+$. It is easy to check in Eq. (2.2) that whenever choosing $X \in R^3_+$ such that $x_i = 0$, then $F_i(x)|_{x_i(t)=0} \geq 0$, $i = 1, 2, 3$. Due to the well-known theorem by Nagumo [12] any solution of Eq.

(2.3) with $X_0 \in R_+^3$, say $X(t) = X(t, X_0)$, is such that $X(t) \in R_+^3$ for all $t > 0$.

Boundedness of Solutions

LEMMA 2.1. *Assume that the initial condition of Eq.* (1.5) *satisfies* $s_0 + i_0 \geq 1$. *Then either* (i) $s(t) + i(t) \geq 1$ *for all* $t \geq 0$ *and therefore as* $t \to +\infty$, $(s(t), i(t), y(t)) \to E_{10} = (1, 0, 0)$, *or* (ii) *there exists a* $t_1 > 0$ *such that* $s(t) + i(t) < 1$ *for all* $t > t_1$. *Finally* (iii) *if* $s_0 + i_0 < 1$, *then* $s(t) + i(t) < 1$ *for all* $t \geq 0$.

Proof. We consider first $s(t) + i(t) \geq 1$ for all $t \geq 0$. From the first two equations of (1.5) we get

$$\frac{d}{dt}(s(t) + i(t)) = as[1 - (s + i)] - b_2 i - \eta(i)y. \tag{2.4}$$

Hence, for all $t \geq 0$, we have that $s'(t) + i'(t) \leq 0$. Let

$$\lim_{t \to \infty} (s(t) + i(t)) = \xi. \tag{2.5}$$

If $\xi > 1$, then by the Barbălat lemma, we have

$$\begin{aligned}
0 &= \lim_{t \to +\infty} \frac{d}{dt}(s(t) + i(t)) \\
&= \lim_{t \to +\infty} [as(t)(1 - s(t) - i(t)) - b_2 i(t) - \eta(i(t))y(t)] \\
&= \lim_{t \to +\infty} [as(t)(1 - \xi) - b_2 i(t) - \eta(i(t))y(t)] \\
&\leq -\min\{a(\xi - 1), b_2\} \lim_{t \to +\infty} (s(t) + i(t)) \\
&= -\xi \min\{b_2, a(\xi - 1)\} < 0.
\end{aligned}$$

This contradiction shows that $\xi = 1$; i.e.,

$$\lim_{t \to +\infty} (s(t) + i(t)) = 1. \tag{2.6}$$

Let us denote by $g(t) = s(t) + i(t)$ for $t \in [0, +\infty)$. Of course, $g(t)$ is differentiable and $g'(t)$ uniformly continuous for $t \in (0, +\infty)$. Thus, with Eq. (2.6) all the assumptions of Barbălat lemma hold true and, therefore,

$$\lim_{t \to +\infty} \frac{d}{dt}(s(t) + i(t)) = 0. \tag{2.7}$$

Since from the first two equations of (1.5)

$$\frac{d}{dt}(s(t)+i(t)) = as(t)[1-(s(t)+i(t))] - b_2 i(t) - \eta(i(t))y(t) \tag{2.8}$$

then Eq. (2.6) implies that

$$\lim_{t\to+\infty} \frac{d}{dt}(s(t)+i(t)) = -\lim_{t\to+\infty}(b_2 i(t) + \eta(i(t))y(t)). \tag{2.9}$$

Hence, Eqs. (2.7) and (2.8) are in agreement if and only if $\lim_{t\to+\infty} i(t) = 0$, which jointly with Eq. (2.6) imply $\lim_{t\to+\infty} s(t) = 1$. From the third equation of (1.5), we have $y(t)$ tends to zero as $t \to +\infty$. This completes the case (i).

Assume that assumption (i) is violated. Then there exists $t_0 > 0$ at which for the first time $s(t_0) + i(t_0) = 1$. According to Eq. (2.8) we have

$$\frac{d}{dt}(s(t)+i(t))|_{t=t_0} = -b_2 i(t_0) - \eta(i(t_0))y(t_0) < 0.$$

This implies that once a solution with $s + i$ has entered into the interval $(0, 1)$ then it remains bounded there for all $t > t_0$; i.e.,

$$s(t) + i(t) < 1 \quad \text{for all } t > t_0. \tag{2.10}$$

Finally, if $s_0 + i_0 < 1$, applying the previous argument, it follows that $s(t) + i(t) < 1$ for all $t > 0$; i.e., (iii) holds true. This completes the proof.

LEMMA 2.2. *There is an $M > 0$ such that for any positive solution $(s(t), i(t), y(t))$ of Eq.* (1.5)

$$y(t) < M \quad \textit{for all large } t, \tag{2.11}$$

where $M = \frac{k_0}{b_1}$, $k_0 = k(1+\epsilon) + k(b_1 - b_2)$, $\epsilon > 0$ is sufficiently small.

Proof. Lemma 2.1 implies that for any (s_0, i_0, y_0) such that $s_0 + i_0 \geq 1$, then either a time $t_0 > 0$ exists for which $s(t) + i(t) < 1$ for all $t > t_0$ or $\lim_{t\to+\infty} s(t) = 1$, $\lim_{t\to+\infty} i(t) = 0$. Furthermore, if $s_0 + i_0 < 1$ then $s(t) + i(t) < 1$ for all $t > 0$. Hence, in any case a nonnegative time, say t^*, exists such that $i(t) < 1$, $s(t) < 1 + \epsilon$, for all $t > t^*$, then we have $\eta(i) < \eta(1)$ for $t > t^*$. Set

$$V = ki(t) + y(t). \tag{2.12}$$

Calculating the derivative of V along the solutions to Eq. (1.5), we find for $t > t^*$

$$\begin{aligned}\dot{V} &= ks(t)i(t) - kb_2 i(t) - b_1 y(t)\\ &\le k(1+\epsilon) - b_1(ki(t) + y(t)) + k|b_1 - b_2|\\ &\le -b_1 V + k_0.\end{aligned}$$

Recall that $i(t) < 1$ for all $t > t^*$. There exists positive constant M, depending only on the parameters of system (1.5), such that $V(t) < M$ for all large t. The assertion of Lemma 2.2 now follows and the proof is completed.

Let Ω be the following subset of R^3_+

$$\Omega = \left\{(s, i, y) \in R^3_+ : \quad s + i \le 1, \quad y \le M\right\}. \tag{2.13}$$

THEOREM 2.1. *The set Ω is a global attractor in R^3_+ and, of course, it is positively invariant.*

Proof. Due to Lemma 2.1 and Lemma 2.2 for all initial conditions in R^3_+ such that $(s_0, i_0, y_0) \notin \Omega$, either there exists a positive time, say $T, T = \max\{t_1, t^*\}$, such that the corresponding solution $(s(t), i(t), y(t)) \in \operatorname{int}\Omega$ for all $t > T$, or the corresponding solution is such that $(s(t), i(t), y(t)) \to E_{10} = (1,0,0)$ as $t \to +\infty$. But $E_{10} \in \partial\Omega$. Hence the global attractivity of Ω in R^3_+ has been proved.

Assume now that $(s_0, i_0, y_0) \in \operatorname{int}\Omega$. Then Lemma 2.1 implies that $s(t) + i(t) < 1$ for all $t > 0$ and also by Lemma 2.2 we know that $y(t) < M$ for all large t. Let us remark that if $(s_0, i_0, y_0) \in \partial\Omega$, because $s_0 + i_0 = 1$ or $y_0 = M$ or both, then still the corresponding solution $(s(t), i(t), y(t))$ must immediately enter $\operatorname{int}\Omega$ or coincide with E_{10}.

3. EQUILIBRIA, LOCAL STABILITY, AND HOPF BIFURCATION

The model equations (1.5) has the following nonnegative equilibria, namely

$$E_0 = (0,0,0), \quad E_{10} = (1,0,0), \quad E_{20} = \left(b_2, \frac{a(1-b_2)}{1+a}, 0\right) \triangleq (\bar{s}, \bar{i}, \bar{y})$$

and $E_2 = (s^*, i^*, y^*)$, where

$$s^* = \frac{a - (a+1)i^*}{a}, \qquad \eta(i^*) = \frac{b_1}{k}, \qquad y^* = \frac{(s^* - b_2)i^*}{\eta(i^*)}. \tag{3.1}$$

The boundary equilibrium E_{20} exists if $b_2 < 1$ and the existence condition for the positive equilibrium E^* is $\eta(\frac{a(1-b_2)}{a+1}) > \frac{b_1}{k}$; i.e.,

$$b_2 < 1 - \frac{1+a}{a}\eta^{-1}\left(\frac{b_1}{k}\right) \triangleq b_2^*. \tag{3.2}$$

It is clear that $b_2 < b_2^*$ is necessary for the existence of component of y^* of the positive equilibrium. It is to be also noted that this condition implies the existence of E_{20}. Hence, we conclude that the existence of E^* implies the existence of E_{20}, but the reverse is not true. It is also interesting to observe that the equilibrium E_{20} arises from E_{10} for the value of the parameter b_2 equal to 1 and persists for all $b_2 < 1$, while E^* arises from E_{20} when b_2 reaches the value b_2^* and persists below this value. We summarize these results.

THEOREM 3.1. *Whenever $b_2 \in [1, +\infty)$ the equilibria of Eq.* (1.5) *are E_0 and E_{10}. Whenever $b_2 \in [b_2^*, 1)$, besides E_0 and E_{10}, equilibrium E_{20} is feasible. As $b_2 \to 1^-$, then $E_{20} \to E_{10}$ and $E_{20} = E_{10}$ when $b_2 = 1$. Whenever $b_2 \in (0, b_2^*)$ besides E_0, E_{10}, and E_{20}, the positive equilibrium E^* is feasible. As $b_2 \to b_2^{*-}$ then $E^* \to E_{20}$ and $E^* = E_{20}$ when $b_2 = b_2^*$.*

Let

$$R_0 = \frac{1}{b_2}, \qquad \sigma = \frac{k}{b_1}\eta\left(\frac{a(1-b_2)}{a+1}\right). \tag{3.3}$$

From Theorem 3.1, we know that if $R_0 > 1$, then the equilibrium point E_{20} exists, and the positive equilibrium E^* is feasible if $\sigma > 1$. In particular, parameter R_0, which controls whether or not the disease persists, is closely related to the "basic reproduction number" of epidemic theory [11], and parameter σ governs whether or not the positive equilibrium exists.

Let $\hat{E} = (\hat{s}, \hat{i}, \hat{y})$ be arbitrary equilibrium. Then the characteristic equation about $\hat{E}$ is given by

$$\det\begin{vmatrix} a - 2a\hat{s} - (a+1)\hat{i} - \lambda & -(a+1)\hat{s} & 0 \\ \hat{i} & \hat{s} - b_2 - \eta'(\hat{i})\hat{y} - \lambda & -\eta(\hat{i}) \\ 0 & k\eta'(\hat{i})\hat{y} & -b_1 + k\eta(\hat{i}) - \lambda \end{vmatrix} = 0. \tag{3.4}$$

For equilibrium $E_0 = (0,0,0)$, (3.4) reduces to

$$(\lambda - a)(\lambda + b_2)(\lambda + b_1) = 0.$$

Obviously, the above formula has a root with a positive real part. Hence E_0 is a saddle point.

In a similar manner, the disease-free equilibrium E_{10} is locally asymptotically stable if $b_2 > 1$, and it is unstable if $b_2 < 1$. Equilibrium E_{20} is locally asymptotically stable if $b_2 > b_2^*$, and it is unstable if $b_2 < b_2^*$.

For positive equilibrium $E^* = (s^*, i^*, y^*)$, characteristic equation (3.4) gives

$$\lambda^3 + Q_1\lambda^2 + Q_2\lambda + Q_3 = 0,$$

where the coefficients Q_i, $i = 1,2,3$, are

$$Q_1 = -s^* + b_2 + \eta'(i^*)y^* + as^*$$
$$Q_2 = as^*(-s^* + b_2 + \eta'(i^*)y^*) + ky^*\eta'(i^*)\eta(i^*) + (a+1)s^*i^*$$
$$Q_3 = as^*ky^*\eta'(i^*)\eta(i^*).$$

From assumption (H_5) and (1.6), we know that $\eta(i^*) > 0$, $\eta'(i^*) > 0$, then $Q_3 > 0$. Define

$$\begin{aligned}
\Delta^{(2)} &= Q_1Q_2 - Q_3\\
&= (A + as^*)\left[as^*A + (a+1)s^*i^* + ky^*\eta(i^*)\eta'(i^*)\right]\\
&\quad - as^*ky^*\eta'(i^*)\eta(i^*)\\
&= (A + as^*)\left[as^*A + as^*(1-s^*)\right] + Ab_1y^*\eta'(i^*)\\
&= as^*\left(\frac{\eta'(i^*)i^* - \eta(i^*)}{\eta(i^*)}\right)^2(s^* - b_2)^2 + \frac{\eta'(i^*)i^* - \eta(i^*)}{\eta(i^*)}\\
&\quad \times(s^* - b_2)\left[(as^*)^2 - as^*(1-s^*) + \frac{\eta'(i^*)b_1i^*}{\eta(i^*)}(s^* - b_2)\right]\\
&\quad +(as^*)^2(1-s^*),
\end{aligned}$$

where

$$\begin{aligned}
A &= -s^* + b_2 + \eta'(i^*)y^* = -(s^* - b_2) + \frac{\eta'(i^*)i^*}{\eta(i^*)}(s^* - b_2)\\
&= \frac{\eta'(i^*)i^* - \eta(i^*)}{\eta(i^*)}(s^* - b_2).
\end{aligned}$$

We classify the following three cases to investigate the local properties of E^*

Case (i). $\frac{\eta'(i^*)i^* - \eta(i^*)}{\eta(i^*)} \geq 0$, in which case $A > 0$, then $Q_1 > 0$, $\Delta^{(2)} > 0$. Hence E^* is locally asymptotically stable according to Routh–Hurwitz criterion.

Case (ii). $-\frac{as^*}{s^* - b_2} < \frac{\eta'(i^*)i^* - \eta(i^*)}{\eta(i^*)} < 0$, in which case $Q_1 > 0$. Further,

$$\begin{aligned}
\Delta^{(2)} &> as^*\left(\frac{\eta'(i^*)i^* - \eta(i^*)}{\eta(i^*)}\right)^2 (s^* - b_2)^2 - \frac{as^*}{s^* - b_2}(s^* - b_2) \\
&\quad \times\left[(as^*)^2 + as^*(1 - s^*) + \frac{\eta'(i^*)b_1 i^*}{\eta(i^*)}(s^* - b_2)\right] + (as^*)^2(1 - s^*) \\
&= as^*\left[\left(\frac{\eta'(i^*)i^* - \eta(i^*)}{\eta(i^*)}\right)^2 (s^* - b_2)^2 - (as^*)^2\right. \\
&\qquad \left. - \frac{\eta'(i^*)b_1 i^*}{\eta(i^*)}(s^* - b_2)\right].
\end{aligned}$$

Then, E^* is locally asymptotically stable provided

$$\begin{aligned}
&(\eta'(i^*)i^* - \eta(i^*))^2 (s^* - b_2)^2 \\
&\qquad > (as^*\eta(i^*))^2 + \eta'(i^*)\eta(i^*)b_1 i^*(s^* - b_2)
\end{aligned} \tag{3.5}$$

holds true.

Case (iii). $\frac{\eta'(i^*)i^* - \eta(i^*)}{\eta(i^*)} < -\frac{as^*}{s^* - b_2}$, in which case $Q_1 < 0$, hence E^* is unstable. Therefore, we have the following proposition.

PROPOSITION 3.1. *E^* is locally asymptotically stable provided one of the following two cases holds*

(1) $\frac{\eta'(i^*)i^* - \eta(i^*)}{\eta(i^*)} \geq 0$

(2) $-\frac{as^*}{s^* - b_2} < \frac{\eta'(i^*)i^* - \eta(i^*)}{\eta(i^*)} < 0$ *and* (3.5) *holds true.*

To study the asymptotic properties of positive equilibrium and Hopf bifurcation at E^* in detail, we consider the response function as Holling type II, given by

$$\eta(i) = \frac{mi}{n + i}, \qquad mk > b_1, \tag{3.6}$$

where m, n are positive constants. Thus Condition (3.2) which ensures the existence of E^* gives

$$b_2 < 1 - \frac{(a+1)b_1 n}{a(mk - b_1)} \triangleq b_2^*. \tag{3.7}$$

To consider the local stability analysis of the positive equilibrium E^* as b_2 varies in $(0, b_2^*)$, we recall that the stability properties of E^* depend on the susceptible dimensionless concentration s^*, which we shall rename as

$$\xi = s^*, \qquad \xi \in (b_2, 1). \tag{3.8}$$

The characteristic equation (3.4) about E^* gives

$$\lambda^3 + Q_1(\xi)\lambda^2 + Q_2(\xi)\lambda + Q_3(\xi) = 0, \tag{3.9}$$

where the coefficients $Q_i(\xi)$, $i = 1, 2, 3$ are

$$\begin{aligned} Q_1(\xi) &= -\xi + b_2 + \frac{mny^*}{(n+i^*)^2} + a\xi \\ Q_2(\xi) &= a\xi\left(-\xi + b_2 + \frac{mny^*}{(n+i^*)^2}\right) + \frac{km^2ni^*y^*}{(n+i^*)^3} \\ &\quad + (a+1)s^*i^* \\ Q_3(\xi) &= aks^*y^*i^*\frac{m^2n}{(n+i^*)^3}, \ \xi \in (b_2, 1). \end{aligned} \tag{3.10}$$

Denote $A(\xi) = -\xi + b_2 + \frac{mny^*}{(n+i^*)^2}$. Applying equations $as^*(1-s^*) = (a+1)s^*i^*$, $s^* - b_2 = \frac{my^*}{n+i^*}$ and $b_1 = \frac{kmi^*}{n+i^*}$, we have

$$A(\xi) = -(\xi - b_2) + \frac{n}{n+i^*}(\xi - b_2) = -\frac{b_1}{mk}(\xi - b_2) \tag{3.11}$$

and then (3.10) can be written as

$$\begin{aligned} Q_1(\xi) &= A(\xi) + a\xi = \left(a - \frac{b_1}{mk}\right)\xi + \frac{b_1 b_2}{mk} \\ Q_2(\xi) &= A(\xi)a\xi + b_1\left(1 - \frac{i^*}{n+i^*}\right)(\xi - b_2) + a\xi(1-\xi) \\ &= A(\xi)a\xi + a\xi(1-\xi) + \frac{b_1(mk - b_1)}{mk}(\xi - b_2) \\ Q_3(\xi) &= a\xi b_1 y^* \frac{mn}{(n+i^*)^2} + \frac{b_1 a\xi(mk - b_1)}{mk}(\xi - b_2). \end{aligned}$$

Obviously, $Q_3(\xi) > 0$ for all $\xi \in (b_2, 1)$. If $Q_1(\xi) > 0$, then we have $A(\xi) > -a\xi$. As for $Q_1(\xi)$ we have two cases:

(i) $b_1 \leq amk$ (i.e., $-a \leq \frac{\eta'(i^*)i^* - \eta(i^*)}{\eta(i^*)} < 0$), in which case $Q_1(\xi) > 0$ for all $\xi \in (b_2, 1)$;

(ii) $b_1 > amk$ (i.e., $\frac{\eta'(i^*)i^* - \eta(i^*)}{\eta(i^*)} < -a$), in which case $Q_1(\xi) < 0$ for all $\xi \in (\xi_1, 1)$, $Q_1(\xi) > 0$ for all $\xi \in (b_2, \xi_1)$ (i.e., $-\frac{as^*}{s^* - b_2} < \frac{\eta'(i^*)i^* - \eta(i^*)}{\eta(i^*)}$) and $Q_1(\xi_1) = 0$ at $\xi = \xi_1$, where

$$\xi_1 = \frac{b_1 b_2}{b_1 - amk}. \tag{3.12}$$

By applying the result [13] we obtain the following theorem.

THEOREM 3.2. *Assume* $b_2 < b_2^* < \xi_1 < \frac{-1 + \sqrt{1 + 8b_2}}{2}$ *and* $ab_2 < 1 - b_2 < \frac{b_1 n}{ab_2}$. *Then a single Hopf bifurcation occurs at the unique value* $\xi_0 \in (b_2, \xi_1)$ *for increasing* ξ; *i.e., the positive equilibrium* E^* *is locally asymptotically stable in* (b_2, ξ_0) *and unstable in* $(\xi_0, 1)$.

Proof. Since $b_2 < b_2^* < \xi_1$, then we have $\xi \in (b_2, \xi_1)$; it follows from (ii) that $Q_1(\xi) > 0$. Moreover, $Q_3(\xi) > 0$ for all $\xi \in (b_2, 1)$. Now let us look at

$$\begin{aligned}
\Delta^{(2)}(\xi) &= Q_1(\xi)Q_2(\xi) - Q_3(\xi) \\
&= (A(\xi) + a\xi)(a\xi A(\xi) + a\xi(1 - \xi)) \\
&\quad + \frac{A(\xi)b_1(mk - b_1)}{mk}(\xi - b_2) \\
&= \left(\frac{b_1}{mk}\right)^2 a\xi(\xi - b_2)^2 - \frac{b_1}{mk}(\xi - b_2) \\
&\quad \times \left[(a\xi)^2 + a\xi(1 - \xi) + \frac{b_1(mk - b_1)}{mk}(\xi - b_2)\right] \\
&\quad + (a\xi)^2(1 - \xi).
\end{aligned}$$

Obviously, $\Delta^{(2)}(b_2) = (ab_2)^2(1 - b_2) > 0$, $\Delta^{(2)}(\xi_1) = -(\frac{b_1}{mk})^2(mk - b_1)(\xi - b_2)^2 < 0$. Since $\Delta^{(2)}(\xi)$ is continuous on (b_2, ξ_1), a value $\xi_0 \in (b_2, \xi_1)$ must exist at which $\Delta^{(2)}(\xi_0) = 0$.

Now, we check the sign of $\frac{d^2\Delta^{(2)}(\xi)}{d\xi^2}$ for $\xi \in (b_2, \xi_1)$.

$$\begin{aligned}\frac{d^2\Delta^{(2)}(\xi)}{d\xi^2} &= 6a\left(\frac{b_1}{mk}+1\right)\left(\frac{b_1}{mk}-a\right)\xi - 2a\left(\frac{b_1b_2}{mk}+1\right)\left(\frac{b_1}{mk}-a\right)\\ &\quad - \frac{2b_1}{mk}\left[ab_2\left(\frac{b_1}{mk}+1\right) + \frac{b_1(mk-b_1)}{mk}\right]\\ &< 6a\left(\frac{b_1}{mk}+1\right)\left(\frac{b_1}{mk}-a\right)\xi_1 - 2a\left(\frac{b_1b_2}{mk}+1\right)\left(\frac{b_1}{mk}-a\right)\\ &\quad - \frac{2b_1}{mk}\left[ab_2\left(\frac{b_1}{mk}+1\right) + \frac{b_1(mk-b_1)}{mk}\right]\\ &= -2a\left[\left(\frac{b_1b_2}{mk}+1\right)\left(\frac{b_1}{mk}-a\right) - \frac{b_1b_2}{mk}\left(\frac{b_1}{mk}+1\right)\right]\\ &\quad - \frac{2b_1}{mk}\left[\frac{b_1}{mk}(mk-b_1) - ab_2\left(\frac{b_1}{mk}+1\right)\right]\\ &< -\frac{2ab_1}{mk}(1-ab_2-b_2) - 2\left(\frac{b_1}{mk}\right)^2\left(1+\frac{1}{a}\right)\left(\frac{b_1n}{1-b_2}-ab_2\right)\\ &< 0,\end{aligned}$$

which implies the value ξ_0 is unique.

Furthermore,

$$\begin{aligned}&\left.\frac{d\Delta^{(2)}(\xi)}{d\xi}\right|_{\xi=\xi_0}\\ &= -A(\xi_0)a\xi_0\left(\frac{b_1}{mk}+2\right) + a(A(\xi_0)+1)(A(\xi_0)+2a\xi_0)\\ &\quad -(a\xi_0)^2\left(\frac{1-\xi_0}{\xi_0-b_2}+3\right) + \frac{A(\xi_0)b_1}{mk}(mk-b_1)\\ &< (a\xi_0)^2\left(\frac{b_1}{mk}+2\right) + 2a^2\xi_0 - (a\xi_0)^2\left(\frac{1-\xi_0}{\xi_0-b_2}+3\right)\\ &\quad + \frac{A(\xi_0)b_1}{mk}(mk-b_1)\end{aligned}$$

$$
\begin{aligned}
&= (a\xi_0)^2\left(\frac{b_1}{mk} - 1\right) + \frac{a^2\xi_0}{\xi_0 - b_2}\left(\xi_0^2 + \xi_0 - 2b_2\right) \\
&\quad + \frac{A(\xi_0)b_1}{mk}(mk - b_1) \\
&< 0.
\end{aligned}
$$

Hence $\Delta^{(2)}(\xi) > 0$ in (b_2, ξ_0) and, according to Routh–Hurwitz criterion, E^* is locally asymptotically stable in (b_2, ξ_0). Furthermore, according to the results [13] we have a single Hopf bifurcations toward periodic solutions for increasing ξ, being $\Delta^{(2)}(\xi) < 0$ in (ξ_0, ξ_1). Of course, E^* is unstable in (ξ_0, ξ_1). Further, $Q_1(\xi) < 0$ for all $\xi \in (\xi_1, 1)$, by Routh–Hurwitz criterion we know that E^* is also unstable in $(\xi_1, 1)$. This completes the proof.

4. GLOBAL STABILITY RESULTS: PERMANENCE

In Section 3, we have shown that whenever the parameter $b_2 < b_2^*$ then the positive equilibrium E^* is feasible and the boundary one $E_{20} = (\bar{s}, \bar{i}, \bar{y})$ is unstable. However, as b_2 increases to b_2^* and when $b_2 = b_2^*$ the positive equilibrium E^* collapses into E_{20}, whereas for $b_2^* < b_2 < 1$ the positive equilibrium is not feasible and boundary one E_{20} becomes locally asymptotically stable. As b_2 increases to 1 and when $b_2 = 1$ the boundary equilibrium E_{20} collapses into $E_{10} = (1, 0, 0)$, whereas for $b_2 > 1$ the equilibrium E_{20} is not feasible and the one E_{10} is locally asymptotically stable. In the following, we show the global stability of E_{10} and E_{20}.

THEOREM 4.1. *If $b_2 \geq 1$, then the boundary equilibrium $E_{10} = (1, 0, 0)$ is globally asymptotically stable.*

Proof. Let Ω be set (2.13) of R^3_+. We proved that any solution to Eq. (1.5) starting outside Ω (in R^3_+) either enters into Ω at some finite time, say $t_0 > 0$, and then it remains in its interior Ω for all $t > t_0$ or tends to the boundary equilibrium $E_{10} \in \partial\Omega$. It is therefore sufficient to prove that E_{10} is asymptotically stable with respect to int Ω to prove global asymptotic stability in R^3_+.

Let $R^3_{+s} = \{(s, i, y) \in R^3_+,\ s > 0,\ i \geq 0,\ y \geq 0\}$ and consider scalar function V: $R^3_{+s} \to R$

$$V(t) = s - 1 - \ln s + i. \tag{4.1}$$

From system (1.5) we get

$$\begin{aligned}\dot{V}(t) &= -a(1-s)(1-s-i) + (1-b_2)i - y\eta(i)\\ &\le -a(1-s)(1-s-i) + (1-b_2)i.\end{aligned}$$

Clearly, the first term on the right of the above formula is always negative in int Ω. If $b_2 > 1$, then $\dot{V}(t)$ is negative in int Ω and vanishes if and only if $(s, i) = (1, 0)$. If $b_2 = 1$, then we have

$$\dot{V}(t) \le -a(1-s)(1-s-i) \le 0$$

in Ω. However, in this case, we have the largest positively invariant subset of the set, where $\dot{V}(t) = 0$ is $(s, i) = (1, 0)$. Hence, for all solutions to system (1.5) starting in int Ω, we know $\lim_{t\to+\infty} s(t) = 1$, $\lim_{t\to+\infty} i(t) = 0$. Thus we have $y(t)$ tends to zero as $t \to +\infty$ from the third equation of system (1.5). This implies global asymptotic stability in int Ω, and hence in R^3_+ too, of E_{10}. This completes the proof.

THEOREM 4.2. *If $b_2^* < b_2 < 1$, then all solutions to system* (1.5) *starting in Ω approach the boundary equilibrium $E_{20} = (\bar{s}, \bar{i}, \bar{y})$ as $t \to +\infty$.*

Proof. Because of the positivity of solutions, we have

$$\frac{di(t)}{dt} \le s(t)i(t) - b_2 i(t). \tag{4.2}$$

Consider the comparison equations

$$\begin{aligned}\dot{u}_1(t) &= au_1(t)\left[1 - (u_1(t) + u_2(t))\right] - u_1(t)u_2(t)\\ \dot{u}_2(t) &= u_1(t)u_2(t) - b_2u_2(t).\end{aligned} \tag{4.3}$$

It is easy to see that for $b_2 < 1$, $(b_2, \frac{a(1-b_2)}{1+a})$ is a unique positive equilibrium of system (4.3) which is globally asymptotically stable. Let $u_1(0) \ge s_0$, $u_2(0) \ge i_0$. If $(u_1(t), u_2(t))$ is a solution to (4.3) with initial value $(u_1(0), u_2(0))$, then by comparison theorem we have $s(t) \le u_1(t)$, $i(t) \le u_2(t)$, for $t > 0$, and hence

$$\limsup_{t\to+\infty} i(t) \le \frac{a(1-b_2)}{1+a}.$$

Since $1 > b_2 > 1 - \frac{1+a}{a}\eta^{-1}(\frac{b_1}{k})$, we can choose $\epsilon > 0$ small enough such that

$$b_1 > k\eta\left(\frac{a(1-b_2)}{1+a} + \epsilon\right). \tag{4.4}$$

Let $T > 0$ be sufficiently large such that

$$i(t) < \frac{a(1-b_2)}{1+a} + \epsilon \quad \text{for } t > T.$$

Then we have, for $t > T$

$$\dot{y}(t) < -b_1 y(t) + k\eta\left(\frac{a(1-b_2)}{1+a} + \epsilon\right) y(t).$$

By (4.4) and comparison theorem we know

$$\limsup_{t \to +\infty} y(t) \leq 0.$$

Therefore $\lim_{t \to +\infty} y(t) = 0$. So all solutions to system (1.5) approach the $s - i$ plane first. Since $(\bar{s}, \bar{i})$ is globally asymptotically stable in $s - i$ plane, then for any solution $(s(t), i(t), y(t))$ to system (1.5) starting in Ω we have $\lim_{t \to \infty} s(t) = \bar{s}$, $\lim_{t \to +\infty} i(t) = \bar{i}$, $\lim_{t \to +\infty} y(t) = 0$. This completes the proof.

In the following we shall prove that the instability of E_{10} and E_{20} implies the system (1.5) is permanent (see definition in [16]).

THEOREM 4.3. *System* (1.5) *is permanent provided* $b_2 < b_2^*$.

In order to prove Theorem 4.3, we present the persistence theory for infinite dimensional systems from [17]. Let X be a complete metric space. Suppose that $X^0 \subset X$, $X_0 \subset X$, $X_0 \cap X^0 = \varnothing$. Assume that $T(t)$ is a C_0 semigroup on X satisfying

$$\begin{aligned} T(t):& \quad X^0 \to X^0 \\ T(t):& \quad X_0 \to X_0. \end{aligned} \tag{4.5}$$

Let $T_b(t) = T(t)|_{X_0}$ and let A_b be the global attractor for $T_b(t)$. The following is a variant of Theorem 4.1 in paper [17].

LEMMA 4.1. *Suppose that* $T(t)$ *satisfies* (4.5) *and we have the following*:

(i) *there is a* $t_0 \geq 0$ *such that* $T(t)$ *is compact for* $t > t_0$

(ii) $T(t)$ *is point dissipative in* X

(iii) $\hat{A}_b = \bigcup_{x \in A_b} \omega(x)$ *is isolated and has an acyclic covering* $\hat{M}$, *where*

$$\hat{M} = \{M_1, M_2, \ldots, M_n\}.$$

(iv) $W^s(M_i) \cap X^0 = \varnothing$ *for* $i = 1, 2, \ldots, n$.

Then X_0 is a uniform repellor with respect to X^0; i.e., there is an $\epsilon > 0$ such that for any $x \in X^0$, $\lim_{t \to +\infty} \inf d(T(t)x, X_0) \geq \epsilon$, where d is the distance of $T(t)x$ from X_0.

We are now able to state the proof of Theorem 4.3.

Proof of Theorem 4.3. We begin by showing that the boundary planes of R_+^3 repel the positive solutions to system (1.5) uniformly. Let us define

$$C_1 = \{(s,i,y) \in R_+^3 : s(0) = 0\}$$

$$C_2 = \{(s,i,y) \in R_+^3 : i(0) = 0,\ s(0) \neq 0\}$$

$$C_3 = \{(s,i,y) \in R_+^3 : y(0) = 0,\ s(0)i(0) \neq 0\}.$$

If $C_0 = C_1 \cup C_2 \cup C_3$ and $C^0 = \operatorname{int} R_+^3$, it suffices to show that there exists an $\epsilon_0 > 0$ such that for any solution u_t to system (1.5) initiating from C^0, $\lim_{t \to +\infty} \inf d(u_t, C_0) \geq \epsilon_0$. To this end, we verify below that the conditions of Lemma 4.1 are satisfied. It is easy to see that C^0 and C_0 are positively invariant. Moreover, Conditions (i) and (ii) of Lemma 4.1 are clearly satisfied. Thus we only need to verify Conditions (iii) and (iv). There are three constant solutions E_0, E_{10}, and E_{20} in C_0, corresponding, respectively, to $s(t) = i(t) = y(t) = 0$, $s(t) = 1$, $i(t) = y(t) = 0$, and $s(t) = \bar{s}$, $i(t) = \bar{i}$, $y(t) = 0$. If $(s(t), i(t), y(t))$ is a solution to system (1.5) initiating from C_1 then $\frac{di(t)}{dt} = -b_2 i - \eta(i)y \leq -b_2 i$. Hence $i(t) \to 0$ and $y(t) \to 0$ as $t \to +\infty$. If $(s(t), i(t), y(t))$ is a solution initiating from C_2 with $s(0) > 0$, it follows that $s(t) \to 1$ as $t \to +\infty$ and $y(t) \to 0$ as $t \to +\infty$. If $(s(t), i(t), y(t))$ is a solution to system (1.5) initiating from C_3 with $s(0) > 0$, $i(0) > 0$, it is easy to prove that $s(t) \to \bar{s}$ and $i(t) \to \bar{i}$ as $t \to +\infty$. This shows that if invariant sets E_0, E_{10}, and E_{20} are isolated, $\{E_0, E_{10}, E_{20}\}$ is isolated and is an acyclic covering. It is obvious that E_0 is an isolated invariant. The isolated invariance of E_{10} and E_{20} will follow from the following proof.

We now show that $W^s(E_0) \cap C^0 = \emptyset$, $W^s(E_{10}) \cap C^0 = \emptyset$, and $W^s(E_{20}) \cap C^0 = \emptyset$, we restrict our attention to the second and third equations, since the proof for the first is simple. Assume that contrary, i.e., $W^s(E_{10}) \cap C^0 \neq \emptyset$, then there exists a positive solution $(s(t), i(t), y(t))$ to system (1.5) such that

$$(s(t), i(t), y(t)) \to (1,0,0) \quad \text{as } t \to +\infty.$$

If we let (3.6) hold, we can choose $\epsilon > 0$ small enough such that

$$\epsilon < \min\left\{\frac{n(1-b_2)}{m}, \frac{an^2}{m}\right\}. \tag{4.6}$$

Let $t_0 > 0$ be sufficiently large such that

$$-\epsilon < y(t) < \epsilon \quad \text{for } t > t_0.$$

Then we have, for $t > t_0$,

$$\begin{aligned} \frac{ds(t)}{dt} &= s(t)\left[a(1 - s(t)) - (a+1)i(t)\right] \\ \frac{di(t)}{dt} &\geq i(t)\left(s(t) - b_2 - \frac{m\epsilon}{n + i(t)}\right). \end{aligned} \tag{4.7}$$

Let us consider

$$\begin{aligned} \dot{x}_1(t) &= x_1(t)\left[a(1 - x_1(t)) - (a+1)x_2(t)\right] \\ \dot{x}_2(t) &= x_2(t)\left(x_1(t) - b_2 - \frac{m\epsilon}{n + x_2(t)}\right). \end{aligned} \tag{4.8}$$

Let $v = (v_1, v_2)$ and let $\mu > 0$ be small enough such that

$$\mu v_1 < s(t_0), \qquad \mu v_2 < i(t_0).$$

If $(x_1(t), x_2(t))$ is a solution to system (4.8) satisfying $x_i(t_0) = \mu v_i$, $i = 1, 2$, we know by comparison theorem $s(t) \geq x_1(t)$, $i(t) \geq x_2(t)$ for all $t > t_0$. It is easy to see that system (4.8) has a unique positive equilibrium (x_1^*, x_2^*), where

$$x_1^* = b_2 + \frac{m\epsilon}{n + x_2^*},$$

$$x_2^* = \frac{a(1-b_2) - n(a+1) + \sqrt{\left(a(1-b_2) - n(a+1)\right)^2 + 4a(a+1)\left(n(1-b_2) - m\epsilon\right)}}{2(a+1)},$$

which is globally asymptotically stable for ϵ given by (4.6). Note that $s(t) \geq x_1(t), i(t) \geq x_2(t)$ for $t > t_0$ and $\lim_{t\to\infty} x_2(t) = x_2^*$. This is a contradiction. Hence $W^s(E_{10}) \cap C^0 = \varnothing$.

Suppose that there exists a positive solution $(s(t), i(t), y(t))$ to system (1.5) such that

$$(s(t), i(t), y(t)) \to (\bar{s}, \bar{i}, 0) \quad \text{as } t \to +\infty.$$

Since $b_2 < b_2^*$, we can choose $\xi > 0$ small enough such that

$$b_2 < b_2^* - \frac{a}{a+1}\xi. \tag{4.9}$$

Let $t_1 > 0$ be sufficiently large such that

$$\bar{i} - \xi < i(t) < \bar{i} + \xi, \quad \text{for } t > t_1.$$

Then we have, for $t > t_1$

$$\frac{dy(t)}{dt} \geq -b_1 y(t) + k\eta(\bar{i} - \xi) y(t).$$

Let us consider

$$\dot{u}(t) = -b_1 u(t) + k\eta(\bar{i} - \xi) u(t). \tag{4.10}$$

Let $u_0 > 0$ be small enough such that

$$u_0 < y(0) = y_0.$$

If $u(t)$ is a solution to (4.10) satisfying $u(t_1) = u_0$, since (4.9) (i.e., $b_1 < k\eta(\bar{i} - \xi)$), it follows that $u(t) \to +\infty$ as $t \to +\infty$. Note that $y(t) \geq u(t)$ for $t > t_1$ we have $y(t) \to +\infty$ as $t \to +\infty$. This contradicts Lemma 2.2. At this time, we are able to conclude from Lemma 4.1 that C_0 repels the positive solutions to (1.5) uniformly. Incorporating into Lemmas 2.1 and 2.2, we know that system (1.5) is permanent.

5. DISCUSSION

In this paper we have proposed and analyzed a model of a three species, eco-epidemiological system, namely, sound prey, infected prey and predator. We have pointed out the well-known phenomenon of "exchange of stability" through simple bifurcation at the crossing point of E_{10} to E_{20} as well as at the crossing point of E_{20} to E^*. We have shown that E_{10} is globally asymptotically stable for $b_2 \geq 1$ and E_{20} is globally asymptotically stable in Ω for $b^* < b_2 < 1$, and we have pointed out the instability of boundary equilibria implies the permanence of the system and existence of the positive equilibrium. Comparing the results [6, 7] in which the nature of equilibria is proved locally, we obtain the global stability of equilibria E_{10} and E_{20}.

Furthermore, we observed that the strictly positive equilibrium enters a Hopf-type bifurcation under the conditions of Theorem 3.2. See Fig. 1.

Two threshold parameters R_0 and σ are found in this paper which control the development of the disease and the growth of the predator population, respectively. The parameter R_0 governs whether or not the disease persists. In the absence of disease, the prey population approaches the carrying capacity K. The threshold parameter

$$R_0 = \frac{1}{b_2} = \frac{\beta K}{c}$$

is the average number of adequate contacts, when the prey population is K, of an infective during the mean infectious period $\frac{1}{c}$. In a totally susceptible population of K, the parameter R_0 is the average number of new infections (secondary cases) produced per infective, so it is often called the basic reproduction number. We know that if $R_0 \le 1$ (i.e.,

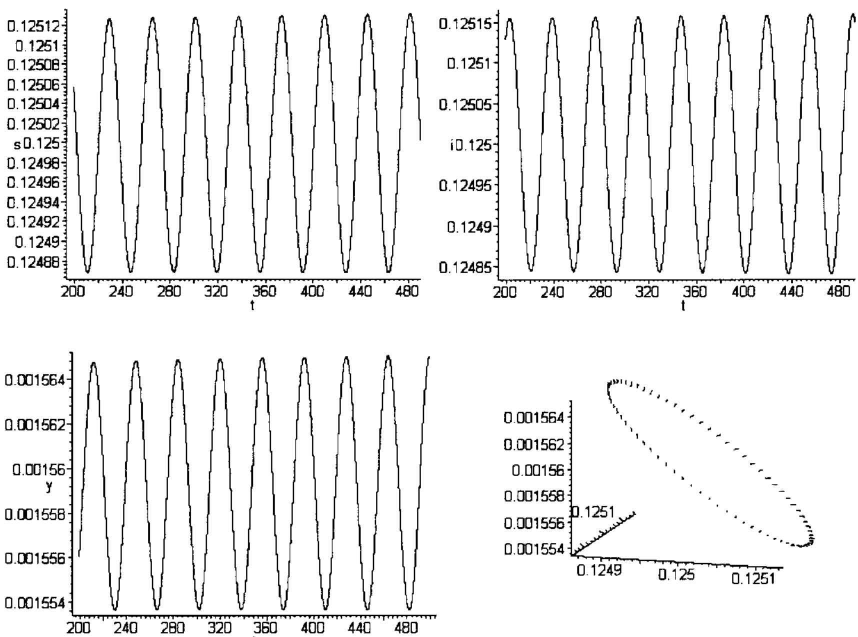

FIG. 1. $a = \frac{1}{6}$, $b_1 = 1$, $k = \frac{1}{2}$, $m = 4$, $n = \frac{1}{8}$, and $b_2 = 0.10005$.

$b_2 \geq 1$), the disease dies out, and of course the predator population goes into extinction; that is to say the disease-free equilibrium E_{10} is globally asymptotically stable. Whereas if $R_0 > 1$ (i.e., $b_2 < 1$) the infective does not tend to zero.

The parameter

$$\sigma = \frac{k}{b_1}\eta\left(\frac{a(1 - b_2)}{a + 1}\right) = \frac{k}{d}\overline{\eta}(\bar{i}K)$$

governs whether or not the positive equilibrium exists. In the absence of predator, according to the proof of Theorem 4.2, we know that the infected prey population approaches the constant $\bar{i} = \frac{a(1 - b_2)}{1 + a}$. Moreover, $\frac{k}{d}$ represents the survival rate of predator. Hence the threshold parameter σ simply says that the predator population can only survive if the number $k\overline{\eta}(\bar{i}K)$ of new predator is enough to maintain the predator with the given mortality d, which is just another way to write the condition $b_2 < b_2^*$; that is, if $\sigma > 1$, the positive equilibrium E^* exists and the system is permanent.

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