

The effect of dispersal on a predator-prey model with Holling type-II functional response

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Abstract. A predator-prey model with prey dispersal and Holling type-II functional response is investigated. In this model, the time delay due to the gestation of the predator and stage-structure for the predator are considered. By analyzing the corresponding characteristic equations, the local stability of each of the nonnegative equilibria is discussed. The existence of Hopf bifurcations at the positive equilibrium is established. By using Lyapunov functionals and LaSalle's invariance principle, sufficient conditions are obtained for the global stability of the positive equilibrium, the nonnegative boundary equilibrium and the trivial equilibrium of the model, respectively. Numerical simulations are carried out to illustrate the main results.

§1 Introduction

The effect of dispersal on ecological system is an important topic from mathematical as well as ecological point of view. Since the pioneering work by Skellam [14], many works have focused on the effect of spatial factors which play a crucial rule in the persistence and stability of a population. Some of the mathematical models dealt with a single population dispersing among patches. Some of them dealt with competition and predator-prey interactions in patchy environments(see, for examples, [1,2,4,9] and references therein). We note that many authors always assumed that the intrinsic growth rates are all continuous and bounded above and below by positive constants. This means that every species lives in a suitable environment. However, the actual living environments of endangered species are not always like this. Because of the ecological effects of human activities and industry, e.g., the location of manufacturing industries and pollution of the atmosphere, rivers and soil, more and more habitats have been broken into patches and some of the patches have been polluted. In some of these patches, and sometimes

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even in every patch, species will become extinct without contributions from other patches, and hence the species live in a weak patchy environment.

In [1,2], Cui and Chen proposed and studied population models with weak patchy environment. In [4], Freedman and Takeuchi are concerned with a model of a single species that disperse among the n patches of a heterogeneous environment with barriers between patches, and with a predator for which the dispersal between patches does not involve a barrier. In [9], Xu and Ma considered the following predator-prey model with prey dispersal between two patches

$$\begin{aligned}\dot{x}_1(t) &= r_1x_1(t) - a_{11}x_1^2(t) - a_{12}x_1(t)y(t) + D_{21}x_2(t) - D_{12}x_1(t), \\ \dot{x}_2(t) &= -r_2x_2(t) + D_{12}x_1(t) - D_{21}x_2(t), \\ \dot{y}(t) &= a_{21}x_1(t - \tau)y(t - \tau) - ry(t) - a_{22}y^2(t).\end{aligned}\tag{1}$$

In model (1), it is assumed that the ecosystem is composed of two isolated patches and the breeding area is damaged in patch 2. $x_1(t)$ and $x_2(t)$ represent the densities of the prey at time t in patches 1 and 2, respectively; $y(t)$ represents the density of the predator population at time t in patch 1. The parameters a_{11} , a_{12} , a_{21} , a_{22} , D_{12} , D_{21} , r_1 , r_2 and r are positive constants, where D_{12} and D_{21} are the dispersal rates of the prey between the two patches, a_{11} and a_{22} are the intra-specific competition rates of the prey and the predator in patch 1, a_{12} is the capturing rate of the predator in patch 1, a_{21}/a_{12} is the conversion rate of nutrients into the reproduction of the predator, r_1 is the intrinsic growth rate of the prey in patch 1, r_2 and r are the death rates of the prey in patch 2 and the predator. $\tau \geq 0$ is a constant delay due to the gestation of the predator, that is, mature adult predators only can contribute to the reproduction of the predator biomass. In [9], by using an iteration technique, a threshold is derived for the permanence and extinction of the model (1).

In the classical predator-prey models, it is assumed that each individual predator admits the same ability to feed on prey and each individual prey admits the same risk to be attacked by predators. This assumption seems not to be realistic for many animals. In the natural world, there are many species whose individuals pass through an immature stage during which they are raised by their parents, and the reproductive rate during this stage can be ignored. Stage-structured models have received great attention in the last two decades (see, for example, [10,15,16] and references therein). In [16], Tian and Xu considered a Holling type II functional response predator-prey model with stage structure for the predator. It is assumed that the predator is divided into two groups, one immature and the other mature, and that only mature predators can attack prey and have reproductive ability, while immature predators do not attack prey and have no reproductive ability.

In this paper, motivated by the works of [9] and [16], we are concerned with the effects of prey dispersal between two patches, Holling type II functional response, stage-structure for the predator and time delay due to the gestation of predator on the global dynamics of a predator-prey model. To this end, we study the following delayed differential model

$$\begin{aligned}\dot{x}_1(t) &= r_1x_1(t) - a_{11}x_1^2(t) - \frac{a_{12}x_1(t)y_2(t)}{1 + mx_1(t)} + D_{21}x_2(t) - D_{12}x_1(t), \\ \dot{x}_2(t) &= -r_2x_2(t) + D_{12}x_1(t) - D_{21}x_2(t),\end{aligned}$$

$$\begin{aligned}\dot{y}_1(t) &= \frac{a_{21}x_1(t-\tau)y_2(t-\tau)}{1+mx_1(t-\tau)} - (r+d_1)y_1(t), \\ \dot{y}_2(t) &= ry_1(t) - d_2y_2(t),\end{aligned}\tag{2}$$

where $x_1(t)$ and $x_2(t)$ represent the densities of the prey at time t in patches 1 and 2, respectively; $y_1(t)$ and $y_2(t)$ represent the densities of the immature and mature predator at time t in patch 1. The parameters a_{11} , a_{12} , a_{21} , D_{12} , D_{21} , r , r_1 , r_2 , d_1 , d_2 and m are positive constants, in which r is the transformation rate from the immature individuals to mature individuals for the predator; d_1 and d_2 are the death rate of the immature predator and mature predator, respectively; $x/(1+mx)$ is the Holling type II functional response. Other parameters are the same biological significance as model (1). In model (2), we assume that only mature predator can capture the prey in patch 1.

The initial conditions for model (2) take the form

$$\begin{aligned}x_1(\theta) &= \varphi_1(\theta) \geq 0, x_2(\theta) = \varphi_2(\theta) \geq 0, y_1(\theta) = \phi_1(\theta) \geq 0, y_2(\theta) = \phi_2(\theta) \geq 0, \theta \in [-\tau, 0], \\ \varphi_1(0) &> 0, \varphi_2(0) > 0, \phi_1(0) > 0, \phi_2(0) > 0, (\varphi_1(\theta), \varphi_2(\theta), \phi_1(\theta), \phi_2(\theta)) \in C([-\tau, 0], R_{+0}^4),\end{aligned}\tag{3}$$

where $R_{+0}^4 = \{(z_1, z_2, z_3, z_4) : z_i \geq 0, i = 1, 2, 3, 4\}$.

It is well known by the fundamental theory of functional differential equations [6] that model (2) has a unique solution $(x_1(t), x_2(t), y_1(t), y_2(t))$ satisfying initial conditions (3). It is easy to show that all solutions of model (2) with initial conditions (3) are defined on $[0, +\infty]$ and remain positive for all $t \geq 0$.

The organization of this paper is as follows. In the next section, we prove the boundedness of solutions of model (2) with initial conditions (3). In section 3, by using the theory on characteristic equation of delay differential equations developed by [6], we discuss the local stability of each of feasible equilibria of model (2). We establish the existence of Hopf bifurcations at the positive equilibrium. In Section 4, by means of Lyapunov functionals and LaSalle's invariance principle, we obtain sufficient conditions for the global stability of each of the nonnegative equilibria of model (2). Some numerical simulations are presented in Section 5 to illustrate the main results. The paper ends with a brief discussion in Section 6.

§2 Boundedness of solutions

In this section, we show the boundedness of the positive solutions of model (2)-(3).

Lemma 2.1 *For model (2)-(3), there are positive constants M_1 and M_2 , such that each positive solution $(x_1(t), x_2(t), y_1(t), y_2(t))$ of model (2)-(3) satisfies*

$$\limsup_{t \rightarrow +\infty} x_i(t) \leq M_1, \quad \limsup_{t \rightarrow +\infty} y_i(t) \leq M_2 (i = 1, 2),$$

that is, positive solutions of (2)-(3) are ultimately bounded.

Proof. Let $(x_1(t), x_2(t), y_1(t), y_2(t))$ be any positive solution of (2)-(3). Define

$$f(t) = x_1(t-\tau) + x_2(t-\tau) + \frac{a_{12}}{a_{21}}(y_1(t) + y_2(t)).$$

Calculating the derivative of $f(t)$ along positive solutions of (2)-(3), it follows that

$$\begin{aligned} \dot{f}(t) &\leq r_1 x_1(t-\tau) - a_{11} x_1^2(t-\tau) - r_2 x_2(t-\tau) - \frac{a_{12}}{a_{21}} d_1 y_1(t) - \frac{a_{12}}{a_{21}} d_2 y_2(t) \\ &\leq -df(t) - a_{11} \left(x_1(t-\tau) - \frac{r_1+d}{2a_{11}} \right)^2 + \frac{(r_1+d)^2}{4a_{11}} \\ &\leq -df(t) + \frac{(r_1+d)^2}{4a_{11}}, \end{aligned} \quad (4)$$

where $d = \min\{r_2, d_1, d_2\}$. We derive from (4) that

$$\limsup_{t \rightarrow +\infty} f(t) \leq \frac{(r_1+d)^2}{4a_{11}d}.$$

If we choose

$$M_1 = \frac{(r_1+d)^2}{4a_{11}d}, \quad M_2 = \frac{a_{21}(r_1+d)^2}{4a_{11}a_{12}d},$$

then

$$\limsup_{t \rightarrow +\infty} x_i(t) \leq M_1, \quad \limsup_{t \rightarrow +\infty} y_i(t) \leq M_2 \quad (i = 1, 2).$$

This completes the proof. $\square$

Lemma 2.2 For any positive solution $(x_1(t), x_2(t), y_1(t), y_2(t))$ of model (2)-(3), we have

$$\liminf_{t \rightarrow +\infty} x_1(t) \geq \frac{|(r_1 - a_{21}M_2)(r_2 + D_{21}) - r_2D_{12}|}{a_{11}(r_2 + D_{21})} := \underline{x}_1,$$

where M_2 is defined in Lemma 2.1.

Proof. Let $(x_1(t), x_2(t), y_1(t), y_2(t))$ be any positive solution of (2)-(3). By Lemma 2.1, it follows that $\limsup_{t \rightarrow +\infty} y_2(t) \leq M_2$. Hence, for $\varepsilon > 0$ sufficiently small, there is a $T_0 > 0$ such that if $t > T_0$, $y_2(t) < M_2 + \varepsilon$. For $\varepsilon > 0$ sufficiently small, we derive from the first and the second equations of model (1.2) that for $t > T_0$,

$$\begin{aligned} \dot{x}_1(t) &\geq r_1 x_1(t) - a_{11} x_1^2(t) - a_{12}(M_2 + \varepsilon)x_1(t) + D_{21}x_2(t) - D_{12}x_1(t), \\ \dot{x}_2(t) &= -r_2 x_2(t) + D_{12}x_1(t) - D_{21}x_2(t). \end{aligned} \quad (5)$$

By comparison and Lemma 2.2 of [10], it follows from (5) that

$$\liminf_{t \rightarrow +\infty} x_1(t) \geq \frac{|(r_1 - a_{12}M_2)(r_2 + D_{21}) - r_2D_{12}|}{a_{11}(r_2 + D_{21})}.$$

This completes the proof. $\square$

§3 Local stability and Hopf bifurcations

In this section, we are concerned with the local stability of each of nonnegative equilibria of model (2) by analyzing the corresponding characteristic equations.

It is easy to show that model (2) always has a trivial equilibrium $E_0(0, 0, 0, 0)$. Model (2) has a nonnegative (i.e., predator-extinction) equilibrium $E_1(x'_1, x'_2, 0, 0)$ provided that

$$r_1(r_2 + D_{21}) > r_2D_{12},$$

where

$$x'_1 = \frac{r_1(r_2 + D_{21}) - r_2D_{12}}{a_{11}(r_2 + D_{21})}, \quad x'_2 = \frac{D_{12}}{r_2 + D_{21}}x'_1.$$

Further, if the following holds

$$(H_1) \quad \frac{r_1(r_2 + D_{21}) - r_2D_{12}}{a_{11}(r_2 + D_{21})} > \frac{d_2(r + d_1)}{a_{21}r - md_2(r + d_1)} > 0,$$

then model (2) has a positive equilibrium $E_+(x_1^+, x_2^+, y_1^+, y_2^+)$, where

$$\begin{aligned} x_1^+ &= \frac{d_2(r+d_1)}{a_{21}r - md_2(r+d_1)}, \quad x_2^+ = \frac{D_{12}}{r_2 + D_{21}}x_1^+, \\ y_1^+ &= \frac{a_{21}x_1^+}{a_{12}(r+d_1)} \left(r_1 - \frac{r_2 D_{12}}{r_2 + D_{21}} - a_{11}x_1^+ \right), \quad y_2^+ = \frac{r}{d_2}y_1^+. \end{aligned}$$

3.1 Local stability of boundary equilibria

The characteristic equation of model (2) at the equilibrium $E_0(0, 0, 0, 0)$ is of the form

$$(\lambda + d_2)(\lambda + r + d_1) [\lambda^2 + (r_2 + D_{21} + D_{12} - r_1)\lambda + r_2 D_{12} - r_1(r_2 + D_{21})] = 0. \quad (6)$$

Clearly, equation (6) always has two negative real roots $\lambda_1 = -d_2$, $\lambda_2 = -(r + d_1)$. All other roots of (6) are determined by the following equation:

$$\lambda^2 + (r_2 + D_{21} + D_{12} - r_1)\lambda + r_2 D_{12} - r_1(r_2 + D_{21}) = 0. \quad (7)$$

If $r_2 D_{12} > r_1(r_2 + D_{21})$, then we have $D_{12} > r_1$. In this case, equation (7) has two negative real roots. Hence, E_0 is locally asymptotically stable. If $r_2 D_{12} < r_1(r_2 + D_{21})$, equation (7) has a positive real root. Accordingly, the equilibrium E_0 is unstable.

The characteristic equation of model (2) at the equilibrium $E_1(x'_1, x'_2, 0, 0)$ takes the form

$$\begin{aligned} &[\lambda^2 + (r_2 + D_{21} + D_{12} + 2a_{11}x'_1 - r_1)\lambda + r_1(r_2 + D_{21}) - r_2 D_{12}] \\ &\times \left[\lambda^2 + (r + d_1 + d_2)\lambda + d_2(r + d_1) - \frac{a_{21}x'_1}{1 + mx'_1}e^{-\lambda\tau} \right] = 0. \end{aligned} \quad (8)$$

Noting that

$$r_2 + D_{21} + D_{12} + 2a_{11}x'_1 - r_1 = r_2 + D_{21} + a_{11}x'_1 + \frac{D_{12}D_{21}}{r_2 + D_{21}} > 0,$$

it is easy to show that the equation

$$\lambda^2 + (r_2 + D_{21} + D_{12} + 2a_{11}x'_1 - r_1)\lambda + r_1(r_2 + D_{21}) - r_2 D_{12} = 0$$

always has two negative real roots. All other roots are given by the roots of equation

$$\lambda^2 + (r + d_1 + d_2)\lambda + d_2(r + d_1) - \frac{a_{21}x'_1}{1 + mx'_1}e^{-\lambda\tau} = 0. \quad (9)$$

Let $g(\lambda) = \lambda^2 + (r + d_1 + d_2)\lambda + d_2(r + d_1) - \frac{a_{21}x'_1}{1 + mx'_1}e^{-\lambda\tau}$. If (H_1) holds, it then follows that for nonnegative real λ ,

$$\begin{aligned} g(0) &= d_2(r + d_1) - \frac{a_{21}x'_1}{1 + mx'_1} \\ &= \frac{a_{21}r - md_2(r + d_1)}{1 + mx'_1} \left(\frac{d_2(r + d_1)}{a_{21}r - md_2(r + d_1)} - \frac{r_1(r_2 + D_{21}) - r_2 D_{12}}{a_{11}(r_2 + D_{21})} \right) \\ &< 0, \end{aligned}$$

$$\lim_{\lambda \rightarrow +\infty} g(\lambda) = +\infty, \quad g'(\lambda) = 2\lambda + r + d_1 + d_2 + \frac{a_{21}x'_1}{1 + mx'_1}e^{-\lambda\tau} > 0.$$

Hence, $g(\lambda) = 0$ has a positive real root. Accordingly, the equilibrium E_1 is unstable.

If the following holds

$$(H_2) \quad 0 < \frac{r_1(r_2 + D_{21}) - r_2 D_{12}}{a_{11}(r_2 + D_{21})} < \frac{d_2(r + d_1)}{a_{21}r - md_2(r + d_1)},$$

then $g(0) > 0$. When $\tau = 0$, equation (9) reduces to

$$\lambda^2 + (r + d_1 + d_2)\lambda + d_2(r + d_1) - \frac{a_{21}x_1'}{1 + mx_1'} = 0. \quad (10)$$

It is easy to show that equation (10) always has two negative real roots. Hence, the equilibrium E_1 is locally asymptotically stable.

If $i\omega$ ($\omega > 0$) is a solution of (9), it is not difficult to show that

$$\omega^4 + h_1\omega^2 + h_0 = 0, \quad (11)$$

where

$$h_1 = (r + d_1)^2 + d_2^2 > 0, \quad h_0 = (d_2(r + d_1))^2 - \left(\frac{ra_{21}x_1'}{1 + mx_1'}\right)^2 > 0.$$

In this case, equation (11) has no positive real roots. Accordingly, the roots of equation (9) have only negative real parts. By the general theory on characteristic equations of delay differential equation from [6], the equilibrium E_1 is locally asymptotically stable for all $\tau \geq 0$.

In conclusion, we have the following results.

Theorem 3.1 For model (2)-(3), we have

- (i) If $r_2D_{12} > r_1(r_2 + D_{21})$, then the equilibrium $E_0(0, 0, 0, 0)$ is locally asymptotically stable for all $\tau \geq 0$; if $r_2D_{12} < r_1(r_2 + D_{21})$, then E_0 is unstable.
- (ii) Let $r_2D_{12} < r_1(r_2 + D_{21})$ hold. If (H_2) holds, then the equilibrium $E_1(x_1', x_2', 0, 0)$ is locally asymptotically stable for all $\tau \geq 0$; if (H_1) holds, then E_1 is unstable.

3.2 Local stability of positive equilibrium and Hopf bifurcations

Now, we study the local stability of the positive equilibrium $E_+(x_1^+, x_2^+, y_1^+, y_2^+)$ of model (1.2). The characteristic equation of model (2) at the equilibrium E_+ takes the form

$$P(\lambda) + Q(\lambda)e^{-\lambda\tau} = 0, \quad (12)$$

where

$$\begin{aligned} P(\lambda) &= \lambda^4 + p_3\lambda^3 + p_2\lambda^2 + p_1\lambda + p_0, \quad Q(\lambda) = q_2\lambda^2 + q_1\lambda + q_0, \\ \alpha &= 2a_{11}x_1^+ + D_{12} + \frac{a_{12}y_2^+}{(1 + mx_1^+)^2} - r_1, \\ p_3 &= r + d_1 + d_2 + r_2 + D_{21} + \alpha, \\ p_2 &= d_2(r + d_1) + (r + d_1 + d_2)(r_2 + D_{21} + \alpha) + \alpha(r_2 + D_{21}) - D_{12}D_{21}, \\ p_1 &= (r + d_1 + d_2)(\alpha(r_2 + D_{21}) - D_{12}D_{21}) + d_2(r + d_1)(r_2 + D_{21} + \alpha), \\ p_0 &= d_2(r + d_1)(\alpha(r_2 + D_{21}) - D_{12}D_{21}), \\ q_2 &= -d_2(r + d_1), \\ q_1 &= -d_2(r + d_1) \left(r_2 + D_{21} + \alpha - \frac{a_{12}y_2^+}{(1 + mx_1^+)^2} \right), \\ q_0 &= -d_2(r + d_1) \left(\alpha(r_2 + D_{21}) - D_{12}D_{21} - \frac{a_{12}y_2^+}{(1 + mx_1^+)^2} (r_2 + D_{21}) \right). \end{aligned}$$

When $\tau = 0$, equation (12) reduces to

$$\lambda^4 + p_3\lambda^3 + (p_2 + q_2)\lambda^2 + (p_1 + q_1)\lambda + p_0 + q_0 = 0. \quad (13)$$

By direct calculations, we obtain

$$\begin{aligned} p_2 + q_2 &= (r + d_1 + d_2)(r_2 + D_{12} + \alpha) + \alpha(r_2 + D_{12}) - D_{12}D_{21}, \\ p_1 + q_1 &= (r + d_1 + d_2)[\alpha(r_2 + D_{12}) - D_{12}D_{21}] + d_2(r + d_1)\frac{a_{12}y_2^*}{(1 + mx_1^*)^2}, \\ p_0 + q_0 &= d_2(r + d_1)\frac{a_{12}y_2^*}{(1 + mx_1^*)^2} > 0. \end{aligned}$$

Hence, if $\alpha(r_2 + D_{12}) > D_{12}D_{21}$, then

$$p_3 > 0, p_2 + q_2 > 0, \text{ and } p_1 + q_1 > 0.$$

Hence the roots of equation (13) have only negative real parts. Accordingly, the positive equilibrium E_+ is locally asymptotically stable when $\tau = 0$.

If $\lambda = i\omega$ ($\omega > 0$) is a solution of (12), separating the real and imaginary parts, we obtain that

$$\begin{aligned} (q_2\omega^2 - q_0)\cos\omega\tau - q_1\omega\sin\omega\tau &= \omega^4 - p_2\omega^2 + p_0, \\ (q_2\omega^2 - q_0)\sin\omega\tau + q_1\omega\cos\omega\tau &= p_3\omega^3 - p_1\omega. \end{aligned} \quad (14)$$

Squaring and adding the two equations of (14), it follows that

$$\omega^8 + h_3\omega^6 + h_2\omega^4 + h_1\omega^2 + h_0 = 0, \quad (15)$$

where

$$h_3 = p_3^2 - 2p_2, \quad h_2 = p_2^2 + 2p_0 - q_2^2 - 2p_1p_3, \quad h_1 = p_1^2 + 2q_0q_2 - q_1^2 - 2p_0p_2, \quad h_0 = p_0^2 - q_0^2.$$

Letting $z = \omega^2$, equation (15) can be written as

$$h(z) = z^4 + h_3z^3 + h_2z^2 + h_1z + h_0 = 0. \quad (16)$$

A direct calculation shows that

$$\begin{aligned} h_3 &= \alpha^2 + r^2 + (d_1 + d_2)^2 + (r_2 + D_{21})^2 + 2D_{12}D_{21} > 0, \\ h_2 &= [\alpha(r_2 + D_{21}) - D_{12}D_{21}]^2 + [(r + d_1)^2 + d_2^2][\alpha^2 + (r_2 + D_{21})^2 + 2D_{12}D_{21}] > 0, \\ h_1 &= [\alpha(r_2 + D_{21}) - D_{12}D_{21}]^2[(r + d_1)^2 + d_2^2] \\ &\quad + d_2^2(r + d_1)^2\frac{a_{12}y_2^+}{(1 + mx_1^+)^2}[2\alpha - \frac{a_{12}y_2^+}{(1 + mx_1^+)^2}] \\ h_0 &= d_2^2(r + d_1)^2\frac{a_{12}y_2^+}{(1 + mx_1^+)^2}[(r_2 + D_{21})(2\alpha - \frac{a_{12}y_2^+}{(1 + mx_1^+)^2}) - 2D_{12}D_{21}]. \end{aligned}$$

If the following holds

$$(H_3) \quad 2\alpha > \frac{2D_{12}D_{21}}{r_2 + D_{12}} + \frac{a_{12}y_2^+}{(1 + mx_1^+)^2},$$

we have $h_1 > 0$ and $h_0 > 0$. Hence, equation (16) has no positive real roots. Accordingly, if (H_1) and (H_3) hold, then the equilibrium E_+ is locally asymptotically stable for all $\tau \geq 0$.

In the following, we assume that

$$(H_4) \quad 0 < 2\alpha - \frac{a_{12}y_2^+}{(1 + mx_1^+)^2} < \frac{2D_{12}D_{21}}{r_2 + D_{12}}.$$

In this case, we have $h_1 > 0$ and $h_0 < 0$. Therefore, equation (16) has a unique positive root z_+ , that is, (12) admits a pair of purely imaginary roots of the form $\pm i\omega_0$. Denote

$$\tau_k = \frac{1}{\omega_0} \arccos \frac{q_1\omega_0^2(p_3\omega_0^2 - p_1) + (q_2\omega_0^2 - q_0)(\omega_0^4 - p_2\omega_0^2 + p_0)}{(q_1\omega_0)^2 + (q_2\omega_0^2 - q_0)^2} + \frac{2k\pi}{\omega_0}, \quad k = 0, 1, 2, \dots \quad (17)$$

Noting that if $\alpha(r_2 + D_{12}) > D_{12}D_{21}$ holds, then E_+ is locally stable when $\tau = 0$, and by the general theory on characteristic equation of delay differential equation from [7] (Theorem 4.1), E^* remains stable for $\tau < \tau_0$.

Differentiating the two sides of (12) with respect τ , it follows that

$$\left(\frac{d\lambda}{d\tau}\right)^{-1} = \frac{4\lambda^3 + 3p_3\lambda^2 + 2p_2\lambda + p_1}{-\lambda(\lambda^4 + p_3\lambda^3 + p_2\lambda^2 + p_1\lambda + p_0)} + \frac{2q_2\lambda + q_1}{\lambda(q_2\lambda^2 + q_1\lambda + q_0)} - \frac{\tau}{\lambda}.$$

Direct calculation, one obtains that

$$\begin{aligned} \operatorname{sign} \left\{ \frac{d(Re\lambda)}{d\tau} \right\}_{\lambda=i\omega_0} &= \operatorname{sign} \left\{ Re \left(\frac{d\lambda}{d\tau} \right)^{-1} \right\}_{\lambda=i\omega_0} \\ &= \operatorname{sign} \left\{ Re \left[\frac{4\lambda^3 + 3p_3\lambda^2 + 2p_2\lambda + p_1}{-\lambda(\lambda^4 + p_3\lambda^3 + p_2\lambda^2 + p_1\lambda + p_0)} + \frac{2q_2\lambda + q_1}{\lambda(q_2\lambda^2 + q_1\lambda)} \right]_{\lambda=i\omega_0} \right\} \\ &= \operatorname{sign} \left\{ -\frac{(p_1 - 3p_3\omega_0^2)(p_3\omega_0^2 - p_1) + 2(p_2 - 2\omega_0^2)(\omega_0^4 - p_2\omega_0^2 + p_0)}{(p_1\omega_0 - p_3\omega_0^3)^2 + (\omega_0^4 - p_2\omega_0^2 + p_0)^2} \right. \\ &\quad \left. - \frac{q_1^2 + 2q_2(q_0 - q_2\omega_0^2)}{(q_0 - q_2\omega_0^2)^2 + (q_1\omega_0)^2} \right\}. \end{aligned}$$

It follows from (14) that

$$(p_1\omega_0 - p_3\omega_0^3)^2 + (\omega_0^4 - p_2\omega_0^2 + p_0)^2 = (q_0 - q_2\omega_0^2)^2 + (q_1\omega_0)^2.$$

Hence, we obtain that

$$\begin{aligned} \operatorname{sign} \left\{ \frac{d(Re\lambda)}{d\tau} \right\}_{\lambda=i\omega_0} &= \operatorname{sign} \left\{ \frac{4\omega_0^6 + 3h_3\omega_0^4 + 2h_2\omega_0^2 + h_1}{(q_2\omega_0^2 - q_0)^2 + (q_1\omega_0)^2} \right\} \\ &> 0. \end{aligned}$$

Therefore, the transversal condition holds and a Hopf bifurcation occurs at $\tau = \tau_0$.

From what has been discussed previously, we obtain the following results.

Theorem 3.2 For model (2)-(3), assume that $\alpha(r_2 + D_{12}) > D_{12}D_{21}$ and (H_1) hold. Then the following results hold true:

- (i) If (H_3) holds, then the equilibrium E_+ is locally asymptotically stable for all $\tau \geq 0$.
- (ii) Let (H_4) hold, then $h(z)$ has at least one positive root z_+ , the equilibrium E_+ of model (2) is locally asymptotically stable for $\tau \in [0, \tau_0)$ and is unstable if $\tau > \tau_0$. Further, model (2) undergoes a Hopf bifurcation at E_+ when $\tau = \tau_0$.

§4 Global stability

Now, we are concerned with the global stability of the positive equilibrium $E_+(x_1^+, x_2^+, y_1^+, y_2^+)$, the predator-extinction equilibrium $E_1(x_1', x_2', 0, 0)$ and the trivial equilibrium $E_0(0, 0, 0, 0)$ of model (2), respectively. The strategy of proofs is to use Lyapunov functionals and LaSalle's invariance principle.

Theorem 4.1 Assume that (H_1) holds, then the positive equilibrium E_+ of model (2) is globally attractive provided

$$(H_5) \quad \underline{x}_1 > \frac{r_1(r_2 + D_{21}) - r_2 D_{12}}{a_{11}(r_2 + D_{21})} - \frac{d_2(r + d_1)}{a_{21}r - md_2(r + d_1)}.$$

Here, $\underline{x}_1$ is defined in Lemma 2.2.

Proof Let $(x_1(t), x_2(t), y_1(t), y_2(t))$ be any positive solution of model (2)-(3). Model (1.2) can be rewritten as

$$\begin{aligned} \dot{x}_1(t) &= \frac{D_{21}}{x_1^+} [-x_2(t)(x_1(t) - x_1^+) + x_1(t)(x_2(t) - x_2^+)] - a_{11}x_1(t)(x_1(t) - x_1^+) \\ &\quad - \frac{a_{12}x_1(t)y_2(t)}{1 + mx_1(t)} + \frac{a_{12}y_2^+}{1 + mx_1^+}x_1(t), \\ \dot{x}_2(t) &= \frac{D_{12}}{x_2^+} [-x_1(t)(x_2(t) - x_2^+) + x_2(t)(x_1(t) - x_1^+)], \\ \dot{y}_1(t) &= \frac{a_{21}x_1(t - \tau)y_2(t - \tau)}{1 + mx_1(t - \tau)} - (r + d_1)y_1(t), \\ \dot{y}_2(t) &= ry_1(t) - d_2y_2(t). \end{aligned} \quad (18)$$

Define

$$\begin{aligned} V_1(t) &= x_1(t) - x_1^+ - x_1^+ \ln \frac{x_1(t)}{x_1^+} + k_1 \left(x_2(t) - x_2^+ - x_2^+ \ln \frac{x_2(t)}{x_2^+} \right) \\ &\quad + c_1 \left(y_1(t) - y_1^+ - y_1^+ \ln \frac{y_1(t)}{y_1^+} \right) + c_2 \left(y_2(t) - y_2^+ - y_2^+ \ln \frac{y_2(t)}{y_2^+} \right). \end{aligned}$$

where $k_1 = D_{21}x_2^+/(D_{12}x_1^+)$, $c_1 = a_{12}(1 + mx_1^+)/a_{21}$, $c_2 = c_1(r + d_1)/r$. Calculating the derivative of $V_1(t)$ along positive solutions of (18), it follows that

$$\begin{aligned} \dot{V}_1(t) &= -\frac{D_{21}}{x_1^+} \left(\sqrt{\frac{x_2(t)}{x_1(t)}}(x_1(t) - x_1^+) - \sqrt{\frac{x_1(t)}{x_2(t)}}(x_2(t) - x_2^+) \right)^2 - a_{11}(x_1(t) - x_1^+)^2 \\ &\quad - a_{12}(1 + mx_1^+) \frac{x_1(t)y_2(t)}{1 + mx_1(t)} + a_{12}(1 + mx_1^+) \frac{x_1(t - \tau)y_2(t - \tau)}{1 + mx_1(t - \tau)} \\ &\quad - a_{12}(1 + mx_1^+) \frac{y_1^+}{y_1(t)} \cdot \frac{x_1(t - \tau)y_2(t - \tau)}{1 + mx_1(t - \tau)} + \frac{a_{12}y_2^+}{1 + mx_1^+} (x_1(t) - x_1^+) \\ &\quad c_1(r + d_1)y_1^+ + c_2d_2y_2^+ - c_2ry_2^+ \frac{y_1(t)}{y_2(t)}. \end{aligned} \quad (19)$$

Define

$$\begin{aligned} V_+(t) &= V_1(t) + \\ &\quad a_{12}(1 + mx_1^+) \int_{t-\tau}^t \left[\frac{x_1(u)y_2(u)}{1 + mx_1(u)} - \frac{x_1^+y_2^+}{1 + mx_1^+} - \frac{x_1^+y_2^+}{1 + mx_1^+} \ln \frac{(1 + mx_1^+)x_2(u)y_2(u)}{x_1^+y_2^+(1 + mx_1(u))} \right] du. \end{aligned} \quad (20)$$

A direct calculation shows that

$$\begin{aligned} \dot{V}_+(t) &= -\frac{D_{21}}{x_1^+} \left(\sqrt{\frac{x_2(t)}{x_1(t)}}(x_1(t) - x_1^+) - \sqrt{\frac{x_1(t)}{x_2(t)}}(x_2(t) - x_2^+) \right)^2 \\ &\quad - a_{12}x_1^+y_2^+ \left[\frac{(1 + mx_1^+)y_1^+x_1(t - \tau)y_2(t - \tau)}{x_1^+y_2^+y_1(t)(1 + mx_1(t - \tau))} - 1 - \ln \frac{(1 + mx_1^+)y_1^+x_1(t - \tau)y_2(t - \tau)}{x_1^+y_2^+y_1(t)(1 + mx_1(t - \tau))} \right] \\ &\quad - a_{12}x_1^+y_2^+ \left[\frac{y_2^+y_1(t)}{y_1^+y_2(t)} - 1 - \ln \frac{y_2^+y_1(t)}{y_1^+y_2(t)} \right] \end{aligned}$$

$$-a_{12}x_1^+y_2^+ \left[\frac{x_1^+(1+mx_1(t))}{x_1(t)(1+mx_1^+)} - 1 - \ln \frac{x_1^+(1+mx_1(t))}{x_1(t)(1+mx_1^+)} \right] \\ - (x_1(t) - x_1^+)^2 \left[a_{11} - \frac{a_{12}y_2^+}{(1+mx_1^+)x_1(t)} \right].$$

Because (H_5) holds, we have $a_{11} > \frac{a_{12}y_2^+}{(1+mx_1^+)x_1(t)}$. Note that the function $g(x) = x - 1 - \ln x$ is always non-negative for any $x > 0$, and $g(x) = 0$ if and only if $x = 1$. Therefore, we have $\dot{V}_+(t) \leq 0$, with equality if and only if $x_1(t) = x_1^+$, $x_2(t) = x_2^+$, $y_1(t) = y_1^+$, $y_2(t) = y_2^+$. Hence, the only invariant set in $M = \{(x_1, x_2, y_1, y_2) : \dot{V}_+(t) = 0\}$ is $\mathcal{M} = \{(x_1^+, x_2^+, y_1^+, y_2^+)\}$. Therefore, the global asymptotic attractive of E_+ follows from LaSalle's invariance principle for delay differential systems (see, for example, [5]). This completes the proof.

Theorem 4.2 Assume that (H_2) holds, then the equilibrium $E_1(x'_1, x'_2, 0, 0)$ of model (2)-(3) is globally asymptotically stable.

Proof By Theorem 3.1, we see that if (H_2) holds, the equilibrium E_1 is locally asymptotically stable for all $\tau \geq 0$. Hence, we only prove that all positive solutions of model (2)-(3) converge to E_1 . Let $(x_1(t), x_2(t), y_1(t), y_2(t))$ be any positive solution of model (2)-(3). For convenience, we rewrite model (1.2) as following

$$\begin{aligned} \dot{x}_1(t) &= \frac{D_{21}}{x'_1} [-x_2(t)(x_1(t) - x'_1) + x_1(t)(x_2(t) - x'_2)] - a_{11}x_1(t)(x_1(t) - x'_1) - \frac{a_{12}x_1(t)y_2(t)}{1+mx_1(t)}, \\ \dot{x}_2(t) &= \frac{D_{12}}{x'_2} [-x_1(t)(x_2(t) - x'_2) + x_2(t)(x_1(t) - x'_1)], \\ \dot{y}_1(t) &= \frac{a_{21}x_1(t-\tau)y_2(t-\tau)}{1+mx_1(t-\tau)} - (r+d_1)y_1(t), \\ \dot{y}_2(t) &= ry_1(t) - d_2y_2(t). \end{aligned} \quad (21)$$

Define

$$V_{21}(t) = x_1(t) - x'_1 - x'_1 \ln \frac{x_1(t)}{x'_1} + k_2 \left(x_2(t) - x'_2 - x'_2 \ln \frac{x_2(t)}{x'_2} \right) + c_3 (y_1(t) + y_2(t)),$$

where $k_2 = D_{21}x'_2/(D_{12}x'_1)$, $c_3 = a_{12}(1+mx'_1)/a_{21}$. Calculating the derivative of $V_{21}(t)$ along positive solutions of model (21), we obtain

$$\begin{aligned} \dot{V}_{21}(t) &= \frac{x_1(t) - x'_1}{x_1(t)} \dot{x}_1(t) + k_2 \frac{x_2(t) - x'_2}{x_2(t)} \dot{x}_2(t) + c_3 (\dot{y}_1(t) + \dot{y}_2(t)) \\ &= -\frac{D_{21}}{x'_1} \left(\sqrt{\frac{x_2(t)}{x_1(t)}} (x_1(t) - x'_1) - \sqrt{\frac{x_1(t)}{x_2(t)}} (x_2(t) - x'_2) \right)^2 - a_{11}(x_1(t) - x'_1)^2 \\ &\quad - a_{12}(1+mx'_1) \frac{x_1(t)y_2(t)}{1+mx_1(t)} + a_{12}(1+mx'_1) \frac{x_1(t-\tau)y_2(t-\tau)}{1+mx_1(t-\tau)} \\ &\quad - c_1 d_1 y_1(t) - (c_1 d_2 - a_{12}x'_1) y_2(t). \end{aligned} \quad (22)$$

Define

$$V_2(t) = V_{21}(t) + a_{12}(1+mx'_1) \int_{t-\tau}^t \frac{x_1(s)y_2(s)}{1+mx_1(s)} ds. \quad (23)$$

A direct calculation shows that

$$\begin{aligned} \dot{V}_2(t) = & -\frac{D_{21}}{x_1'} \left(\sqrt{\frac{x_2(t)}{x_1(t)}}(x_1(t) - x_1') - \sqrt{\frac{x_1(t)}{x_2(t)}}(x_2(t) - x_2') \right)^2 - a_{11}(x_1(t) - x_1')^2 \\ & - c_1 d_1 y_1(t) - (c_1 d_2 - a_{12} x_1') y_2(t). \end{aligned} \quad (24)$$

Hence, it follows from (24) that if (H_2) holds, then $\dot{V}_2(t) \leq 0$ with equality if and only if $x_1(t) = x_1'$, $x_2(t) = x_2'$, $y_1(t) = 0$ and $y_2(t) = 0$. Using a similar argument as that in the proof of Theorem 4.1, we show that the only invariant set in $M = \{(x_1, x_2, y_1, y_2) : \dot{V}_2(t) = 0\}$ is $\mathcal{M} = \{(x_1', x_2', 0, 0)\}$. Accordingly, the global asymptotic stability of E_1 follows from LaSalle's invariant principle for delay differential systems. This completes the proof.

Theorem 4.3 *Let $r_1(r_2 + D_{21}) < r_2 D_{12}$, then the trivial equilibrium $E_1(0, 0, 0, 0)$ of model (2) is globally asymptotically stable.*

Proof By Theorem 3.1, we see that if $r_1(r_2 + D_{21}) < r_2 D_{12}$, E_0 is locally asymptotically stable. Hence, we only prove that all positive solutions of model (2)-(3) converge to E_0 . Let $(x_1(t), x_2(t), y_1(t), y_2(t))$ be any positive solution of model (2)-(3). Define

$$V_0(t) = x_1(t) + \frac{D_{21}}{r_2 + D_{21}} x_2(t) + \frac{a_{12}}{a_{21}} (y_1(t) + y_2(t)) + a_{12} \int_{t-\tau}^t \frac{x_1(u) y_2(u)}{1 + m x_1(u)} du.$$

Calculating the derivative of $V_0(t)$ along positive solutions of model (2), we have

$$\begin{aligned} \dot{V}_0(t) = & \dot{x}_1(t) + \frac{D_{21}}{r_2 + D_{21}} \dot{x}_2(t) + \frac{a_{12}}{a_{21}} (\dot{y}_1(t) + \dot{y}_2(t)) + \frac{a_{12} x_1(t) y_2(t)}{1 + m x_1(t)} - \frac{a_{12} x_1(t - \tau) y_2(t - \tau)}{1 + m x_1(t - \tau)} \\ & - \frac{D_{12} r_2 - r_1(r_2 + D_{21})}{r_2 + D_{21}} x_1(t) - a_{11} x_1^2(t) - \frac{a_{12}}{a_{21}} d_1 y_1(t) - \frac{a_{12}}{a_{21}} d_2 y_2(t). \end{aligned} \quad (25)$$

If $r_1(r_2 + D_{21}) < r_2 D_{12}$, it then follows from (25) that $\dot{V}_0(t) \leq 0$. Clearly, we see from (25) that $\dot{V}_0(t) = 0$ if and only if $x_1(t) = 0$, $x_2(t) = 0$, $y_1(t) = 0$ and $y_2(t) = 0$. Accordingly, the global asymptotic stability of E_0 follows from LaSalle's invariant principle for delay differential systems. This completes the proof.

§5 Numerical simulation

In this section, we give two examples to illustrate the main results in Section 3 and Section 4.

Example 1 In model (2), let $a_{11} = 0.25$, $a_{12} = 1.5$, $a_{21} = 3.2$, $m = 0.55$, $D_{12} = 0.5$, $D_{21} = 0.1$, $r = 2$, $r_1 = 0.25$, $r_2 = 0.5$, $d_1 = 0.2$, $d_2 = 0.2$. It is easy to show that $r_2 D_{12} - r_1(r_2 + D_{21}) = 0.1 > 0$, model (2) has only the trivial equilibrium $E_0(0, 0, 0, 0)$. By Theorem 4.3, we see that the equilibrium E_0 is globally asymptotically stable. Numerical integration can be carried out using the standard MATLAB algorithm. Numerical simulation illustrates the result above (see, Figure 1).

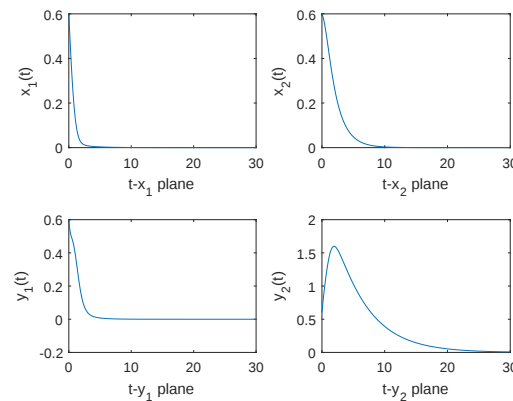


Figure 1. The temporal solution found by numerical integration of model (2) with $\tau = 0.1$ and $(\varphi_1(0), \varphi_2(0), \phi_1(0), \phi_2(0)) = (0.6, 0.6, 0.6, 0.6)$.

Example 2 In model (2), let $a_{11} = 4, a_{12} = 2, a_{21} = 1, m = 0.2, D_{12} = 4, D_{21} = 2, r = 3, r_1 = 2, r_2 = 1, d_1 = 0.2, d_2 = 0.2$. Noting that $r_1(r_2 + D_{21}) - r_2 D_{12} = 2 > 0$, model (2) has a nonnegative boundary equilibrium $E_1(0.1667, 0.2222, 0, 0)$. Clearly, $0 < \frac{r_1(r_2 + D_{21}) - r_2 D_{12}}{a_{11}(r_2 + D_{21})} = 0.1667 < \frac{d_2(r + d_1)}{a_{21}r - m d_2(r + d_1)} = 0.2228$. By Theorem 4.2, we see that the equilibrium E_1 is globally asymptotically stable. Numerical simulation illustrates the result above (see Figure 2).

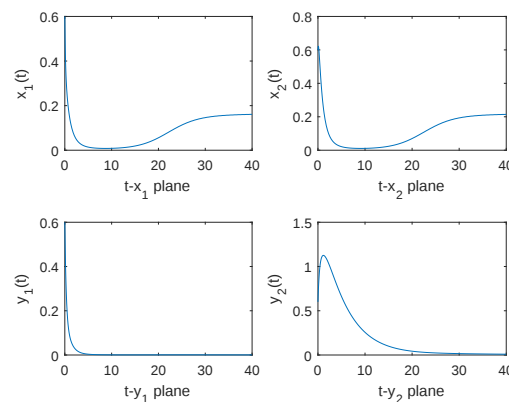


Figure 2. The temporal solution found by numerical integration of model (2) with $\tau = 0.1$ and $(\varphi_1(0), \varphi_2(0), \phi_1(0), \phi_2(0)) = (0.6, 0.6, 0.6, 0.6)$.

Example 3 In model (2), let $a_{11} = 4, a_{12} = 2, a_{21} = 1, m = 0.2, D_{12} = 4, D_{21} = 2, r = 3, r_1 = 2, r_2 = 1, d_1 = 0.2, d_2 = 0.2$.

By calculation, we obtain $\frac{r_1(r_2 + D_{21}) - r_2 D_{12}}{a_{11}(r_2 + D_{21})} = 0.6061 > \frac{d_2(r + d_1)}{a_{21}r - m d_2(r + d_1)} = 0.1112 > 0$, and therefore, the model (2) has a unique positive equilibrium $E_+(0.1112, 0.1011, 0.1501, 1.5010)$. Noting that $0 < 2\alpha - \frac{a_{12}y_2^+}{(1 + m x_1^+)^2} = 2.8029 < \frac{2D_{12}D_{21}}{r_2 + D_{12}} = 3.6364$ and $\tau_0 = 1.6524$. By Theorem

3.2, we see that the equilibrium E_+ is locally asymptotically stable if $0 \leq \tau < \tau_0$ and model (2) undergoes a Hopf bifurcation at E_+ when $\tau = \tau_0$. Numerical simulation illustrates the previous result (see Figures 3 and 4).

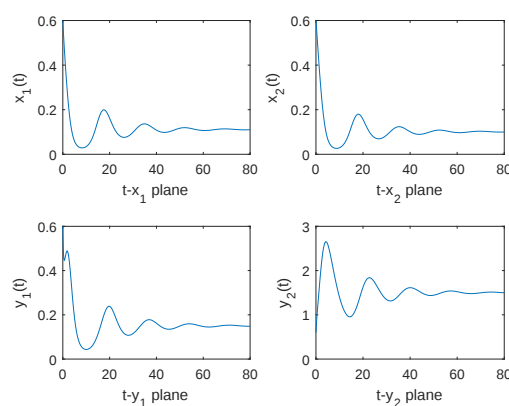


Figure 3. The temporal solution found by numerical integration of model (2) with $\tau = 0.1$ and $(\varphi_1(0), \varphi_2(0), \phi_1(0), \phi_2(0)) = (0.6, 0.6, 0.6, 0.6)$.

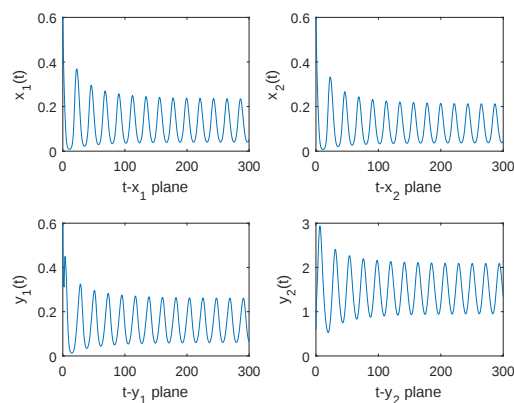


Figure 4. The temporal solution found by numerical integration of model (2) with $\tau = \tau_0$ and $(\varphi_1(0), \varphi_2(0), \phi_1(0), \phi_2(0)) = (0.6, 0.6, 0.6, 0.6)$.

§6 Discussion

In this paper, we have investigated the global dynamics of a delayed predator-prey model with prey dispersal and Holling type-II functional response. By analysing the corresponding characteristic equations, the local stability of each of feasible equilibria has been established.

From the analysis in Sections 3 and 4, if $r_1(r_2 + D_{21}) < r_2D_{12}$, then the trivial equilibrium $E_0(0, 0, 0, 0)$ is globally asymptotically stable. If $r_1(r_2 + D_{21}) > r_2D_{12}$ and $\frac{r_1(r_2 + D_{21}) - r_2D_{12}}{a_{11}(r_2 + D_{21})} < \frac{d_2(r + d_1)}{a_{21}r - md_2(r + d_1)}$ hold, then the equilibrium $E_1(x'_1, x'_2, 0, 0)$ is globally asymptotically stable. If $x_1 > \frac{r_1(r_2 + D_{21}) - r_2D_{12}}{a_{11}(r_2 + D_{21})} - \frac{d_2(r + d_1)}{a_{21}r - md_2(r + d_1)} > 0$ holds, then the positive equilibrium E_+ is globally attractive. At the positive equilibrium, a threshold τ_0 for the time delay is identified such that below it, the equilibrium is locally asymptotically stable, but if the delay is greater than the threshold, sustained oscillation arise.

Declarations

Conflict of interest The authors declare no conflict of interest.

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