

ROLE OF FORCE OF INFECTION IN AN ECO-EPIDEMIOLOGICAL MODEL

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In this paper, the model of Chattopadhyay and Bairagi¹ has been modified by considering the horizontal incidence as standard incidence in lieu of mass action incidence. Our observations indicate that the modified system around the positive equilibrium is stable for a wider range of force of infection. Numerical experiments are performed to observe the effect of disease transmission on different types of functional responses. We finally conclude that the mechanistic nature of disease transmission should be known for predicting the dynamics of such systems.

Keywords: Horizontal Incidence; Mass Action Incidence; Standard Incidence; Functional Response.

1. Introduction

Mathematical models have become important tools to analyze the spread and control of infectious diseases. Most models for the transmission of infectious diseases descend from the classical SIR model of Kermack and McKendrick. Susceptible become infectious by contact with infectious individuals. In the natural world, however, species does not exist alone. While species spreads the disease, it also competes with the other species for space or food, or is predated by other species. This type of model has been termed an eco-epidemiological model (see Chattopadhyay and Arino²). In eco-epidemiological models, the horizontal incidence (the infection rate of susceptible individuals through their contacts with infectives) is usually of the type $\lambda(N) = \lambda$ (mass action incidence) or $\lambda(N) = \frac{\lambda}{N}$ (standard incidence).

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Ebert *et al.*³ formulated the following plausible epidemiological microparasite model with horizontal transmission.

$$\begin{aligned}\frac{dx}{dt} &= a(x + \theta y)(1 - c(x + y)) - dx - bxy \\ \frac{dy}{dt} &= bxy - (d + \alpha)y \\ x(0) &= x_0 > 0, \quad y(0) = y_0 > 0,\end{aligned}\tag{1.1}$$

where $x(t)$, $y(t)$ represent the densities of susceptible and infected hosts at time t , respectively. A careful examination of the above deterministic model reveals an often misinterpreted and misunderstood model assumption. Namely, b , if understood as an infection rate, it is the maximum number of infections that an infective host can cause in a unit time. This shows that the infection term bxy (the simple mass action law bxy , with b as a mass action coefficient, has sometimes been used for the horizontal incidence) should be replaced by $\frac{bxy}{x+y}$ (standard incidence). When the total population is constant, a fact if the disease is not fatal and the model does not address vital dynamics (the normal birth and death dynamics), then the infection term bxy may be justified (since $\frac{b}{x+y}$ is now a constant) but the meaning of b becomes the encounter infection rate. For large populations, individuals finite and often slow movement prevents it to make contact to a large number of individuals in a unit time. Such a mechanism is better described by $\frac{bxy}{x+y}$ than bxy . Consequently, encounter infection rate makes sense only when the total population is small and steady. For more information about the difference in models using these forms of horizontal incidence, see Gao and Hethcote,⁴ Gao *et al.*,⁵ Gao *et al.*,⁶ Hethcote,⁷ Hethcote and Van Ark,⁸ and Mena-Lorca and Hethcote⁹).

Using an incidence of the form $\frac{\eta N^v SI}{N}$, data for five human diseases in communities with population sizes ranging from 1000 to 400,000 [see Anderson and May¹⁰ (p. 157), and Anderson and May¹¹ (p. 306)] imply that v is between 0.03 and 0.07. This strongly suggests that the standard mass action incidence corresponding to $v = 0$ is more realistic for human diseases than the simple mass action incidence corresponding to $v = 1$. It is also noticed that the standard incidence is also a better formulation than the simple mass action law for animal populations such as mice in a mouse-room or animals in a herd (see De Jong *et al.*¹²), and disease transmission primarily occurs locally from nearby animals. So ultimately one can say that in a large population system where force of infection plays a vital role, standard incidence should be taken as horizontal incidence to get an appropriate and correct result.

Keeping the above observations in mind, we modify the model of Chattopadhyay and Bairagi¹ by considering horizontal incidence as standard incidence. Our observations indicate that the modified system around the positive interior equilibrium is stable for a wider range of force of infection. Moreover in eco-epidemiological situations, the use of different functional form may lead to different dynamical behavior of the system. Numerical experiments have been performed to observe the effect of horizontal incidence on different types of functional responses.

2. Basic Mathematical Model

To study an eco-epidemiological model of the Salton Sea, Chattopadhyay and Bairagi¹ considered the following assumptions:

- (1) There are two populations in the Salton Sea: The fishes, Tilapia, whose population is denoted by $N([N])$, number of Tilapia per unit designated area, and the birds, whose population is denoted by $p([p])$, number of birds per unit designated area.
- (2) In the presence of bacterial infection, total fish population N is divided into two classes, namely susceptible fish population, denoted by s , and infected fish population, denoted by i .
- (3) The susceptible fish population, s , is capable of reproducing with logistic law and the infective fish population, i , dies before having the capability of reproducing. However the infective fish, i , still contributes with s to population growth towards the carrying capacity.
- (4) The mode of disease transmission follows the simple law of mass action.
- (5) The disease is only spread amongst the prey population and the disease is not genetically inherited. The infected population does not recover or become immune.
- (6) The predator (bird) population preys only on the infected fish population. The reason behind this assumption is that the infected Tilapia population is present in the Salton Sea in a considerable number.

Based on the above assumptions, their model equations become

$$\begin{aligned}\frac{ds}{dt} &= rs \left(1 - \frac{s+i}{k} \right) - \lambda is \\ \frac{di}{dt} &= \lambda is - \frac{mip}{a+i} - \mu i \\ \frac{dp}{dt} &= \frac{\theta ip}{a+i} - dp.\end{aligned}\tag{2.1}$$

Here $s = s(t)$ = concentration of the susceptible prey population at time t ; $i = i(t)$ = concentration of the infected prey population at time t ; $p = p(t)$ concentration of the predator population at time t ; r is the logistic growth rate; m is the search rate of infected prey population; a is the half saturation coefficient; μ is the natural death rate of infected prey population; d is the natural death rate of predator population; and λ is the force of infection between susceptible and infected prey populations.

In this paper, we assume that horizontal incidence follows standard incidence and with this assumption, the model (2.1) takes the following form

$$\begin{aligned}\frac{ds}{dt} &= rs \left(1 - \frac{s+i}{k} \right) - \frac{\lambda is}{s+i} = F_1(s, i, p) \\ \frac{di}{dt} &= \frac{\lambda is}{s+i} - \frac{mip}{a+i} - \mu i = F_2(s, i, p) \\ \frac{dp}{dt} &= \frac{\theta ip}{a+i} - dp = F_3(s, i, p).\end{aligned}\tag{2.2}$$

System (2.2) needs to be analyzed with the following initial conditions:

$$s(0) \geq 0, \quad i(0) \geq 0, \quad p(0) \geq 0. \quad (2.3)$$

3. Boundedness of the System

Lemma 3.1. *All the solutions which initiate in \mathfrak{R}_3^+ are uniformly bounded.*

Note: The proof is obvious.

3.1. Equilibria and existence

Remark 3.1. The system Eq. (2.2) has four equilibria, namely, $E_0(0,0,0)$, $E_1(k,0,0)$, $E_2\left(\frac{\mu k(r+\mu-\lambda)}{r\lambda}, \frac{k(\lambda-\mu)(r+\mu-\lambda)}{r\lambda}, 0\right)$ and $E^*(s^*, i^*, p^*)$ where s^* is the real positive root of the quadratic equation $f(s) = rs^2 + Bs + C = 0$ and is given by $s^* = \frac{-B + \sqrt{B^2 - 4rC}}{2r}$, where $B = \left(\frac{2rad}{\theta-d} - rk\right)$; $C = \frac{ad}{\theta-d} \left(r\frac{ad}{\theta-d} + \lambda k - rk\right)$, i^* and p^* are given by $i^* = \frac{ad}{\theta-d}$ and $p^* = \frac{ad}{(\theta-d)m} \left(\frac{\lambda s^*}{r s^* + i^*} - \mu\right)$, respectively.

Remark 3.2. It is easy to see that equilibria E_0 and E_1 exists for all parameter values. The planar equilibria E_2 exists if the condition $\mu < \lambda < r + \mu$ is satisfied.

Remark 3.3. If the condition $k > \frac{rad}{(r-\lambda)(\theta-d)}$ is satisfied then there exists a unique positive real root s^* of the equation $f(s) = 0$. In order to have $p^* > 0$ we must have $s^* > \frac{\mu ad}{(\theta-d)(\lambda-\mu)}$. Moreover $i^* > 0$ implies $\theta > d$. Therefore the interior equilibrium $E^*(s^*, i^*, p^*)$ exists if the conditions

(i) $k > \frac{rad}{(r-\lambda)(\theta-d)}$, (ii) $s^* > \frac{\mu ad}{(\theta-d)(\lambda-\mu)}$ and (iii) $\theta > d$ are satisfied.

4. Dynamical Behavior of the System Around the Biological Feasible Equilibria

The main interest of this section to observe the dynamical behavior around the positive interior equilibrium when horizontal incidence has been taken as mass action incidence and standard incidence, respectively. The stability analysis of the system around the trivial equilibrium $E_0(0,0,0)$ may be obtained following the approach of Jost *et al.*¹³ or Arino *et al.*¹⁴

Theorem 4.1. *The axial equilibrium $E_1(k,0,0)$ is unstable saddle along the s -axis if $\lambda > \mu$ (existence condition of E_2). If the condition $k > \frac{adr\lambda}{(\theta-d)(\lambda-\mu)(r+\mu-\lambda)}$ is satisfied then $E_2\left(\frac{\mu k(r+\mu-\lambda)}{r\lambda}, \frac{k(\lambda-\mu)(r+\mu-\lambda)}{r\lambda}, 0\right)$ is saddle in nature.*

Note. Using variational matrix method one can easily prove the theorem.

Next we assume that the interior equilibrium exists and study its local stability. This will yield some analytic and computational conditions for stable co-existence of all three species.

Theorem 4.2. *If the condition $\frac{mi^*p^*}{(a+i^*)^2} < \frac{\lambda s^*i^*}{(s^*+i^*)^2} < \frac{rs^*}{k}$ then the interior equilibrium E^* is locally asymptotically stable.*

Note. By applying Routh-Hurwitz criterion the theorem can be proved easily.

Example. We have taken the hypothetical set of parameter values, $r = 15 \text{ day}^{-1}$, $k = 45 \text{ individuals ha}^{-1}$, $m = 14.5 \text{ day}^{-1}$, $a = 14 \text{ individuals ha}^{-1}$, $\lambda = 0.006 \text{ day}^{-1}$, $\mu = 0.0019 \text{ day}^{-1}$, $\theta = 11.1 \text{ day}^{-1}$, $d = 6 \text{ day}^{-1}$ which were considered by Chattopadhyay and Bairagi.¹ Substituting these parameter values in the equation $f(s) = 0$ and solving we get $s^* = 28.5228$. We also get $i^* = 16.4706$. Again substituting the value of s^* and i^* in the expression of p^* we observe that system Eq. (2.2) possesses one positive interior equilibrium $E^*(s^* = 28.5228, i^* = 16.4706, p^* = 0.0040)$. Using these set of parametric values and the values of s^* , i^* and p^* , we observe that condition for local asymptotic stability of the interior equilibrium (as stated in Theorem 4.2) is satisfied. Moreover the eigenvalues associated with the variational matrix of the system Eq. (2.2) at E^* is $(-9.505, -0.0006 + 0.724i, -0.0006 - 0.724i)$. So from the above observation we can say that E^* is locally asymptotically stable.

5. Numerical Simulation

The aim of the section is to observe the role of force of infection on different horizontal incidence as well as on different functional response. Numerical simulations have been carried out with the help of MATLAB software.

5.1. Role of force of infection on different horizontal incidence

We start this section with numerical experiments to confirm our analytical findings. The dynamics of system Eq. (2.2) around the positive interior equilibrium has been numerically simulated for the hypothetical set of parametric values which we have used in the previous example. The existence and stability conditions have been satisfied for these set of parametric values. Keeping all other parameter values fixed, varying the parameter λ and taking 30 susceptible individuals ha^{-1} , five infective individuals ha^{-1} , 15 predator individuals ha^{-1} as our initial populations, we observe the following dynamical behavior of the two systems. System (2.1) is stable for a small range of λ (see Fig. 1) whereas system (2.2) is stable for a wider range of λ (see Fig. 2). These observations indicate that standard incidence is a better formulation than the simple mass action incidence.

To visualize the above dynamics more transparently we present the Table 1.

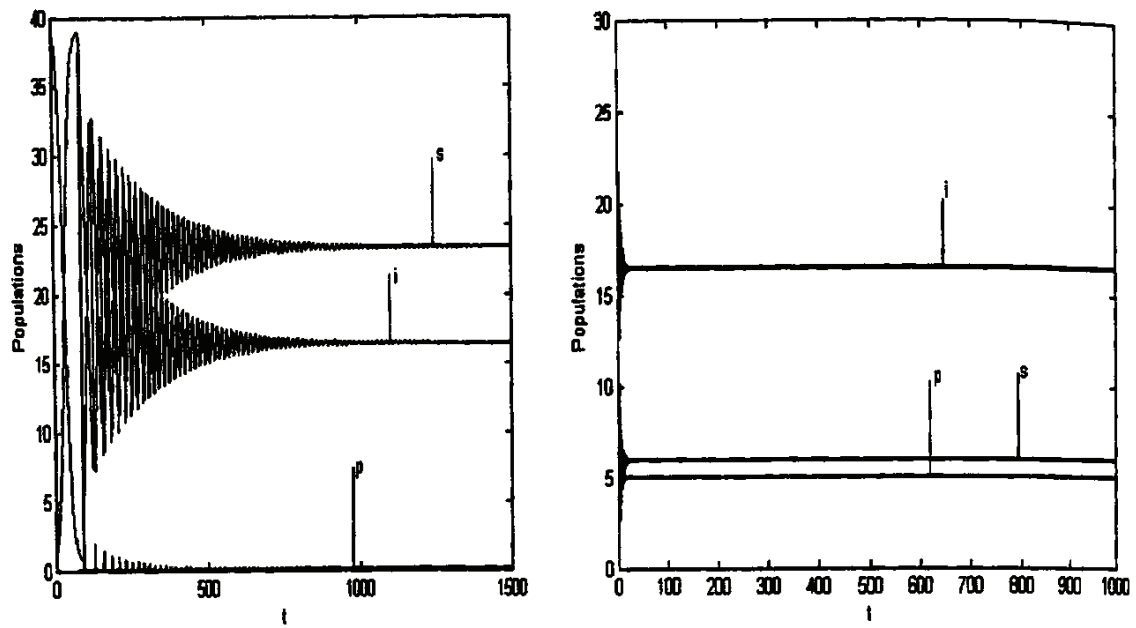


Fig. 1. Stable co-existence of three populations for $r = 15$, $k = 45$, $m = 14.5$, $a = 14$, $\mu = 0.0019$, $\theta = 11.1$, $d = 6$, and for $\lambda = 0.0026$ and $\lambda = 0.4$ when horizontal incidence follows mass action incidence.

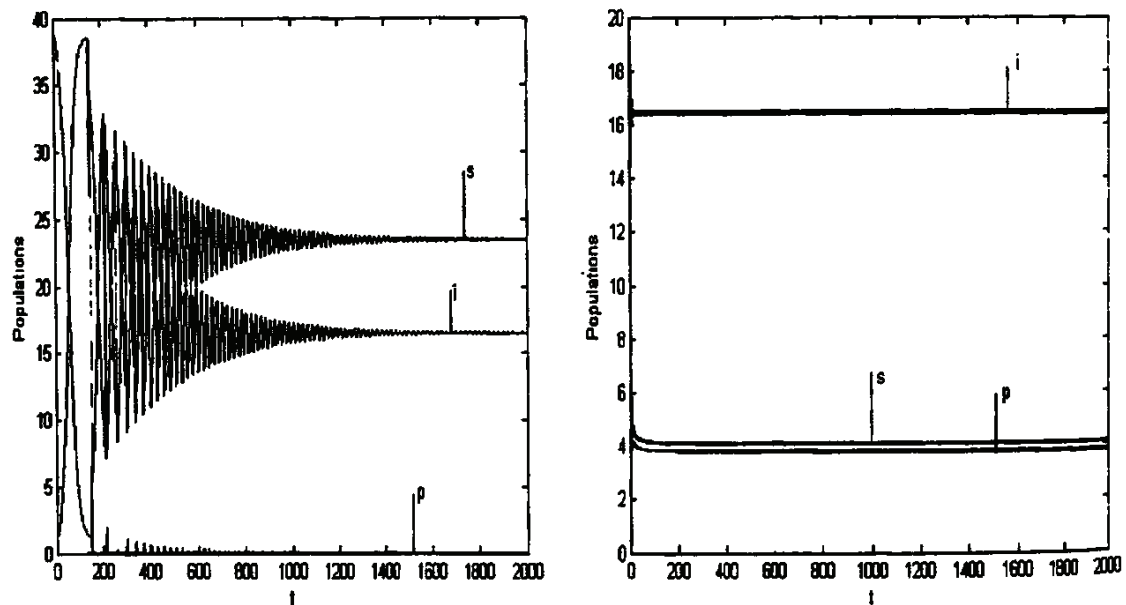


Fig. 2. Stable co-existence of three populations for $\lambda = 0.065$ and for $\lambda = 9.1$, when horizontal incidence follows standard incidence, keeping all other parameters fixed as described in Fig. 1.

Table 1. Simulation experiment of model system (2.1) and (2.2) by taking horizontal incidence as mass action incidence and standard incidence, respectively with fixed parameter values $r = 15, k = 45, m = 14.5, a = 14, \lambda = 0.006, \mu = 0.0019, \theta = 11.1, d = 6$.

Variation in λ	Horizontal incidence follows mass action incidence	Horizontal incidence follows standard incidence
Greater than 0.0025	Stable	Unstable
Greater than 0.0064	Stable	Stable
Less than 0.5	Stable	Stable
Less than 9.2	Unstable	Stable

5.2. Role of force of infection on different horizontal incidence as well as on different functional responses

Apart from the force of infection, the impact of functional response on ecological system cannot be ignored. The dynamic stability of ecological system depends on the type of functional response used (for example, see Williams and Martinez¹⁵). Recently Fussmann and Blasius¹⁶ observed that the use of several nearly indistinguishable functions can serve as phenomenological descriptors of resource uptake and may lead to alarmingly different dynamical behaviors in a simple community model. It is well established that force of infection in epidemiological models and functional response in ecological systems have remarkable influence on the dynamics of the system behavior. It is quite intuitive that joint variation of these two factors in eco-epidemiological systems may describe some interesting dynamics. To observe this role, we shall consider different functional responses in the following model.

$$\begin{aligned}
 \frac{ds}{dt} &= rs \left(1 - \frac{s+i}{k} \right) - h(s, i) - f\left(\frac{s}{p}\right)p \\
 \frac{di}{dt} &= h(s, i) - g(i)p - \mu i \\
 \frac{dp}{dt} &= f_1\left(\frac{s}{p}\right)p - g_1(i)p - \delta p
 \end{aligned}
 \tag{5.1}$$

Here r is the growth rate of the susceptible prey and k is the carrying capacity. The predator, p , consumes the prey s and i and grows according to the functional responses $f\left(\frac{s}{p}\right)$ and $g(i)$, respectively. Here $h(s, i) = \lambda si$ when horizontal incidence is mass action incidence and $h(s, i) = \frac{\lambda si}{s+i}$ when horizontal incidence is standard incidence, $f\left(\frac{s}{p}\right) = \frac{\theta_1 s}{a p + s}$, $g(i) = m_1 i$, $f_1(s) = \frac{\theta_2 s}{a + s}$ and $g_1(i) = m_2 i$ where θ_1 and m_1 are the search rates for susceptible prey population and infected prey population respectively, a is the half saturation coefficient, θ_2 and m_2 are the conversion factors due to predation of susceptible prey and infected prey, respectively. If we consider $p = 1$ in the functional response then it will be considered as prey-dependent functional response, otherwise it is called ratio-dependent functional response.

Considering the parametric values as $r = 3 \text{ day}^{-1}$, $K = 45 \text{ individuals ha}^{-1}$, $a = 15 \text{ day}^{-1}$, $m_1 = 0.05 \text{ ha per individuals day}^{-1}$, $\theta_1 = 0.5 \text{ day}^{-1}$, $\theta_2 = 0.2 \text{ ha}$

per individuals day⁻¹, $m_2 = 0.04$, $\mu = 0.24$ day⁻¹, $\delta = 0.09$ day⁻¹, varying only parameter λ , the above model has been simulated for different horizontal incidence on different type of functional responses. In the case of standard incidence, we note that when functional response due to predation of susceptible prey is of Holling type II or ratio-dependent and functional response due to predation of infected prey is of type I, we get infected prey-free region and at the same time

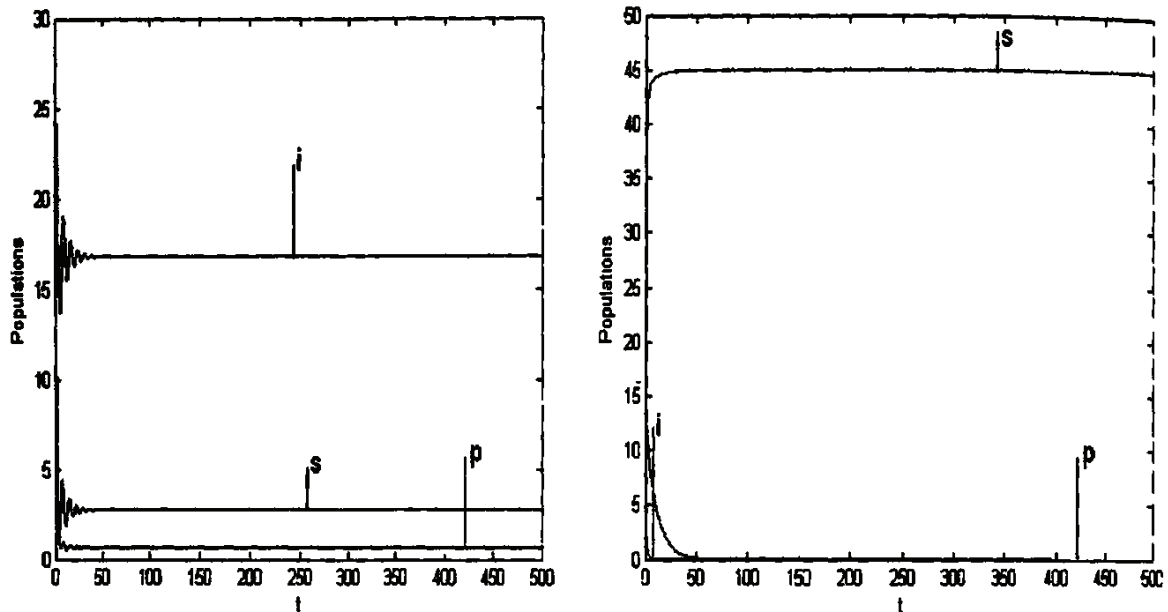


Fig. 3. Stable population distribution of three species in the case of mass action incidence and extinction of i and p population in the case of standard incidence respectively for $r = 3$, $K = 45$, $a = 15$, $m_1 = 0.05$, $\theta_1 = 0.5$, $\theta_2 = 0.2$, $m_2 = 0.04$, $\mu = 0.24$, $\delta = 0.09$ and for $\lambda = 0.1$.

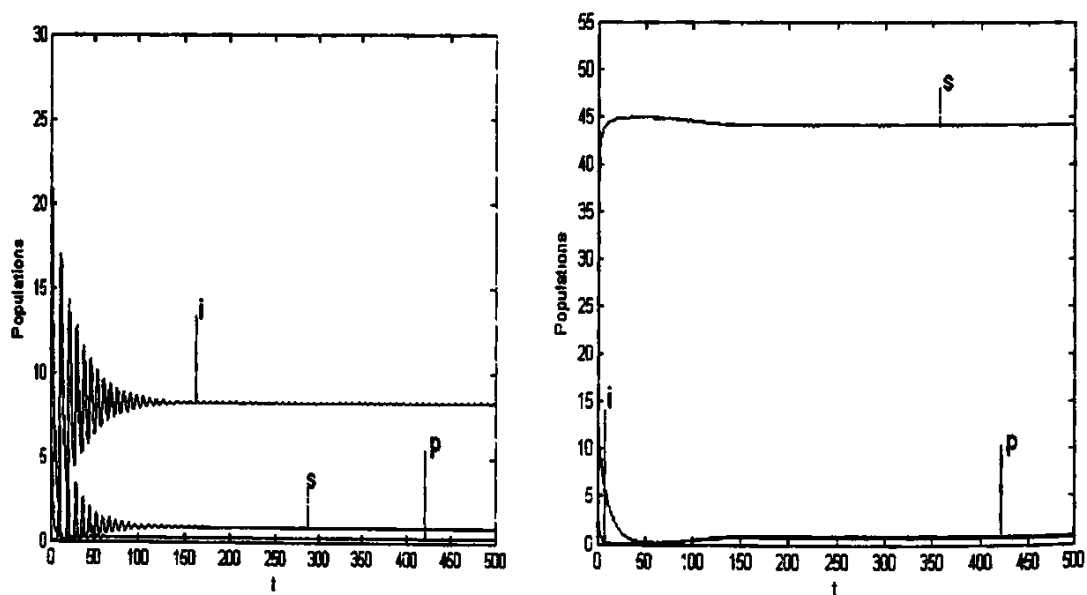


Fig. 4. Keeping all other parameters fixed as described in Fig. 3, and for $\lambda = 0.29$ stable population distribution of three species in the case of mass action incidence, and standard incidence, respectively.

predator population goes to extinction. In these cases, λ lies between 0.006 to 0.24 (see Fig. 3). If the value of λ is increased from 0.24 to 3.1 we observe the stable population distribution of three species (see Figs. 4–6). This reflects that if susceptible prey becomes more infected, then in the case of standard incidence stable co-existence of three population is possible. Arino *et al.*¹⁴ described in their paper that infection in prey population may act as a biological control in ratio-dependent predator-prey models. In our paper, we can also say that when horizontal incidence has been taken as standard incidence then infection in prey population

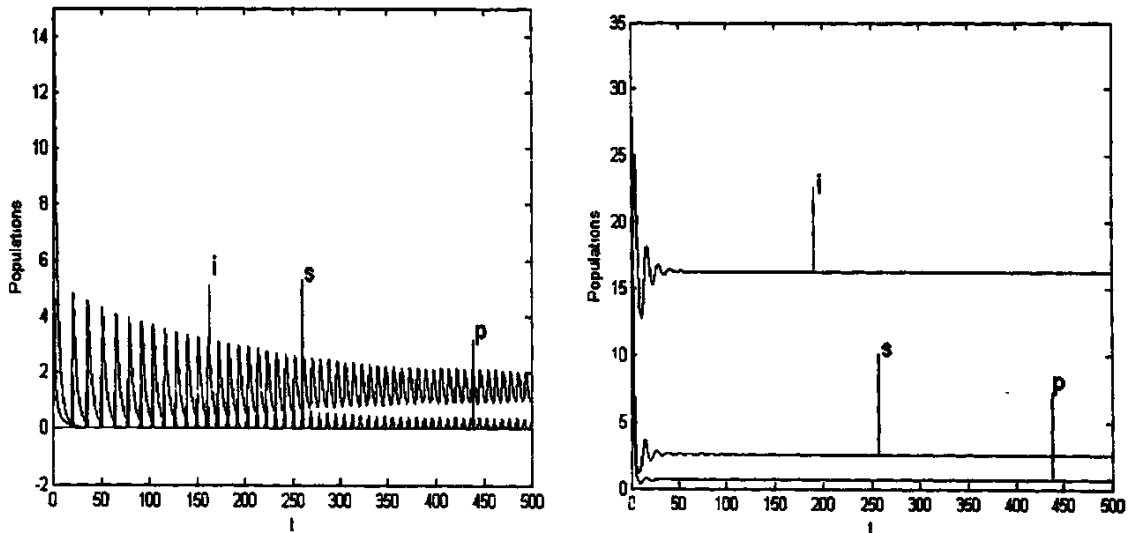


Fig. 5. Keeping all other parameters fixed as described in Fig. 3, and for $\lambda = 2$ susceptible population goes to extinction in the case of mass action incidence and stable population distribution of three species in the case of standard incidence, respectively.

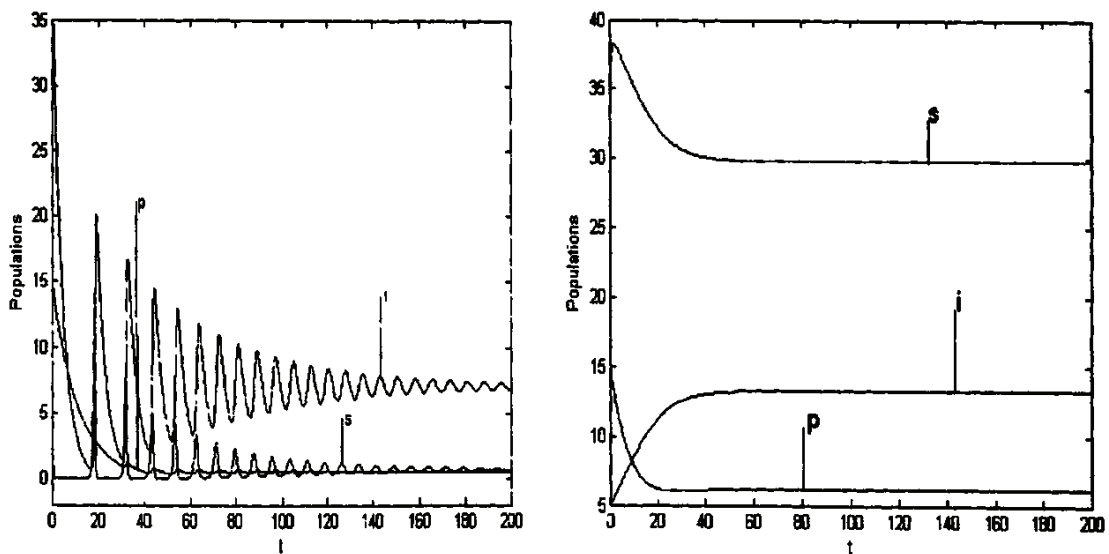


Fig. 6. Keeping all other parameters fixed as described in Fig. 3, and for $\lambda = 0.35$ s goes to extinction in the case of mass action incidence and stable population distribution of three species in the case of standard incidence, respectively.

may act as a biological control. This situation is also true when both functional responses have been taken as ratio-dependent (see Fig. 6). But the remark is not true when horizontal incidence has been taken as mass action incidence. In that case if we increase λ , then the population distribution has been shifted from stable to unstable region.

The Table 2 shows the dynamical stability around the positive equilibrium of the model system (5.1) with different functional responses by varying only λ .

From the table it is clear that the dynamic stability of the modified model depends on horizontal incidence (i.e. mass action incidence and standard incidence, respectively). Our goal was to investigate the effect of λ on different functional responses when horizontal incidence has been taken as mass action incidence and standard incidence, respectively. We observed that two types of horizontal incidences, give completely different outcomes in terms of model dynamics. Using the standard incidence on different functional responses, we observe that predator and prey abundance are always far from zero and therefore the population has a high expectation of persistence for large values of λ (here three species co-exist for λ greater than 2.85). In contrast, with mass action incidence there is an extinction risk for higher values of λ . We observed that when the value of λ is greater than 1.6, there is no chance of co-existence of three species.

6. Conclusion

A three species eco-epidemiological model in which horizontal incidence follows standard incidence is proposed by means of three ordinary differential equations. Our analysis shows that if the force of infection is high, the possibility of the extinction of the species is increased in the case of mass action incidence than that of standard incidence. As in eco-epidemiological situations, the different functional forms may lead to different dynamical behaviors, we used different functional forms and varied the force of infection. In such cases we also observed that the risk of extinction is much less in the case of standard incidence. It has also been seen that when horizontal incidence follows standard incidence, the three populations persist for a wider range of λ whereas in the case of mass action incidence, co-existence of three populations occur for small range of λ . Hence, we finally conclude that unless the exact mechanistic nature of disease transmission between susceptible prey and infected prey is known, caution should be used for predicting dynamics.

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