Classical predator–prey system with infection of prey population—a mathematical model

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SUMMARY

The present paper deals with the problem of a classical predator–prey system with infection of prey population. A classical predator–prey system is split into three groups, namely susceptible prey, infected prey and predator. The relative removal rate of the susceptible prey due to infection is worked out. We observe the dynamical behaviour of this system around each of the equilibria and point out the exchange of stability. It is shown that local asymptotic stability of the system around the positive interior equilibrium ensures its global asymptotic stability. We prove that there is always a Hopf bifurcation for increasing transmission rate. To substantiate the analytical findings, numerical experiments have been carried out for hypothetical set of parameter values. Our analysis shows that there is a threshold level of infection below which all the three species will persist and above which the disease will be epidemic. Copyright © 2003 John Wiley & Sons, Ltd.

KEY WORDS: susceptible and infected prey; predator; global stability; Hopf-bifurcation

1. INTRODUCTION

Ecology and epidemiology are major fields of study in their own right. Lotka [1] and Volterra [2] established their original works on the expression of predator–prey and competing species relations in terms of simultaneous non-linear differential equations, making the first break through in modern mathematical ecology. Similarly most models for the transmission of infectious diseases descend from the classical SIR model of Kermack and McKendrick [3]. Eco-epidemiology study is becoming important as it involves persistence-extinction threshold of each population in systems of two or more interacting species subjected to parasitism (for example, see References [4–7]). In this paper, we consider a prey–predator system where the prey is subjected to an epidemic disease with possibly different predation rates on infected and uninfected prey. This is in accordance with the fact that the infected individuals can be caught more easily. For example; Reference [8] indicated that wolf attacks on moose are more

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often successful if the moose is heavily infected by 'Echinococcus granucosus'. We have two species ecological system:

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

We make the following assumptions

(A1) In the absence of diseases the prey population follows the law of logistic growth with carrying capacity $K(\in R+)$ with an intrinsic birth rate constant $a(a \in R+)$:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = aN\left(1 - \frac{N}{K}\right) \tag{1}$$

(A2) In the presence of disease the total prey population is divided into two classes, namely, susceptible prey (R) and infected prey (U).

(A3) We assume only the susceptible prey are capable of reproducing with logistic law (Equation (1)). In this case, Equation (1) becomes:

$$\frac{\mathrm{d}R}{\mathrm{d}t} = aR\left(1 - \frac{R}{K}\right) \tag{2}$$

(A4) We also assume that the infected prey does not grow, recover and reproduce. Experiment on dinoflagellate Noctiluca scintillans (miliaris) in the German Bight by Uhlig and Sahling [9] indicated that the cells become damaged and they do not feed anymore nor reproduce. The model of Hamilton *et al.* [10] showed that no infected individuals contribute in the reproduction process, it rather reduces the remaining capacity due to the inability to compete for resources.

In this case, it can be argued that the infected prey does not contribute to the carrying capacity and Equation (2) becomes:

$$\frac{\mathrm{d}R}{\mathrm{d}t} = aR - bR^2$$

where $b = a/K$.

(A5) We assume that the disease is spreading among the prey only and the predator population is not affected due to predation of infected prey.

(A6) A susceptible prey R becomes infected under the attack of many parasites. The attacking rate as well as the predation rates follow the law of mass action. The contact process is admittedly debatable. Some researchers argue that a proportional mixing rate is more appropriate than that of simple mass action. But the data of Greenwood experiment suggest that there is no change in the qualitative properties upon the contact process, whether it follows the law of mass action or proportional mixing rate (see, Reference [11]).

Considering the above basic assumptions we can now write the following dynamical system:

$$\frac{\mathrm{d}R}{\mathrm{d}t} = R(a - bR - cF - \lambda U)$$

$$\frac{\mathrm{d}U}{\mathrm{d}t} = U(\lambda R - kF - \gamma) \tag{3}$$

$$\frac{\mathrm{d}F}{\mathrm{d}t} = F(-d + eR - fF + hU)$$

as our model. Here $R = R(t)$ is the concentration of the susceptible prey population at time t; $U = U(t)$ the concentration of the infected prey population at time t; $F = F(t)$ the concentration of the predator population at time t; a denotes the rate of increase of susceptible prey in the absence of predators and d denotes the death rate of predators in the absence of prey; b and f denote the rate of crowding effects on the susceptible prey and predator respectively; c and k are the capturing rates of susceptible prey and infected prey respectively by the predator; $e(\leqslant c)$ and $h(\leqslant k)$ are the growth rates of predators due to predation of susceptible prey and infected prey respectively. λ is the force of infection between susceptible and infected prey populations; γ is the death rate of infected prey.

System (3) needs to be analysed with the following initial conditions:

$$R(0) \geqslant 0, \quad U(0) \geqslant 0, \quad F(0) \geqslant 0 \tag{4}$$

Our model is similar to Venturino [6]. However, in Venturino's predator–prey system, the predator can survive in the absence of the prey and both predator and prey grow logistically. Venturino also considered that a portion of infected prey will become susceptible again after recovery. Venturino's analysis includes SI and SIS models, mass action and standard incidence. The author showed that under suitable assumptions the disease can act as a control of the system but did not discuss the nature of the solutions of the system arising from Hopf bifurcation.

The main objective of this paper is not only to discuss the nature of Hopf-bifurcating solutions arising from the system but also to find out the threshold level of infection below which all the three species co-exist and above which the dynamics of the system represent the epidemic situation.

2. PRELIMINARIES

It is easy to verify that the existence, uniqueness and continuous dependence of initial conditions are evidently satisfied.

2.1. Boundedness of the system

Lemma 1
All the solutions of (3) which initiate in R_+^3 are uniformly bounded.

Proof
We define a function.

$$W = R + U + F \tag{5}$$

The time derivative of (5) along the solutions of (3) is

$$\frac{\mathrm{d}W}{\mathrm{d}t} = R(a - bR) + (e - c)FR - \gamma U - F(d + fF) + FU(h - k)$$

As $e \leqslant c$ and also $h \leqslant K$, for each $\mu > 0$, the following inequality holds:

$$\frac{\mathrm{d}W}{\mathrm{d}t} + \mu W \leqslant R(a - bR + \mu) + U(\mu - \gamma) + F(\mu - d - fF)$$

$$\leqslant \frac{(\mu + a)^2}{4b} + U(\mu - \gamma) + \frac{(\mu - d)^2}{4f}$$

If we take $\mu \leqslant \gamma$, the above expression becomes:

$$\frac{\mathrm{d}W}{\mathrm{d}t} + \mu W \leqslant \frac{(\mu + a)^2}{4b} + \frac{(\mu - d)^2}{4f} \qquad (6)$$

It is clear that the right-hand side of (6) is bounded.

Then we can find a constant $m > 0$ such that

$$\frac{\mathrm{d}W}{\mathrm{d}t} + \mu W < m$$

Applying the theory of differential inequalities [12], we obtain

$$0 < W(R, U, F) \leqslant \frac{m}{\mu}(1 - \mathrm{e}^{-\mu t}) + W(R(0), U(0), F(0))\mathrm{e}^{-\mu t}$$

and for $t \to \infty$, we have

$$0 < W < \frac{m}{\mu} \qquad (7)$$

Hence all the solutions of (3) which originate in R_3^+ are eventually confined in the region:

$$B = \left\{ (R, U, F) \in R_+^3 : R + U + F = \frac{m}{\mu} + \varepsilon \forall \varepsilon > 0 \right\}$$

2.2. Equilibria

System (3) possesses the following equilibria: $E_0(0, 0, 0), E_1(a/b, 0, 0),$ $E_2(af + cd)/(ec + bf), 0, (ae - bd)/(ec + bf), E_3(\gamma/\lambda, (a\lambda - b\gamma)/\lambda^2, 0)$ and the positive equilibrium $E^*(R^*, U^*, F^*)$, where

$$R^* = \frac{\lambda \gamma f - \lambda k d + ahk + c\gamma h}{A_2} \qquad (8)$$

$$U^* = \frac{a\lambda f - aek - b\gamma f + c\lambda d - c\gamma e + bkd}{A_2} \qquad (9)$$

$$F^* = \frac{-\lambda^2 d + \lambda e\gamma + a\lambda h - bh\gamma}{A_2} \qquad (10)$$

where

$$A_2 = \lambda^2 f + c\lambda h - \lambda ke + bkh \qquad (11)$$

The equilibrium E_2 exists only if $a/d > b/e$. The steady state E_3 exists only if $\gamma/\lambda < a/b$.

We find that $\mathrm{d}U/\mathrm{d}t|_{t=0} < 0$ if $R(0) < \gamma/\lambda$ and since $R \leqslant R(0)$ at any time t, we find that in this case $R \leqslant R(0) < \gamma/\lambda$, so that $\lambda R - \gamma < 0$. Hence $\mathrm{d}U/\mathrm{d}t < 0$ for all t when $R(0) < \rho$ where $\rho = \gamma/\lambda$, is the *relative removal rate* of the susceptible prey due to infection. Infection in the susceptible prey population cannot spread unless $R(0) > \rho$. The initial concentration of the susceptible prey population must exceed the threshold value ρ in order to spread the infection. Thus the existence of E_3 implies that the relative removal rate due to infection must be lower than that of the ratio of the birth rate of susceptible prey to its crowding coefficient.

3. STABILITY ANALYSIS

In this section, we investigate the local behaviour of system (3) around each of the equilibria.

Let $\tilde{E} = (\tilde{R}, \tilde{U}, \tilde{F})$ be any one of the equilibria. Local stability analysis (LAS) of the equilibria can be studied by computing the following variational matrix corresponding to each $\tilde{E}$.

$$V(\tilde{R}, \tilde{U}, \tilde{F}) = \begin{bmatrix} a - 2b\tilde{R} - c\tilde{F} - \lambda\tilde{U} & -\lambda\tilde{R} & -c\tilde{R} \\ \lambda\tilde{U} & \lambda\tilde{R} - k\tilde{F} - \gamma & -k\tilde{U} \\ e\tilde{F} & +h\tilde{F} & -d + e\tilde{R} - 2f\tilde{F} + h\tilde{U} \end{bmatrix}$$

It is easy to verify that E_0 is always unstable. LAS of E_1 implies non-existence of E_2 and E_3.

Existence of positive interior equilibrium E^* ensures that E_2 and E_3 are unstable.

Now, if we project our system on the plane, we can prove by constructing suitable Liapunov functions that E_2 and E_3 are globally asymptotically stable.

A graph of IR^3 (see Figure 1) and insights into the two-dimensional subsystems should tell us the following facts:

(1) There will be an uninfected prey–predator equilibrium E_2 (if prey capacity is sufficiently high and/or predator mortality is low). This equilibrium is a local attractor for low transmission rate and a 2–1 saddle point for high transmission rate.
(2) There will be epidemic equilibrium E_3 without predator which is an attractor for poorly performing predators and becomes a 2–1 saddle point for effective predators.

Hence, with respect to the three equilibria E_2, E_3 and E^*, we should have the four standard cases.

$$E_2 \rightarrow E_3$$
$$E_2 \leftarrow E_3$$
$$E_2 \leftarrow E^* \rightarrow E_3$$
$$E_2 \rightarrow E^* \leftarrow E_3$$

Observation (1) is confirmed by the roots μ_1, μ_2 and μ_3 of the characteristic equation associated with E_2

$$\mu_1 = \frac{\lambda(af + dc) - k(ae - bd) - \gamma(ec + bf)}{ec + bf}$$

μ_2 and μ_3 are the roots of the following equation:

$$\mu^2 - \mu(K_1 + K_2) + K_1 K_2 \left(1 + \frac{ec}{bf}\right) = 0$$

where $K_1 = f(ae - bd)/(ec + bf) > 0$, $K_2 = b(af + dc)/(ec + bf) > 0$.

Observation (2) is also confirmed by the following roots η_1, η_2 and η_3 of the characteristic equation associated with E_3

$$\eta_1 = \frac{-d\lambda^2 + e\gamma\lambda + h(a\lambda - b\gamma)}{\lambda^2}$$
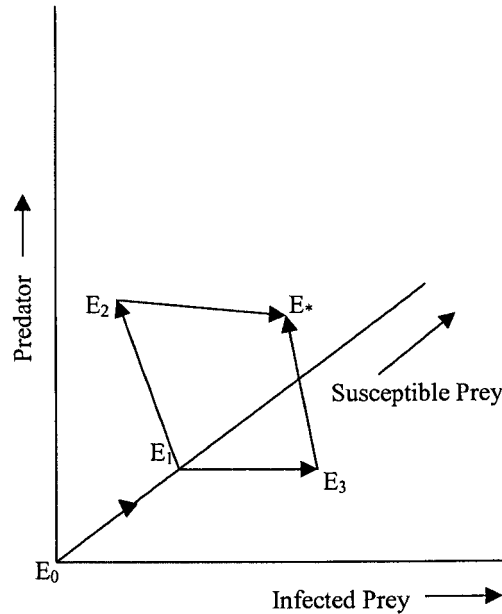
Figure 1. A schematic diagram representing the exchange of stability for different equilibria of system 3.

and the other eigenvalues are the roots of the following equation:

$$\eta^2 + \eta l + l' = 0$$

where $l = b\gamma/\lambda > 0$, $l' = \gamma(a\lambda - b\gamma)/\lambda > 0$.

Now, we are in a position to see the dynamical behaviour of the system around the positive equilibrium E^*. We make the following hypothesis which will be required for local and global asymptotic stability of the positive equilibrium.

Hypothesis 1
Let us assume that $e/c = h/k = m$ (say) $(0 \leqslant m \leqslant 1)$, which is biologically realistic in the sense that an infected prey has the same effects as a susceptible prey has on the growth of predator.

The variational matrix for E^* is

$$V_* = \begin{bmatrix} -bR^* & -\lambda R^* & -cR^* \\ \lambda U^* & 0 & -kU^* \\ eF^* & hF^* & -fF^* \end{bmatrix} \tag{12}$$

The characteristic equation is given by

$$\mu^3 + d_1\mu^2 + d_2\mu + d_3 = 0 \tag{13}$$

where

$$d_1 = bR^* + fF^*$$

$$d_2 = bfF^*R^*khU^*F^* + \lambda^2 U^*R^* + ceR^*F^* \tag{14}$$

$$d_3 = khbR^*U^*F^* + \lambda^2 fR^*U^*F^* - ke\lambda R^*U^*F^* + c\lambda kR^*U^*F^*$$

A set of necessary and sufficient conditions for all the roots of (13) to have negative real part is $d_1 > 0$, $d_3 > 0$ and $d_1 d_2 - d_3 > 0$. In our case d_1 is always greater than zero and the last two conditions are evidently satisfied for the hypothesis. Hence the system around E^* is LAS.

Now we shall study the global asymptotic stability of the system around E^* by constructing a suitable Liapunov function.

Theorem 1
Local asymptotic stability of the positive interior equilibrium of (3) $E^*(R^*, U^*, F^*)$ ensures its global asymptotic stability.

Proof
Let us consider the positive definite Liapunov function:

$$M = \left(R - R^* - R^* \log\left(\frac{R}{R^*}\right) \right) + \left(U - U^* - U^* \log\left(\frac{U}{U^*}\right) \right)$$

$$+ \frac{c}{e}\left(F - F^* - F^* \log\left(\frac{F}{F^*}\right) \right)$$

The time derivative of M along the solutions of (3) is

$$\frac{\mathrm{d}M}{\mathrm{d}t} = (R - R^*)(a - bR - cF - \lambda U) + (U - U^*)(\lambda R - kF - \gamma)$$

$$+ \frac{c}{e}(F - F^*)(-d + eR - fF + hU)$$

$$= -b(R - R^*)^2 - \frac{(ke - ch)}{e}(U - U^*)(F - F^*) - \frac{cf}{e}(F - F^*)^2$$

Now, using hypothesis 1 in the above expression, we have

$$\frac{\mathrm{d}M}{\mathrm{d}t} = -b(R - R^*)^2 - \frac{cf}{e}(F - F^*)^2 < 0$$

We can therefore apply Lasalle's theorem [13] and deduce that any trajectory goes towards the maximal invariant set Q included in the set:

$$S = \{(R, U, F) \in B; R = R^*, F = F^*\}$$

On this straight line S, in the positive space, the only invariant set is the equilibrium E^*. Thus the trajectory converges towards E^* and hence positive interior equilibrium of (3) is globally and asymptotically stable.

Now, we shall find out the conditions for which the strictly positive interior equilibrium enters into Hopf-bifurcation.

Theorem 2
If the positive equilibrium E^* of system (3) exists then system (3) around E^* enters Hopf-bifurcation when λ passes through λ^* (λ^* is given by (15)).

Proof
Necessary and sufficient conditions for Hopf bifurcation to occur is that there exists $\lambda = \lambda^*$, such that

$$\text{(i)} \quad g(\lambda^*) \equiv d_1(\lambda^*)d_2(\lambda^*) - d_3(\lambda^*) = 0$$

$$\text{(ii)} \quad \frac{\mathrm{d}}{\mathrm{d}\lambda} Re(\mu(\lambda))_{\lambda=\lambda^*} \neq 0$$

The condition $d_1 d_2 - d_3 = 0$ is given by

$$H \equiv fceF^{*2}R^* + b\lambda^2 U^*R^{*2} + ke\lambda F^*R^*U^* - c\lambda hR^*U^*F^* + bf^2F^{*2}R^*$$
$$+ b^2fF^*R^{*2} + hfkU^*F^{*2} + bceF^*R^{*2} = 0 \tag{15}$$

For $\lambda = \lambda^*$, we have

$$(\mu^2 + d_2)(\mu + d_1) = 0 \tag{16}$$

which has three roots $\mu_1 = +\mathrm{i}\sqrt{d_2}$, $\mu_2 = -\mathrm{i}\sqrt{d_2}$, $\mu_3 = -d_1$. For all λ, the roots are in general of the form

$$\mu_1(\lambda) = \beta_1(\lambda) + \mathrm{i}\beta_2(\lambda)$$
$$\mu_2(\lambda) = \beta_1(\lambda) - \mathrm{i}\beta_2(\lambda)$$
$$\mu_3(\lambda) = -d_1(\lambda)$$

Now, we shall verify the transversality condition

$$\frac{\mathrm{d}}{\mathrm{d}\lambda}(Re(\mu_j(\lambda))_{\lambda=\lambda^*} \neq 0, \quad j = 1, 2 \tag{17}$$

Substituting $\mu_j(\lambda) = \beta_1(\lambda) + \mathrm{i}\beta_2(\lambda)$ into (16) and calculating the derivative, we have

$$K(\lambda)\beta_1'(\lambda) - L(\lambda)\beta_2'(\lambda) + M(\lambda) = 0$$
$$L(\lambda)\beta_1'(\lambda) + K(\lambda)\beta_2'(\lambda) + N(\lambda) = 0 \tag{18}$$

where

$$K(\lambda) = 3\beta_1^2(\lambda) + 2d_1(\lambda)\beta_1(\lambda) + d_2(\lambda) - 3\beta_2^2(\lambda)$$
$$L(\lambda) = 6\beta_1(\lambda)\beta_2(\lambda) + 2d_1(\lambda)\beta_2(\lambda)$$

$$M(\lambda) = \beta_1^2(\lambda)d_1'(\lambda) + d_2'(\lambda)\beta_1(\lambda) + d_3'(\lambda) - d_1'(\lambda)\beta_2^2(\lambda)$$

$$N(\lambda) = 2\beta_1(\lambda)\beta_2(\lambda)d_1'(\lambda) + d_2'(\lambda)\beta_2(\lambda)$$

Since $L(\lambda^*)N(\lambda^*) + K(\lambda^*)M(\lambda^*) \neq 0$,
we have

$$\frac{\mathrm{d}}{\mathrm{d}\lambda} Re(\mu_j(\lambda))_{\lambda=\lambda^*} = \frac{LN + KM}{K^2 + L^2}\bigg|_{\lambda=\lambda^*} \neq 0$$

and

$$\mu_3(\lambda^*) = -d_1(\lambda^*) \neq 0$$

Therefore the transversality condition holds. This implies that a Hopf-bifurcation occurs at $\lambda = \lambda^*$ and is non-degenerate. This complete the proof.

4. CONCLUSION

In this paper, we proposed and analysed a predator–prey system in which some members of the prey population are infected by some transmissible disease and thus form a new group, namely, the infected prey. We have subdivided the prey into two classes, namely, susceptible and infected. We have modeled the above situation by means of three ordinary differential equations. The behaviour of the system near each of the equilibria has been studied. Threshold value of the relative removal rate which determines the spread of infection has been worked out and is closely related to the basic reproductive ratio, R_0, of epidemic theory. Local and global asymptotic stability analysis of the system near the positive interior equilibrium has been performed. We also proved that there is always a Hopf bifurcation for increasing the transmission rate.

Table I.

λ	H
0.01599	0.792416
0.016	0.7909747
0.017	0.6560341
0.018	0.537175
0.019	0.431783
0.02	0.3377763
0.023	0.1087768
0.024	0.0463195
0.0248	0.0350319
0.02481	−0.0203458
0.02482	−0.0007568
0.02483	−0.0013097
0.02481	−0.0018619
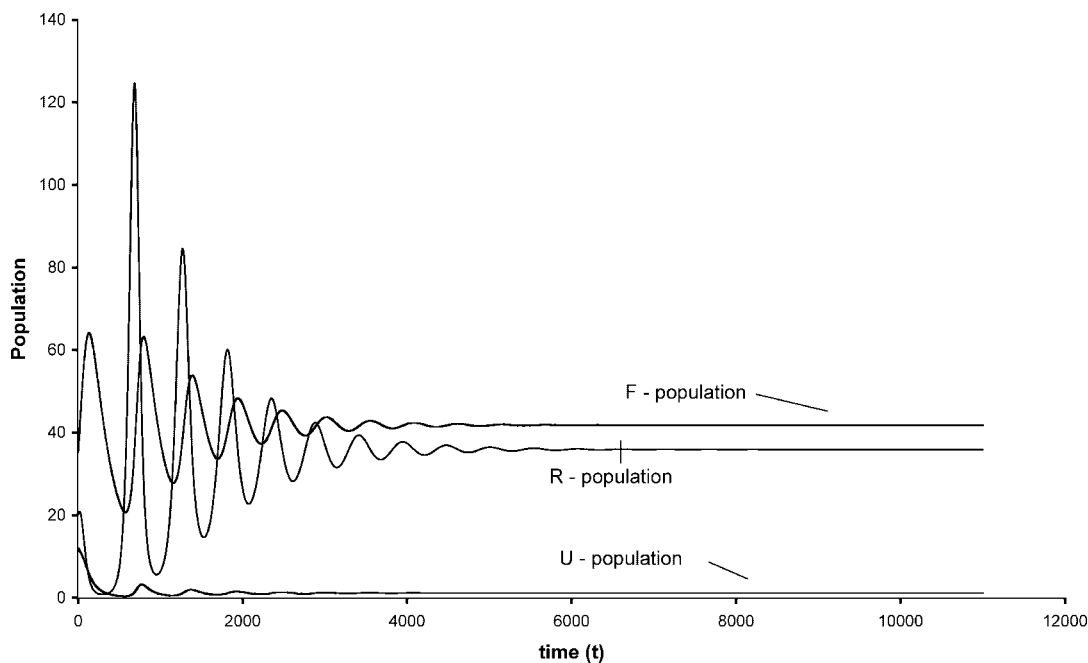
Figure 2. Stable solution for $\lambda = 0.02$.
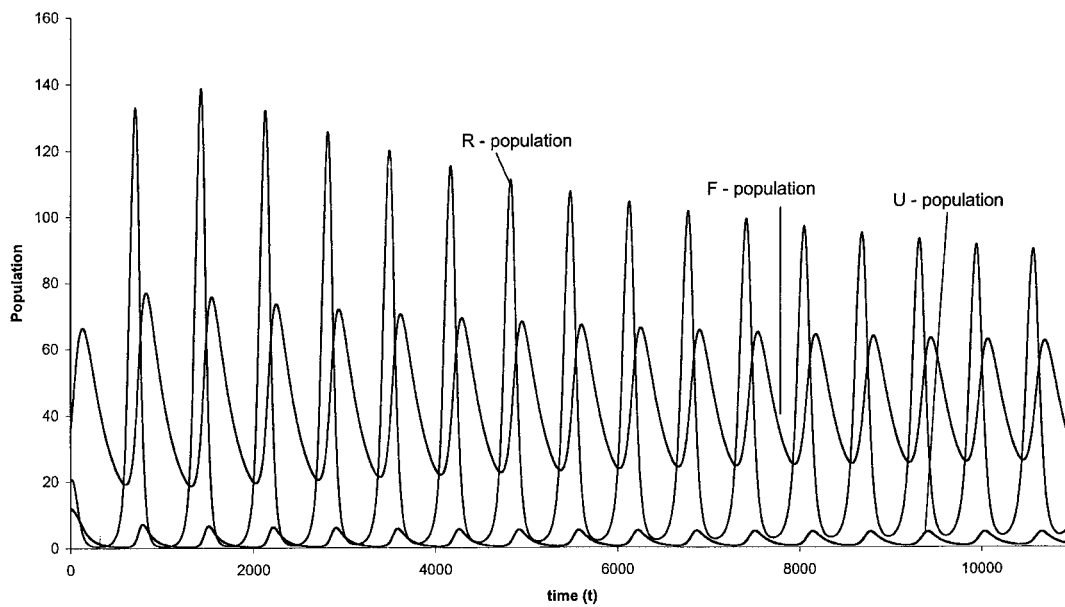
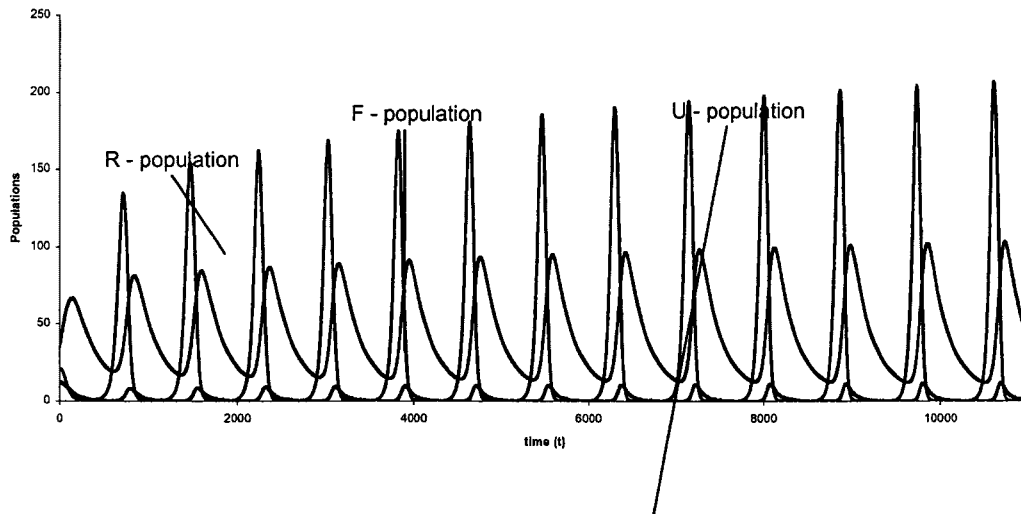Figure 3. Decaying oscillations of system (3) for $\lambda = 0.025$.

Figure 4. Growing oscillations of system (3) for $\lambda = 0.026$.
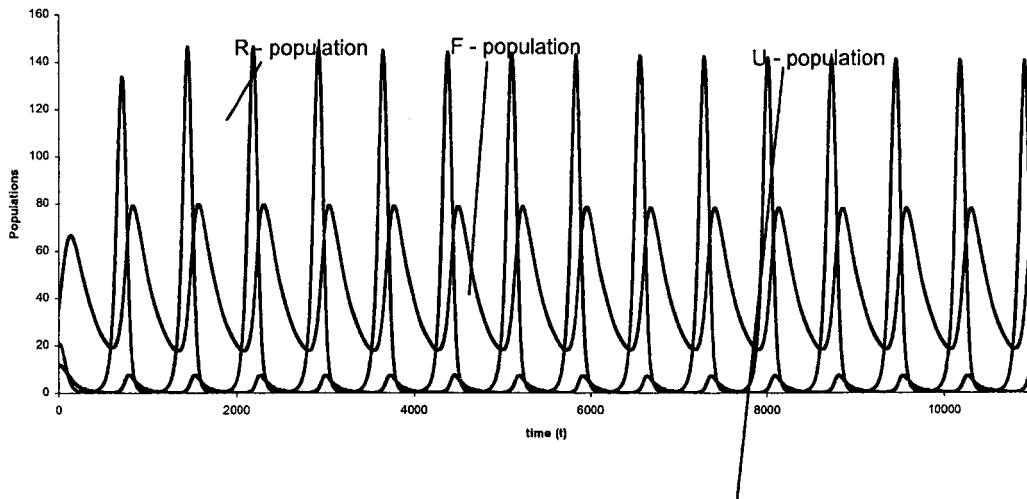

Figure 5. Limit cycles of system (3) for $\lambda = 0.0255$.

To substantiate analytical findings we performed some numerical experiments based on the formulas of Section 3 and obtained solutions for the hypothetical values $a = 4$, $b = 0.006$, $c = 0.09$, $d = 0.25$, $e = 0.01$, $f = 0.005$, $h = 0.09$, $k = 0.01$, $\gamma = 0.3$ and for different values of λ. Using these sets of parameter values in (15) we obtained the results for which system (3) about E^* is stable (if $H > 0$) or unstable (if $H < 0$). Table I summarizes the results. For the above set of parameter values and for $\lambda = 0.02$, we observed that the system settles down to steady-state solutions, depicting stable situation (Figure 2). Now if we increase the force of infection from $\lambda = 0.02$ to 0.025, the system settles down to steady state solution

through decaying oscillations (Figure 3). If we further increase $\lambda = 0.025$ to $\lambda = 0.026$, the system is unstable through growing oscillations (Figure 4) and limit cycle oscillations occurs at $\lambda = 0.0255$ (Figure 5). Hence we may conclude that there is a threshold level of the force of infection, below which all the three species will persist and above which the disease will be epidemic.

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