



On a Predator–Prey System with Digestion Delay and Anti-predation Strategy

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Abstract

Predator–prey interactions are among the most complicated interactions between biological species, in which there may be both direct effect (through predation) and indirect effect (e.g., fear effect). In the literature, the indirect effect has been largely missing in predator–prey models, until some recent works. Based on the recent work (Wang et al. in *J Math Biol* 73:1179–1204, 2016) where a fear effect is considered in an ODE model as a cost, in this paper, we also consider a benefit from the anti-predation response in addition to the cost, as well as a time delay in the transfer of biomass from the prey to the predator after predation. This results in a system of delay differential equations (DDEs). By analyzing this nonlinear DDE system, we obtain some insights on how the anti-predation response level (indirect effect) and the biomass transfer delay jointly affect the population dynamics; particularly we show how the nonlinearity in the predation term mediated by the fear effect affects the long term dynamics of the model system. We also perform some numerical computations and simulations to demonstrate our results. These results seem to suggest a need to revisit existing predator–prey models in the literature by incorporating the indirect effect and biomass transfer delay.

Keywords Predator–prey · Specialist predator · Digestion delay · Anti-predation strategy · Stability · Hopf bifurcation

Mathematics Subject Classification 34K13 · 34K20 · 37N25 · 92B05

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1 Introduction

Predator–prey system is one of the most important topics in mathematical biology. Since the early pinioning model by Lotka (1920, 1925) and Volterra (1926, 1931), there has been a vast and rich literature on the models for predator–prey interactions. Without considering spatial and age structure, a predator–prey model can be generally described by a system of ordinary differential equations of the form

$$\begin{cases} \frac{du}{dt} = f_1(u(t)) - p(u(t), v(t))v(t), \\ \frac{dv}{dt} = f_2(v(t)) + cp(u(t), v(t))v(t), \end{cases} \quad (1.1)$$

where $u(t)$ and $v(t)$ are the population densities of the prey and predator, respectively, under consideration. Here, $f_1(u)$ is the growth rate of the prey population in the absence of the predator, and $f_2(v)$ is the growth rate of the predator population in the absence of the prey; $p(u, v)$ is referred to as the functional response which accounts for the predation rate and biomass transfer after predation, from the prey to the predator, and the constant c explains the efficiency in biomass transfer. For some frequently used forms of the functional response $p(u, v)$, see, e.g., Arditi and Ginzburg (1989), Holling (1965) and Rosenzweig and MacArthur (1963) for some earlier works and Abrams and Ginzburg (2000), Jeschke et al. (2002) and Skalski and Gilliam (2001) for some more recent works.

Predator–prey ODE models of the form (1.1) only consider the direct effect between the predator and prey, reflected by the predation term. In the real world however, presence of predators also has indirect effects on prey population, in various ways. For example, according to a recent field experimental study on song sparrow population by Zanette et al. (2011), the perception of predation risk can reduce the number of prey's offspring by as much as 40%, even without any direct predation. This evidence showed that the indirect effect can be as significant as direct predation for some species, sometimes even more significant. This phenomenon has attracted some biologists, both theoretical and experimental, and there have been some biological hypotheses proposed on such effects and some field experiments reported confirming such effects. See, e.g., Creel and Christianson (2008), Cresswell (2011), Lima (1998, 2009), Zanette et al. (2011) and the references therein.

The aforementioned preliminary biological studies strongly suggest that the neglect of indirect effect due to fear in the traditional predator–prey models, such as models of the form of (1.1), may not be reasonable for many species. This means that the existing mathematical models for predator–prey interactions need to be modified to include the fear effect that is indirect. Recently, Wang et al. (2016) and Wang and Zou (2017, 2018) made some initial efforts along this direction by an ordinary differential equation (ODE) model, a delay differential equation (DDE) model, and a partial differential equation (PDE) model, respectively, to address different aspects of the anti-predation responses of the prey caused by the fear. This work is mainly motivated by Wang et al. (2016) which proposed the following ODE model

$$\begin{cases} \frac{du}{dt} = f(k, v(t)) r_0 u(t) - d u(t) - a u^2(t) - g(u(t)) v(t), \\ \frac{dv}{dt} = c g(u(t)) v(t) - m v(t), \end{cases} \tag{1.2}$$

where u is the population density of prey species, v is the population density of predator species, r_0 is the reproduction rate of prey in the absence of predator, d is the natural (density independent) death rate and the term $au^2 = (au)u$ reflects the crowding effect with au accounting for density dependent death rate, c is the biomass transform efficiency constant. The function $g(u)$ is the functional response which is assumed to depend on the prey population only. Here, the function $f(k, v)$ is incorporated into the model to account for the prey’s anti-predation response with the positive parameter k measuring the response level due to the prey’s perceived fear, and hence, $f(k, v)$ is decreasing in k and v . By analyzing this model, Wang et al. (2016) obtained some interesting results on how the anti-predation response affects the population dynamics of this predator–prey model.

Obviously, in (1.2) *only the cost* of the anti-predation response in prey’s reproduction is considered, but the benefits of such responses are ignored. However, there should be some *benefits*, as the prey’s anti-predation response will obviously decrease the chance of the prey being caught by predators. This suggests a replacement of $g(u)$ in (1.2) by $g(k, u)$ which is decreasing in the response level parameter k . Moreover, in (1.2) it is assumed that the biomass transfer from prey to predator after predation is instantaneous. But in reality, such transfer takes time [see, e.g., Cushing (1977), Wangersky and Cunningham (1957), Li and Li (2012), Xu (2011) and the references therein]. With the above observations of the mentioned two drawbacks in (1.2), we propose, in this paper, the following modification:

$$\begin{cases} \frac{du}{dt} = f(k, v(t)) r_0 u(t) - d u(t) - a u^2(t) - g(k, u(t)) v(t), \\ \frac{dv}{dt} = c g(k, u(t - \tau)) v(t - \tau) - m v(t). \end{cases} \tag{1.3}$$

where $\tau \geq 0$ is the average time needed for biomass transfer after predation from prey to predator. Here, by the meanings of the parameter k , and the nonnegative functions $f(k, v)$ and $g(k, u)$, it is reasonable to pose the following assumptions:

$$\begin{cases} f(0, v) = 1, f(k, 0) = 1, \frac{\partial f}{\partial k} < 0, \frac{\partial f}{\partial v} < 0, \\ \lim_{k \rightarrow \infty} f(k, v) = 0, \lim_{v \rightarrow \infty} f(k, v) = 0, \\ g(k, 0) = 0, \frac{\partial g}{\partial k} < 0, \\ \lim_{k \rightarrow \infty} g(k, u) = 0. \end{cases} \tag{1.4}$$

This model is a system of delay differential equations and hence is of infinite dimension. In the rest of the paper, we will analyze this infinite dimensional dynamical system. To make the analysis more explicit and for convenience of comparison, we will follow Wang et al. (2016) to consider two particular forms for the functional response g : (i) Holling Type I (linear) and (ii) Holling type II. The main concern is

the longtime dynamics, and thus, we will perform stability analysis by employing the stability theory and methods for delay differential equations. For the linear functional response mediated by the prey's anti-predation response, we find that there are two thresholds for the anti-predation strategy k : when k is large, the prey species can always survive from the predation and predator species will die out; an intermediate value of k will lead to a stable coexistence equilibrium; when k is further decreased to a very small level, the coexistence equilibrium becomes unstable and a Hopf bifurcation occurs, leading to the occurrence of a stable periodic solution. This is in strong contrast to the results for (1.2) in Wang et al. (2016), where there is no Hopf bifurcation when the functional response is linear. For the Holling Type II functional response mediated by the prey's anti-predation response, we do similar analysis and the analytic results reveal how the cost and benefit of the prey's anti-predation response interplay to affect the population dynamics. We also perform some numerical simulations to confirm our analytic results, and to explore, more visually, how the anti-predation strategies and the biomass transfer delay will impact the population dynamics.

The remainder of this paper is organized as follows. In Sect. 2, we will address the well-posedness of the model system (1.3) including the existence and uniqueness of solution to (1.3) with biologically meaningful initial conditions, the positivity and boundedness of the solution. In Sect. 3, we investigate the existence and stability of equilibria. To this end, we consider two particular forms for the functional response g , with Sect. 3.1 dealing with the linear functional response mediated by the prey's anti-predation response, and Sect. 3.2 covering the case of Holling Type II functional response. In Sect. 4, we present some numeric results to confirm and demonstrate our analytic results. In Sect. 5, we summarize our main results and discuss their biological implications. We also discuss some possible future projects along this direction of fear effect in predator–prey interactions.

2 Well-Posedness of the Model

The model (1.3) is a system of delay differential equations for which an initial condition needs to be specified on the interval $[-\tau, 0]$. Considering the biological meanings of the variables u and v , nonnegativity is required, motivating the following initial condition

$$\begin{cases} u(\theta) = u_0(\theta), \\ v(\theta) = v_0(\theta), \end{cases} \quad (2.1)$$

where $(u_0(\theta), v_0(\theta)) \in \mathcal{C}([-\tau, 0], \mathcal{R}_+^2)$.

By the fundamental theory of functional differential equations (see, e.g., Hale and Lunel 1993), the system (1.3)–(2.1) has a unique solution $(u(t), v(t)) = (u(t, u_0, v_0), v(t, u_0, v_0))$ which exists in a maximal interval $[0, T_m)$. We now prove the well-posedness of (1.3) in the sense that $u(t) \geq 0$ and $v(t) \geq 0$ for all $t \in [0, T_m)$, and $T_m = \infty$ meaning that the solution exists globally. Indeed, the nonnegativity of $u(t)$ and $v(t)$ is a direct result of Theorem 2.1 in Smith (1995). To prove that $T_m = \infty$, by the extension theory for delay differential equations (see, e.g., Hale and Lunel

1993), we just need to establish a priori boundedness for the solution. To this end, we consider $W(t, \tau) = u(t - \tau) + v(t)/c$. Simple calculations lead to

$$\begin{aligned} W'(t) &= r_0 u(t - \tau) f(k, v(t - \tau)) - d(u(t - \tau)) - a u^2(t - \tau) - \frac{m}{c} v(t) \\ &\leq (r_0 - d) u(t - \tau) - \frac{m}{c} v(t) - a u^2(t - \tau) \\ &\leq r_0 u(t - \tau) - a u^2(t - \tau) - \min\left(d, \frac{m}{c}\right) W \\ &\leq \frac{r_0^2}{4a} - \min\left(d, \frac{m}{c}\right) W =: \frac{r_0^2}{4a} - \mu W, \end{aligned}$$

where $\mu = \min(d, m/c)$. This implies that $\limsup_{t \rightarrow \infty} W(t) \leq r_0^2/(4a\mu)$, concluding the boundedness of $u(t - \tau) + v(t)/c$. Since we have already shown that $u(t)$ and $v(t)$ are nonnegative, $u(t)$ and $v(t)$ are also bounded.

Combining the above, we have proved the well-posedness of (1.3)–(2.1) as stated in the following theorem.

Theorem 2.1 *Initial value problem (1.3)–(2.1) has a unique solution which exists for all $t \geq 0$ and is bounded in $[0, \infty)$.*

3 Equilibria and Their Stability

In this section, we investigate the longtime behavior of solutions to (1.3)–(2.1). To be more concrete, we will consider two particular forms for the functional response $g(k, u)$: (i) linear; (ii) Holling Type II.

3.1 Model with Linear Functional Response

In this subsection, we consider $g(k, u)$ being linear in u , that is, $g(k, u) = \rho(k)u$. With this choice, (1.3) becomes

$$\begin{aligned} \frac{du}{dt} &= r_0 u(t) f(k, v(t)) - d u(t) - a u^2(t) - \rho(k) u(t) v(t), \\ \frac{dv}{dt} &= c \rho(k) u(t - \tau) v(t - \tau) - m v(t), \end{aligned} \tag{3.1}$$

The dependence of $g(k, u)$ on k assumed in (1.4) naturally poses the following condition on $\rho(k)$:

$$\begin{cases} \rho(k) \text{ is a decreasing function with respect to } k, \\ \lim_{k \rightarrow \infty} \rho(k) = 0. \end{cases} \tag{3.2}$$

System (3.1) has three possible equilibrium solutions. The trivial equilibrium $E_0 = (0, 0)$ always exists. When $r_0 > d$, there exists a predator-free equilibrium $E_u =$

$(\frac{r_0-d}{a}, 0)$. A unique positive (coexistence) equilibrium exists when

$$r_0 > \frac{am}{c\rho(k)} + d. \quad (3.3)$$

The positive equilibrium is denoted by $E^+ = (\bar{u}, \bar{v})$ with \bar{u} and \bar{v} satisfying

$$\begin{aligned} \bar{u} &= \frac{m}{c\rho(k)}, \\ r_0 f(k, \bar{v}) - d - a\bar{u} - \rho(k)\bar{v} &= 0. \end{aligned} \quad (3.4)$$

Remark 3.1 Notice that $\rho(k)$ is a decreasing function and $\lim_{k \rightarrow \infty} \rho(k) = 0$. Therefore, for any set of other parameters in (3.1), there exists a critical value $k^* \geq 0$, such that, when $k > k^*$, the condition (3.3) fails, implying that there is no positive solution when $k > k^*$.

3.1.1 Local Stability and Hopf Bifurcation

In this section, we study the local stability for each of the equilibrium solution. The linearization of (3.1) near an equilibrium (u^*, v^*) is given by

$$\begin{aligned} \frac{du}{dt} &= [r_0 f(k, v^*) - d - 2au^*]u(t) - \rho(k)u^*v(t) - \rho(k)v^*u(t) \\ &\quad + \left(r_0 u^* \frac{\partial f}{\partial v} \Big|_{v^*} \right) v(t), \\ \frac{dv}{dt} &= c\rho(k)u^*v(t-\tau) + c\rho(k)v^*u(t-\tau) - mv(t), \end{aligned} \quad (3.5)$$

where (u^*, v^*) denotes the corresponding equilibrium.

The characteristic equation of (3.5) at $E_0 = (0, 0)$ is

$$(r_0 - d - \lambda)(-m - \lambda) = 0. \quad (3.6)$$

Therefore, if $r_0 < d$, E_0 is locally asymptotically stable. If $r_0 > d$, E_0 is unstable.

Now if $r_0 > d$, there exists a predator-free (semi-trivial) equilibrium $E_u = (\frac{r_0-d}{a}, 0)$, the characteristic equation of which is given by

$$(-r_0 + d - \lambda) \left[c\rho(k) e^{-\lambda\tau} \frac{r_0 - d}{a} - m - \lambda \right] = 0. \quad (3.7)$$

Since $r_0 - d > 0$, $-r_0 + d - \lambda = 0$ only has a negative root. Other roots are determined by the equation

$$c\rho(k) e^{-\lambda\tau} \frac{r_0 - d}{a} - m - \lambda = 0. \quad (3.8)$$

This transcendental equation is in the form of the Hayes equation, and hence, the existing results for this equation can be employed. Note that $c \rho(k) \frac{r_0-d}{a} > 0 > -m$ provided that $r_0 > d$, by Hayes (1950) (also see Hale and Lunel 1993 or Smith 2010), E_u is locally asymptotically stable if $c \rho(k) \frac{r_0-d}{a} - m < 0$ and E_u is unstable if $c \rho(k) \frac{r_0-d}{a} - m > 0$. In other words, $r_0 < \frac{am}{c \rho(k)} + d$ [reverse of (3.3)] is a necessary and sufficient condition for E_u to be locally asymptotically stable.

When condition (3.3) holds, there is a unique positive equilibrium $E^+ = (\bar{u}, \bar{v})$, at which, the corresponding characteristic equation reads

$$\lambda^2 + (a \bar{u} + m)\lambda + m a \bar{u} + e^{-\lambda \tau} \left[-m \lambda + m \rho(k) \bar{v} - r_0 m \bar{v} \frac{\partial f}{\partial v} \Big|_{\bar{v}} - a m \bar{u} \right] = 0. \tag{3.9}$$

When $\tau = 0$, since $a \bar{u} > 0$ and $m \rho(k) \bar{v} - r_0 m \bar{v} \frac{\partial f}{\partial v} \Big|_{\bar{v}} > 0$, by the Routh–Hurwitz criterion, all roots of the resulting quadratic equation have negative real parts. Now, we check if pure imaginary roots are possible for $\tau > 0$. Plugging $\lambda = \omega i$ ($\omega > 0$) into (3.8) and separating the real and imaginary parts, we obtain

$$\begin{cases} m \omega \sin(\omega \tau) - \left[m \rho(k) \bar{v} - r_0 m \bar{v} \frac{\partial f}{\partial v} \Big|_{\bar{v}} - a m \bar{u} \right] \cos(\tau \omega) = -\omega^2 + m a \bar{u}, \\ m \omega \cos(\omega \tau) + \left[m \rho(k) \bar{v} - r_0 m \bar{v} \frac{\partial f}{\partial v} \Big|_{\bar{v}} - a m \bar{u} \right] \sin(\tau \omega) = (a \bar{u} + m)\omega, \end{cases} \tag{3.10}$$

By eliminating the trigonometric functions in (3.10), we obtain the following equation for $\omega > 0$:

$$\omega^4 + (p_1^2 - q_1^2 - 2p_0)\omega^2 + p_0^2 - q_0^2 = 0 \tag{3.11}$$

where $p_0 = m a \bar{u}$, $p_1 = a \bar{u} + m$, $q_0 = m \rho(k) \bar{v} - r_0 m \bar{v} \frac{\partial f}{\partial v} \Big|_{\bar{v}} - a m \bar{u}$ and $q_1 = -m$. Simple calculation shows $p_1^2 - q_1^2 - 2p_0 = (a\bar{u})^2 > 0$. Now, we distinguish two exclusive cases: (A) $p_0^2 > q_0^2$; and (B) $p_0^2 < q_0^2$.

For (A), Eq. (3.11) has no positive solution, implying that (3.9) can not have pure imaginary roots for all $\tau > 0$. Therefore, the coexistence equilibrium is locally asymptotically stable for all $\tau > 0$.

For (B), (3.11) has a unique positive root

$$\omega_0 = \left(\frac{-a^2 \bar{u}^2 + \sqrt{a^4 \bar{u}^4 - 4 p_0^4 + 4 q_0^4}}{2} \right)^{\frac{1}{2}}. \tag{3.12}$$

Plugging $\omega = \omega_0$ into (3.10) and solving the resulting equation for $\sin \omega_0 \tau$ and $\cos \omega_0 \tau$, we obtain

$$\begin{cases} \cos(\omega_0 \tau) = \frac{q_0 \omega_0^2 - q_0 p_0 - p_1 q_1 \omega_0^2}{q_0^2 + q_1^2 \omega_0^2} =: P_0 \\ \sin(\omega_0 \tau) = \frac{p_1 \omega_0 + q_1 \omega_0 P_0}{q_0} =: Q_0 \end{cases} \quad (3.13)$$

From this, we obtain a sequence of critical values for the delay parameter τ :

$$\tau_n = \begin{cases} \frac{1}{\omega_0} \arccos \frac{q_0 \omega_0^2 - q_0 p_0 - p_1 q_1 \omega_0^2}{q_0^2 + q_1^2 \omega_0^2} + \frac{2n\pi}{\omega_0}, & n = 0, 1, \dots, \text{ if } Q_0 > 0; \\ \frac{1}{\omega_0} \left[2\pi - \arccos \frac{q_0 \omega_0^2 - q_0 p_0 - p_1 q_1 \omega_0^2}{q_0^2 + q_1^2 \omega_0^2} \right] + \frac{2n\pi}{\omega_0}, & n = 0, 1, \dots, \text{ if } Q_0 < 0. \end{cases} \quad (3.14)$$

Therefore, in this case, the coexistence equilibrium is locally asymptotically stable when $\tau < \tau_0$. At $\tau = \tau_0$, (3.8) has a pair of pure imaginary roots $\pm i\omega_0$. We now verify the transversality condition at $\tau = \tau_0$. We claim that

$$\left. \frac{d(\Re(\lambda))}{d\tau} \right|_{\tau=\tau_0} > 0. \quad (3.15)$$

Indeed, differentiating Eq. (3.9) with respect to τ , we obtain

$$\left(\frac{d\lambda}{d\tau} \right)^{-1} = \frac{2\lambda + p_1 + q_1 e^{-\lambda\tau}}{e^{-\lambda\tau} \lambda(q_1 \lambda + q_0)} - \frac{\tau}{\lambda}. \quad (3.16)$$

Thus, at $\tau = \tau_0$ ($\lambda = i\omega_0$), we have

$$\begin{aligned} \operatorname{sgn} \left(\left. \frac{d\Re(\lambda)}{d\tau} \right|_{\tau=\tau_0} \right) &= \operatorname{sgn} \left(\Re \left. \frac{d(\lambda)}{d\tau} \right|_{\tau=\tau_0} \right) = \operatorname{sgn} \left(\Re \left(\left. \frac{d(\lambda)}{d\tau} \right|_{\tau=\tau_0} \right)^{-1} \right) \\ &= \operatorname{sgn} \left(\Re \left[\left. \frac{2\lambda + p_1 + q_1 e^{-\lambda\tau}}{e^{-\lambda\tau} \lambda(q_1 \lambda + q_0)} - \frac{\tau}{\lambda} \right] \right|_{\lambda=i\omega_0} \right) \\ &= \operatorname{sgn} \left(\frac{-\omega_0(p_1 q_1 - 2q_0) \cos(\omega_0 \tau) + (2q_1 \omega_0^2 + p_1 q_0) \sin(\omega_0 \tau) - q_1^2 \omega_0}{\omega_0(q_1^2 \omega_0^2 + q_0^2)} \right). \end{aligned} \quad (3.17)$$

Plugging (3.13) into (3.17) and simplifying, we obtain

$$\Re \left(\left. \frac{d(\lambda)}{d\tau} \right|_{\tau=\tau_0} \right)^{-1} = \frac{p_1^2 - q_1^2 - 2p_0 + 2\omega^2}{q_1^2 \omega_0^2 + q_0^2} = \frac{a^2 \bar{u}^2 + 2\omega^2}{q_1^2 \omega_0^2 + q_0^2} > 0, \quad (3.18)$$

implying

$$\left. \frac{d(\Re(\lambda))}{d\tau} \right|_{\tau=\tau_0} > 0.$$

This verifies the transversality condition at $\tau = \tau_0$. Therefore, when τ increases to pass τ_0 , Hopf bifurcation occurs.

Summarizing the above analysis, we have proved the following theorem.

Theorem 3.1 *For model system (3.1), the following results hold.*

- (i) *When $r_0 < d$, there is only the trivial equilibrium $E_0 = (0, 0)$ and it is locally asymptotically stable.*
- (ii) *When $d < r_0 < d + \frac{am}{c\rho(k)}$, then $E_0 = (0, 0)$ becomes unstable and there is the predator-free equilibrium $E_u = \left(\frac{r_0-d}{a}, 0\right)$ which is locally asymptotically stable.*
- (iii) *When $r_0 > d + \frac{am}{c\rho(k)}$, both E_0 and E_u are unstable and there is a third equilibrium, the positive (or coexistence) equilibrium E^+ . Moreover,*
 - (iii)-1 *if $p_0 > q_0$, then $E^+ = (\bar{u}, \bar{v})$ is locally asymptotically stable for all $\tau > 0$;*
 - (iii)-2 *if $p_0 < q_0$, there is a $\tau_0 > 0$ such that $E^+ = (\bar{u}, \bar{v})$ is locally asymptotically stable when $0 < \tau < \tau_0$ and is unstable when $\tau > \tau_0$. Furthermore, there is a Hopf bifurcation of E^+ at $\tau = \tau_0$, leading to the occurrence of periodic solutions.*

Remark 3.2 By Theorem (3.2) in Wang et al. (2016), we know that the ODE model (1.2) with the linear functional response can never have periodic solutions. But in our modified model (3.1) with both cost and benefit of the anti-predation response and biomass transfer delay incorporated, even for the linear functional response, within certain range of other parameters and time delay, the stability of the coexistence equilibrium can be destroyed, leading to the occurrence of periodic solutions through Hopf bifurcation. Although we used the delay τ as the bifurcation parameter, we can also use an alternative parameter as the bifurcation parameter. For example, if we use k as bifurcation parameter, we can also confirm Hopf bifurcation when k passes some critical value. We will discuss this in more detail in Sect. 5.

3.1.2 Global Stability of the Boundary Equilibria E_0 and E_u

Theorem 3.1-(i) and (ii) established the local asymptotical stability of E_0 and E_u , respectively. In this subsection, we show that E_0 and E_u are actually globally asymptotically stable under the respective condition.

Theorem 3.2 *When $r_0 < d$, there is only one trivial equilibrium $E_0 = (0, 0)$ and it is globally asymptotically stable.*

Proof Consider the Lyapunov functional $V(t) = u(t) + \frac{v(t)}{c} + \rho(k) \int_{t-\tau}^t u(s) v(s) ds$. Calculating the derivative of V along the trajectory of (3.1) yields

$$\dot{V} = r_0 u(t) f(k, v(t)) - d u(t) - a u^2(t) - \frac{m v(t)}{c}. \tag{3.19}$$

Therefore, $\dot{V} \leq 0$ provided $r_0 < d$ [note that $f(k, v(t)) \leq 1$ by (1.4)]. $\dot{V} = 0$ if and only if $u(t) = v(t) = 0$. Thus, $u(t) \rightarrow 0$ and $v(t) \rightarrow 0$ as $t \rightarrow \infty$, implying that $E_0 = (0, 0)$ is globally asymptotically stable. \square

Theorem 3.3 When $d < r_0 < d + \frac{am}{c\rho(k)}$, $E_u = \left(\frac{r_0-d}{a}, 0\right)$ is globally asymptotically stable.

Proof Note that

$$\begin{aligned}\frac{du}{dt} &= r_0 u(t) f(k, v(t)) - d u(t) - a u^2(t) - \rho(k) u(t) v(t) \\ &\leq r_0 u(t) - d u(t) - a u^2(t)\end{aligned}$$

since $f(k, v(t)) \leq 1$. By the property of the logistic equation and the comparison theorem, for any $\epsilon > 0$, there exist a $T = T(\epsilon) > 0$, such that $u(t) < \frac{r_0-d}{a} + \epsilon$ when $t > T$. Then, for $t > T + \tau$, the DDE for $v(t)$ satisfies

$$\begin{aligned}\frac{dv}{dt} &= c \rho(k) u(t - \tau) v(t - \tau) - m v(t) \\ &< c \rho(k) \left(\frac{r_0-d}{a} + \epsilon\right) v(t - \tau) - m v(t).\end{aligned}\quad (3.20)$$

This establishes the following comparison (from above) equation for the variable $v(t)$

$$\frac{dx}{dt} = c \rho(k) \left(\frac{r_0-d}{a} + \epsilon\right) x(t - \tau) - m x(t).\quad (3.21)$$

Since $r_0 < d + \frac{am}{c\rho(k)}$ and ϵ is arbitrary, we can choose $\epsilon < \frac{m}{c\rho(k)} - \frac{r_0-d}{a}$ so that $c \rho(k) \left(\frac{r_0-d}{a} + \epsilon\right) - m < 0$ and $c \rho(k) \left(\frac{r_0-d}{a} + \epsilon\right) > 0 > -m$. For such chosen ϵ , by Theorem 4.7 in Smith (2010), the trivial solution $x = 0$ of (3.21) is globally asymptotically stable, meaning that every solution $x(t)$ of (3.21) satisfies $x(t) \rightarrow 0$ as $t \rightarrow \infty$. Since (3.21) is linear and cooperative, by (3.20) and the comparison theorem [see, e.g., Theorem 4.1 in Smith (1995)], we have $0 \leq v(t) \leq x(t)$, implying that $v(t) \rightarrow 0$ as $t \rightarrow \infty$. Now by the theory of asymptotically autonomous systems in Castillo-Chavez and Thieme (1995), the behavior of u is governed by the limiting equation

$$\frac{du}{dt} = r_0 u(t) - d u(t) - a u^2(t).$$

By the result on a logistic equation, we then conclude that $u(t) \rightarrow \frac{r_0-d}{a}$ as $t \rightarrow \infty$. Therefore, we have proved that $E_u = \left(\frac{r_0-d}{a}, 0\right)$ is globally asymptotically stable. \square

3.2 Model with the Holling Type II Functional Response

In this subsection, we study the model system (1.3) with Holling Type II functional response

$$g(u(t), k) = \rho(k) \frac{p u(t)}{1 + q u(t)}. \tag{3.22}$$

To make the model more mathematically tractable, in this subsection we also choose some particular forms for the functions $\rho(k)$ and $f(v, k)$ that represent the fear effect through the response level parameter k as below:

$$\rho(k) = \frac{1}{1 + c_1 k}, \quad f(v(t), k) = \frac{1}{1 + c_2 k v(t)}. \tag{3.23}$$

With the above adoptions, model (1.3) becomes

$$\begin{cases} \frac{du}{dt} = \frac{r_0 u(t)}{1 + c_2 k v(t)} - d u(t) - a u^2(t) - \frac{p u(t) v(t)}{1 + q u(t)} \cdot \frac{1}{1 + c_1 k}, \\ \frac{dv}{dt} = \frac{c}{1 + c_1 k} \cdot \frac{p u(t - \tau) v(t - \tau)}{1 + q u(t - \tau)} - m v(t), \end{cases} \tag{3.24}$$

Here, we introduce two constants c_1 and c_2 to describe the decreasing rate of reproduction and predation, respectively, with respect to the response level k .

This system also has three possible equilibrium solutions. The trivial equilibrium $E_0 = (0, 0)$ always exists. When $r_0 > d$, there exists the predator-free equilibrium $E_u = (\frac{r_0 - d}{a}, 0)$. A positive (coexistence) equilibrium is determined by solving the system

$$\begin{cases} 0 = \frac{r_0}{1 + c_2 k \bar{v}} - d - a \bar{u} - \frac{p \bar{v}}{1 + q \bar{u}} \cdot \frac{1}{1 + c_1 k}, \\ 0 = \frac{c}{1 + c_1 k} \cdot \frac{p \bar{u}}{1 + q \bar{u}} - m. \end{cases} \tag{3.25}$$

The second equation does not contain variable v , and it has a positive solution for u if and only if

$$c p > m q(1 + c_1 k), \tag{3.26}$$

and the solution is given by

$$\bar{u} = \frac{m(1 + c_1 k)}{c p - m q(1 + c_1 k)}.$$

Plugging this \bar{u} into the first equation in (3.25) gives the following quadratic equation for the variable v :

$$a_2 v^2 + a_1 v + a_0 = 0 \tag{3.27}$$

where

$$\begin{cases} a_2 = c_2 k p, \\ a_1 = p + (d + a \bar{u})(1 + q \bar{u})(1 + c_1 k)c_1 k, \\ a_0 = (1 + q \bar{u})(1 + c_1 k)(d + a \bar{u} - r_0). \end{cases}$$

Note that under (3.26), both a_1 and a_2 are positive, and $a_0 < 0$ if and only if $d + a\bar{u} - r_0 < 0$ which is equivalent to

$$\frac{m(1 + c_1 k)}{c p - m q(1 + c_1 k)} < \frac{r_0 - d}{a}. \quad (3.28)$$

By the property of quadratic functions, we conclude that (3.27) has a positive solution \bar{v} if and only if (3.28) holds. Summarizing the above, when $r_0 > d$, there exists a unique positive equilibrium (\bar{u}, \bar{v}) if and only if

$$0 < \frac{m(1 + c_1 k)}{c p - m q(1 + c_1 k)} < \frac{r_0 - d}{a}. \quad (3.29)$$

3.2.1 Local Stability and Hopf Bifurcation

In this subsection, we study the local stability for each of the equilibrium solutions. The linearization of (3.24) at an equilibrium (u^*, v^*) is given by

$$\begin{pmatrix} \frac{du}{dt} \\ \frac{dv}{dt} \end{pmatrix} = \begin{pmatrix} J_{11} & J_{12} \\ 0 & -m \end{pmatrix} \begin{pmatrix} u(t) \\ v(t) \end{pmatrix} + \begin{pmatrix} 0 & 0 \\ K_{21} & K_{22} \end{pmatrix} \begin{pmatrix} u(t - \tau) \\ v(t - \tau) \end{pmatrix} \quad (3.30)$$

where

$$\begin{aligned} J_{11} &= \frac{r_0}{1 + c_2 k v^*} - d - 2 a u^* - \frac{p v^*}{(1 + c_1 k)(1 + q u^*)^2}, \\ J_{12} &= -\frac{c_2 k r_0 u^*}{(1 + c_2 k v^*)^2} - \frac{p u^*}{(1 + c_1 k)(1 + q u^*)}, \\ K_{21} &= \frac{c p v^*}{(1 + c_1 k)(1 + q u^*)^2}, \\ K_{22} &= \frac{c p u^*}{(1 + c_1 k)(1 + q u^*)}. \end{aligned}$$

From (3.30), we can derive the characteristic equation as

$$(\lambda - J_{11})(\lambda + m - K_{22}e^{-\tau\lambda}) - J_{12} K_{21}e^{-\tau\lambda} = 0. \quad (3.31)$$

At $E_0 = (0, 0)$, $J_{11} = r_0 - d$, $J_{12} = J_{21} = K_{12} = K_{22} = 0$, and hence, the characteristic equation of (3.31) becomes

$$(\lambda - r_0 + d)(\lambda + m) = 0.$$

Therefore, if $r_0 < d$, E_0 is locally asymptotically stable. If $r_0 > d$, E_0 is unstable.

Now if $r_0 > d$, there exists the predator-free (semi-trivial) equilibrium $E_u = (\frac{r_0-d}{a}, 0)$, at which the characteristic equation is given by

$$(\lambda - d + r_0) \left(\lambda + m - \frac{c p \hat{u}}{(1 + c_1 k)(1 + q \hat{u})} e^{-\tau \lambda} \right) = 0 \tag{3.32}$$

where $\hat{u} = \frac{r_0-d}{a}$. Since $r_0 - d > 0$, $\lambda - d + r_0 = 0$ only has a negative root. Other roots of (3.32) are determined by the equation

$$\lambda + m - \frac{c p \hat{u}}{(1 + c_1 k)(1 + q \hat{u})} e^{-\tau \lambda} = 0. \tag{3.33}$$

Noting that $\frac{c p \hat{u}}{(1+c_1 k)(1+q \hat{u})} > 0 > -m$, again by the results for the Hayes equation given in Hayes (1950) (also see Hale and Lunel 1993 or Smith 2010), E_u is locally asymptotically stable if

$$\frac{c p \hat{u}}{(1 + c_1 k)(1 + q \hat{u})} - m < 0, \tag{3.34}$$

and E_u is unstable if (3.34) is reversed. Calculation shows that (3.34) is equivalent to

$$m(1 + c_1 k) > [c p - m q(1 + c_1 k)] \frac{r_0 - d}{a},$$

which holds if

$$\begin{aligned} &\text{either } \{c p < m q(1 + c_1 k)\}, \\ &\text{or } \left\{ c p > m q(1 + c_1 k) > 0 \text{ and } \frac{m(1 + c_1 k)}{c p - m q(1 + c_1 k)} > \frac{r_0 - d}{a} \right\}. \end{aligned} \tag{3.35}$$

Note that (3.35) is nothing but precisely the violation of (3.29). Therefore, it is the loss of stability of E_u that leads to the occurrence of the positive equilibrium $E^+ = (\bar{u}, \bar{v})$.

When condition (3.29) holds, there is a unique positive equilibrium $E^+ = (\bar{u}, \bar{v})$ with the following characteristic equation

$$\lambda^2 + (m - J_{11})\lambda - J_{11} m + e^{-\lambda \tau} (-m \lambda + J_{11} m - J_{12} K_{21}) = 0 \tag{3.36}$$

where K_{22} has been simplified to m for this case.

When $\tau = 0$, (3.36) reduces to

$$\lambda^2 - J_{11}\lambda - J_{12}K_{21} = 0. \quad (3.37)$$

Note that $J_{12} < 0$ and $K_{21} > 0$. Thus, if $J_{11} < 0$, then by the Routh–Hurwitz criterion, the above quadratic equation only has roots with negative real parts. Now we check, under the condition $J_{11} < 0$, if the roots of (3.36) will cross the pure imaginary axis to enter the right half plane in the complex plane as τ increases.

Plugging $\lambda = \omega i$ into (3.36) and separating the real and imaginary parts, we obtain

$$\begin{cases} m\omega \sin(\omega\tau) - (J_{11}m - J_{12}K_{21})\cos(\tau\omega) = -\omega^2 - J_{11}m, \\ m\omega \cos(\omega\tau) + (J_{11}m - J_{12}K_{21})\sin(\tau\omega) = (-J_{11} + m)\omega, \end{cases} \quad (3.38)$$

Eliminating the cosine and sine functions by trigonometric identity leads to the following equation for ω :

$$\omega^4 + J_{11}^2\omega^2 + (2mJ_{11}J_{12}K_{21} - J_{12}^2K_{21}^2) = 0. \quad (3.39)$$

Note that this is indeed a quadratic equation for ω^2 and $J_{11}^2 > 0$. Thus, when

$$2mJ_{11}J_{12}K_{21} - J_{12}^2K_{21}^2 > 0, \quad (3.40)$$

then (3.39) has no positive solution, implying that no root of (3.36) will cross the pure imaginary axis for all $\tau \geq 0$; that is, all roots remain in the left half complex plane for all $\tau \geq 0$. Therefore, the coexistence equilibrium is locally asymptotically stable for all $\tau \geq 0$, provided that $J_{11} < 0$ and (3.40) holds.

If $J_{11} < 0$ but (3.40) is reversed, then (3.38) has a unique positive root

$$\omega_0 = \sqrt{\frac{-J_{11}^2 + \sqrt{J_{11}^4 - 4 \cdot (2mJ_{11}J_{12}K_{21} - J_{12}^2K_{21}^2)}}{2}},$$

corresponding to which, τ has a sequence of values

$$\begin{aligned} \tau_n = & \frac{1}{\omega_0} \arccos \frac{\omega_0^2 m(-J_{11} + m) + (\omega_0^2 + J_{11}m)(J_{11}m - J_{12}K_{21})}{m^2\omega_0^2 + (J_{11}m - J_{12}K_{21})^2} \\ & + \frac{2n\pi}{\omega_0}, \quad n = 0, 1, 2, \dots, \end{aligned}$$

which are possible critical values for τ at which Hopf bifurcation may occur. Therefore, the coexistence equilibrium is locally asymptotically stable when $\tau < \tau_0$ where

$$\tau_0 = \frac{1}{\omega_0} \arccos \frac{\omega_0^2 m(-J_{11} + m) + (\omega_0^2 + J_{11}m)(J_{11}m - J_{12}K_{21})}{m^2\omega_0^2 + (J_{11}m - J_{12}K_{21})^2}. \quad (3.41)$$

When $\tau = \tau_0$, (3.36) has a pair of pure imaginary roots $\pm i\omega_0$. In order to confirm Hopf bifurcation at the first critical value $\tau = \tau_0$, we need to verify the transversality condition, that is,

$$\frac{d\Re(\lambda)}{d\tau} \Big|_{\tau=\tau_0} > 0. \tag{3.42}$$

Indeed, differentiating Eq. (3.36) with respect to τ , we have

$$\left(\frac{d\lambda}{d\tau}\right)^{-1} = \frac{m - J_{11} + 2\lambda - m e^{-\lambda\tau}}{e^{-\lambda\tau} \lambda(-m\lambda + J_{11}m - J_{12}K_{21})} - \frac{\tau}{\lambda}.$$

Hence, at $\tau = \tau_0$ ($\lambda = i\omega_0$),

$$\begin{aligned} \operatorname{sgn}\left(\frac{d\Re(\lambda)}{d\tau} \Big|_{\tau=\tau_0}\right) &= \operatorname{sgn}\left(\Re \frac{d(\lambda)}{d\tau} \Big|_{\tau=\tau_0}\right) = \operatorname{sgn}\left(\Re \left(\frac{d(\lambda)}{d\tau} \Big|_{\tau=\tau_0}\right)^{-1}\right) \\ &= \operatorname{sgn}\left(\Re \left[\frac{m - J_{11} + 2\lambda - m e^{-\lambda\tau}}{e^{-\lambda\tau} \lambda(-m\lambda + J_{11}m - J_{12}K_{21})} - \frac{\tau}{\lambda}\right] \Big|_{\lambda=i\omega_0}\right) \\ &= \operatorname{sgn}\left(\frac{k_1 \cos(\omega_0\tau) + k_2 \sin(\omega_0\tau) - m^2\omega_0}{\omega_0[(J_{11}^2 + \omega_0^2)m^2 - 2mJ_{11}J_{12}K_{21} + J_{12}^2K_{21}^2]}\right) \end{aligned}$$

where $k_1 = \omega_0(I_{11}m - 2J_{12}K_{21} + m^2)$ and $k_2 = m^2J_{11} + m(-J_{11}^2 - J_{12}K_{21} - 2\omega_0^2) + J_{11}J_{12}K_{21}$.

From system (3.38), we have

$$\begin{aligned} \cos(\omega_0\tau) &= \frac{\omega_0^2 m(-J_{11} + m) + (\omega_0^2 + J_{11}m)(J_{11}m - J_{12}K_{21})}{m^2\omega_0^2 + (J_{11}m - J_{12}K_{21})^2}, \\ \sin(\omega_0\tau) &= \frac{-\omega_0^2 - J_{11}m + (J_{11}m - J_{12}K_{21})\cos(\omega_0\tau)}{m\omega_0}. \end{aligned} \tag{3.43}$$

Consequently,

$$\Re \left(\frac{d(\lambda)}{d\tau} \Big|_{\tau=\tau_0}\right)^{-1} = \frac{J_{11}^2 + 2\omega^2}{(J_{11}^2 + \omega_0^2)m^2 - 2mJ_{11}J_{12}K_{21} + J_{12}^2K_{21}^2} > 0. \tag{3.44}$$

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

If (3.29) holds but $J_{11} > 0$, then Eq. (3.36) only has roots with positive real parts when $\tau = 0$, meaning that the positive equilibrium $E^+ = (\bar{u}, \bar{v})$ is unstable when $\tau = 0$. Now, we follow the same procedure to check if the roots of (3.36) will cross the pure imaginary axis to enter the left half plane in the complex plane as τ increases.

Plugging $\lambda = \omega i$ into (3.36) and separating the real and imaginary parts, we still obtain the system (3.38) and Eq. (3.39) for ω . But now, since $J_{11} > 0$, the condition (3.40) is reversed, and thus, (3.38) has a unique positive root ω_0 . Differentiating Eq. (3.36) and evaluating at $\lambda = i\omega_0$, we find that (3.44) still holds, implying that any roots on the right half of the complex plane will remain on the right half plane as τ increases. This means that the positive equilibrium $E^+ = (\bar{u}, \bar{v})$ remains unstable for all $\tau > 0$.

Summarizing the above analysis, we have proven the following theorem,

Theorem 3.4 For model system (3.24), the following hold.

- (i) When $r_0 < d$, there is only the trivial equilibrium $E_0 = (0, 0)$ and it is locally asymptotically stable; when $r_0 > d$, it becomes unstable and there is the predator-free equilibrium E_u .
- (ii) For E_u , when (3.29) is violated (i.e., (3.35) holds), E_u is locally asymptotically stable; when (3.29) holds, then E_u becomes unstable and there is the positive (coexistence) equilibrium E^+ .
- (iii) Assume (3.29) holds so that E^+ exists and suppose $J_{11} < 0$ holds.
 - (iii)-1 If (3.40) is satisfied, then $E^+ = (\bar{u}, \bar{v})$ is locally asymptotically stable for all $\tau > 0$
 - (iii)-2 If (3.40) is reversed, then there is a $\tau_0 > 0$ such that $E^+ = (\bar{u}, \bar{v})$ is locally asymptotically stable when $0 < \tau < \tau_0$ and unstable when $\tau > \tau_0$. Furthermore, there is a Hopf bifurcation around E^+ at $\tau = \tau_0$, causing periodic solutions around E^+ .
- (iv) Assume (3.29) holds so that E^+ exists and suppose $J_{11} > 0$ holds, then $E^+ = (\bar{u}, \bar{v})$ is unstable for all $\tau > 0$.

Remark 3.3 Comparing with the results for the case with linear functional response (i.e., (3.1)) in Sect. 3.1, as far as the stability of the coexistence equilibrium is concerned, we have required a condition “ $J_{11} < 0$ ” which is needed for the corresponding ODE when $\tau = 0$ to have its coexistence equilibrium being stable. This should not be surprising as it is well-known that for an ODE predator–prey model (i.e., without delay) with a functional response of Holling Type II, the positive equilibrium may also lose its stability to periodic solutions through Hopf bifurcation. It is very natural to expect Hopf bifurcation to occur as well when J_{11} changes signs. But this is quite analytically demanding, hence we will explore along this line numerically in Sect. 4.

3.2.2 Global Stability of the Boundary Equilibria E_0 and E_u

Parallel to Sect. 3.1.2, in this subsection, we study the global asymptotical stability of the equilibria E_0 and E_u .

Theorem 3.5 When $r_0 < d$, the trivial equilibrium $E_0 = (0, 0)$ is indeed globally asymptotically stable.

Proof Consider

$$V(t) = u(t) + \frac{v(t)}{c} + \frac{1}{1 + c_1 k} \int_{t-\tau}^t \frac{p u(s) v(s)}{1 + q u(s)} ds.$$

Then,

$$\dot{V} = \frac{r_0 u(t)}{1 + c_2 k v(t)} - d u(t) - a u^2(t) - \frac{m v(t)}{c}. \tag{3.45}$$

Therefore, $\dot{V} \leq 0$ provided $r_0 < d$, and $\dot{V} = 0$ if and only if $u(t) = v(t) = 0$. Thus, $u(t) \rightarrow 0$ and $v(t) \rightarrow 0$ as $t \rightarrow \infty$, and hence, $E_0 = (0, 0)$ is globally asymptotically stable. \square

Theorem 3.6 *When $d < r_0$ and (3.34) holds (i.e., (3.29) is violated), $E_u = \left(\frac{r_0-d}{a}, 0\right)$ is globally asymptotically stable.*

Proof Consider

$$\begin{aligned} \frac{du}{dt} &= \frac{r_0 u(t)}{1 + c_2 k v(t)} - d u(t) - a u^2(t) - \frac{p u(t) v(t)}{(1 + q u(t))(1 + c_1 k)} \\ &\leq r_0 u(t) - d u(t) - a u^2(t). \end{aligned}$$

By the property of logistic equation and the comparison theorem, for any $\epsilon > 0$, there exist a $T = T(\epsilon) > 0$, such that when $t > T$, $u(t) < \frac{r_0-d}{a} + \epsilon$. Then, for $t > T + \tau$, the DDE for $v(t)$ satisfies

$$\begin{aligned} \frac{dv}{dt} &= \frac{c}{1 + c_1 k} \cdot \frac{p u(t - \tau) v(t - \tau)}{1 + q u(t - \tau)} - m v(t) \\ &< \frac{c}{1 + c_1 k} \cdot \frac{p \left(\frac{r_0-d}{a} + \epsilon\right)}{1 + q \left(\frac{r_0-d}{a} + \epsilon\right)} v(t - \tau) - m v(t). \end{aligned} \tag{3.46}$$

By (3.34), we can choose $\epsilon > 0$ sufficiently small so that

$$\frac{c}{1 + c_1 k} \cdot \frac{p (\hat{u} + \epsilon)}{1 + q (\hat{u} + \epsilon)} - m < 0.$$

By Smith (2010), the trivial solution of

$$\frac{dx}{dt} = \frac{c}{1 + c_1 k} \cdot \frac{p (\hat{u} + \epsilon) x(t - \tau)}{1 + q (\hat{u} + \epsilon)} - m x(t), \tag{3.47}$$

is globally asymptotically stable. Note that (3.47) is monotone, by (3.46) and the comparison theorem, $v(t) \rightarrow 0$ as $t \rightarrow \infty$. This means that the first equation in (3.24) is asymptotically autonomous having the following logistic equation as its limit equation:

$$\frac{du}{dt} = r_0 u(t) - d u(t) - a u^2(t).$$

Since $\hat{u} = (r_0 - d)/a$ attracts every positive solution to this logistic equation, by the theory of asymptotically autonomous systems (see, e.g., Castillo-Chavez and Thieme 1995), we conclude that in the system (3.24) $u(t) \rightarrow \hat{u} = \frac{r_0 - d}{a}$ as $t \rightarrow \infty$. Therefore, every positive solution of (3.24) converges to $E_u = (\hat{u}, 0)$. This together with the local stability established in Theorem 3.4 implies that E_u is globally asymptotically stable. \square

4 Numerical Simulations

In this section, we present some numerical simulations to illustrate the main analytic results obtained in Sect. 3, and also to more visually explore the impact of the anti-predation response level and the biomass transfer time.

We begin with the model (3.1) that adopts the linear functional response, with two response functions $f(k, v)$ and $\rho(k)$ given by (3.23), that is, the following system:

$$\begin{cases} \frac{du}{dt} = \frac{r_0 u(t)}{1 + c_2 k v(t)} - d u(t) - a u^2(t) - \frac{u(t) v(t)}{1 + c_1 k}, \\ \frac{dv}{dt} = \frac{c u(t - \tau) v(t - \tau)}{1 + c_1 k} - m v(t). \end{cases} \quad (4.1)$$

We fix the parameters

$$r_0 = 0.03, \quad d = 0.01, \quad a = 0.01, \quad m = 0.05, \quad c = 0.4, \quad c_1 = 1, \quad c_2 = 1, \quad (4.2)$$

and demonstrate how k and τ impact the population dynamics. To this end, we transfer the threshold for r_0 in comparison with $d + am/c\rho(k)$ for the stability of E_u in (ii) and (iii) of Theorem 3.1 to a threshold value for k . By setting $r_0 = d + \frac{am}{c\rho(k)}$ and using the parameter values in (4.2), we obtain $k^* = 15$. By Theorem 3.1, when $k > 15$, the predator-free equilibrium E_u is stable (as demonstrated in Fig. 1a for $k = 20$); when $k < 15$, E_u becomes unstable and there occurs the unique coexistence equilibrium E^+ . For $k = 11 < k^*$ and with the above parameters, we can numerically calculate to obtain $p_0 = 0.00075$ and $|q_0| = 0.0005250388635$, giving a situation of $p_0 > |q_0|$ (Theorem 3.1-(iii)-1), and hence, E^+ is asymptotically stable for any $\tau > 0$, as demonstrated in Fig. 1b.

When k is further decreased to $k = 1$, we still have the coexistence equilibrium E^+ , and p_0 and q_0 are numerically computed to be $p_0 = 0.000125$ and $q_0 = 0.0007484621132$, corresponding to the scenario in Theorem 3.1-(iii)-(2). Further calculations reveal that $\tau_0 = 3.678038406$. The numeric solutions are illustrated in Fig. 2, for $\tau < \tau_0$ and $\tau > \tau_0$, respectively in (a) and (b). For latter case ($\tau = 4 > \tau_0$), the periodic solutions are also illustrated in the $u - v$ plane in Fig. 3. With the parameters given in (4.2), we also plot the bifurcation diagrams with respect to time delay τ (with $k = 1$ fixed) and anti-predation strategy k (with $\tau = 2$ fixed), respectively, in Fig. 4a, b. There, the curve represents either the predator population of the stable positive equilibrium point, or the maximum and the minimum value of the predator population in the bifurcated periodic solution.

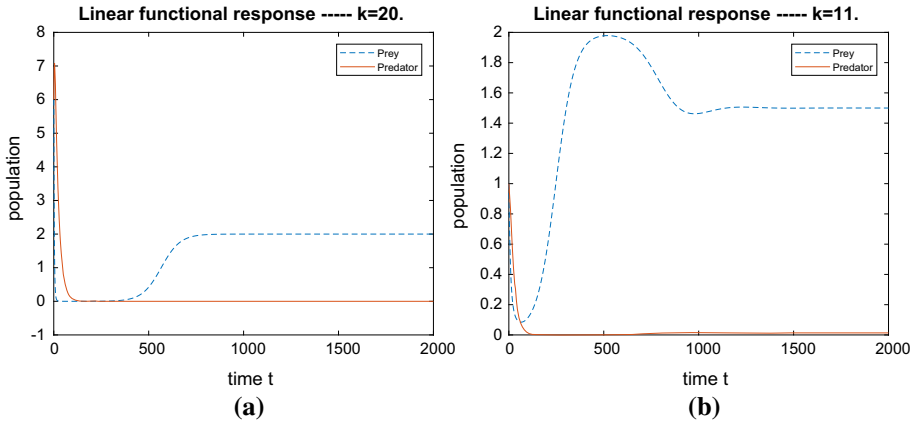


Fig. 1 Population dynamics of (4.1). **a** When $k = 20 > k^* = 15$, the predator-free equilibrium E_u is stable, the predator species goes extinct and the prey species eventually goes to its carrying capacity. **b** When $k = 11 < k^* = 15$, E_u is unstable and there is the coexistence equilibrium E^+ which is asymptotically stable for all $\tau \geq 0$ since $p_0 = 0.00075 > |q_0| = 0.0005250388635$

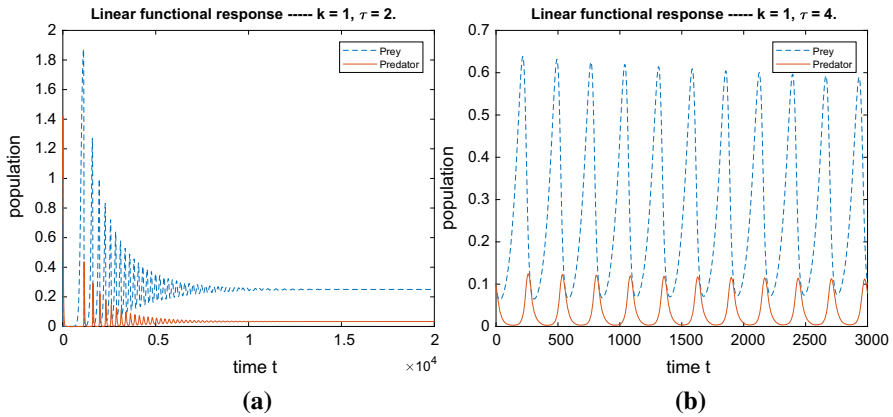


Fig. 2 Population dynamics of (4.1). **a** When $k = 1 < k^*$, $p_0 = 0.000125 < q_0 = 0.0007484621132$, $\tau = 2 < \tau_0 = 3.678038406$, the coexistence equilibrium is stable. **b** $\tau = 4 > \tau_0 = 3.678038406$, there occurs a periodic solution

Next demonstrate the results for the model system (3.24) with the following parameter values

$$\begin{aligned}
 r_0 &= 0.03, \quad d = 0.01, \quad a = 0.01, \quad m = 0.05, \quad c = 0.4, \\
 c_1 &= 1, \quad c_2 = 1, \quad p = 0.5, \quad q = 0.6.
 \end{aligned}
 \tag{4.3}$$

Since $r_0 > d$, the predator-free equilibrium E_u exists. For its stability, we can similarly transfer the threshold value for r_0 in Theorem 3.4 to a critical value k^* of k , by setting

$$r_0 = \frac{a m (1 + c_1 k)}{c p - m q (1 + c_1 k)} + d$$

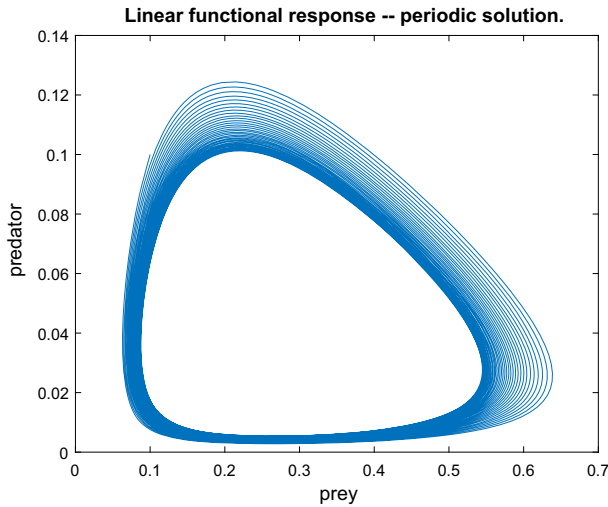


Fig. 3 Plot of periodic orbit of (4.1) in $u = v$ plane when $k = 1$ and $\tau = 4 > \tau_0 = 3.678038406$

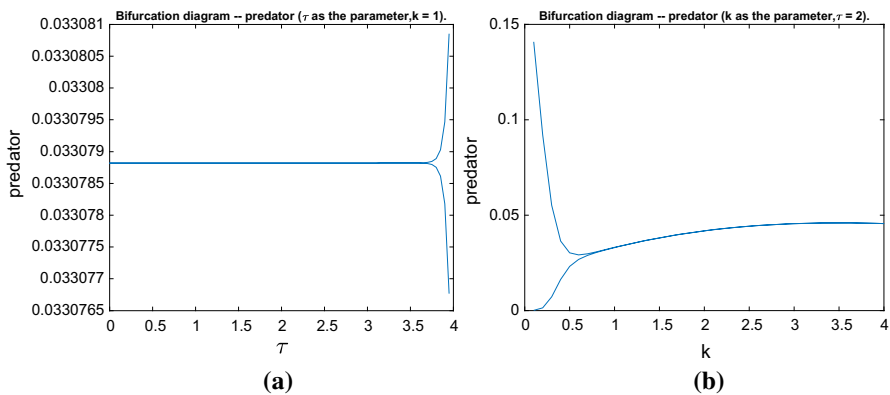


Fig. 4 Bifurcation diagram for (4.1): **a** fixing $k = 1$ and choosing τ as the bifurcation parameter; **b** fixing $\tau = 2$ and choosing k as the bifurcation parameter

and solving it for k , leading to the a numeric value $k^* = 2.636363636$. Thus, by Theorem (3.4), when $k > 2.636363636$, the predator-free equilibrium E_u is stable (as demonstrated in Fig. 5a), and when $k < 2.636363636$, E_u becomes unstable and there occurs the unique coexistence equilibrium E^+ . As far as the stability of E^+ is concerned under $k < k^* = 2.636363636$, it depends on whether $J_{11} < 0$ or $J_{11} > 0$. When $k = 2$, numeric calculations give $J_{11} = -0.01184921799 < 0$ and $2m J_{11} J_{12} K_{21} - J_{12}^2 K_{21}^2 = 1.723290120 \times 10^{-7} > 0$ [i.e., (3.40) holds]. By Theorem 3.4-(iii)-1, E^+ is asymptotically stable (see Fig. 5b).

However, when k is further decreased to $k = 1$, computations give $J_{11} = -0.003821249991 < 0$ (still negative) but $2m J_{11} J_{12} K_{21} - J_{12}^2 K_{21}^2 = -2.86322377 \times 10^{-8} < 0$ [i.e., (3.40) is reversed now]. This is the scenario of Theorem 3.4-(iii)-2,

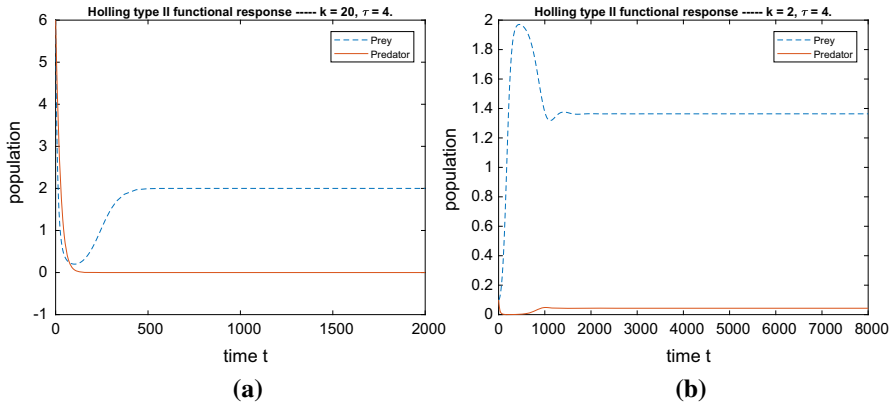


Fig. 5 Population dynamics of (3.24). **a** When $k = 20 > k^* = 2.636363636$, the predator-free equilibrium E_U is stable. **b** When $k = 2 < k^*$, E_U becomes unstable and there occurs the positive equilibrium E^+ which is asymptotically stable for all $\tau > 0$ because $J_{11} = -0.01184921799 < 0$ and $(2m J_{11} J_{12} K_{21} - J_{12}^2 K_{21}^2) = 1.723290120 \cdot 10^{-7} > 0$

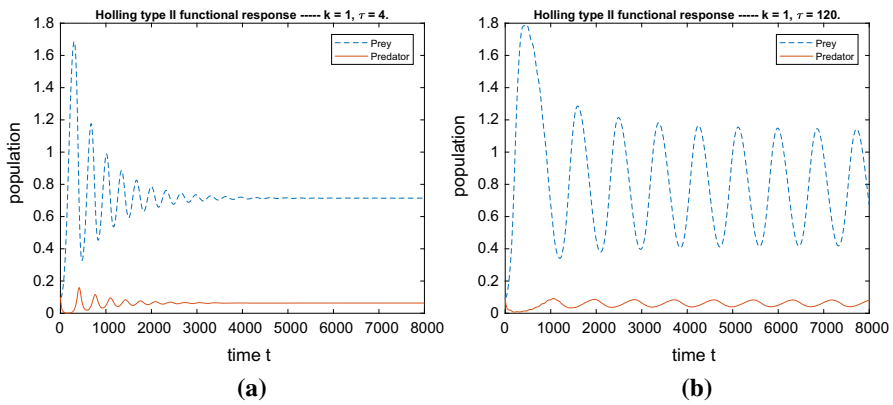


Fig. 6 When $k = 1 < k^*$, $J_{11} = -0.003821249991 < 0$, $(2m J_{11} J_{12} K_{21} - J_{12}^2 K_{21}^2) = -2.86322377 \cdot 10^{-8} < 0$. **a** When $\tau = 4 < \tau_0 = 33.27610729$, the coexistence equilibrium E^+ is still stable; **b** When $\tau = 120 > \tau_0 = 33.27610729$, E^+ loses its stability and a periodic solution occurs

meaning that the stability of E^+ further depends on the size of delay τ . By (3.41), we compute to obtain $\tau_0 = 33.27610729$. The numeric solutions for $\tau < \tau_0$ and $\tau > \tau_0$ are shown in Fig. 6a and b, respectively, for $\tau = 4$ and $\tau = 120$; and plotting in the $u - v$ plane for the case of Fig. 6b is given in Fig. 7.

Parallel to Fig. 4, we also plot the bifurcation diagrams with respect to delay τ (with $k = 1$ fixed) and anti-predation response level k (with $\tau = 2$ fixed), respectively, in Fig. 8a and b, with the parameters given in (4.3).

We have seen in Theorem 3.4 and mentioned in Remark 3.3 that when $J_{11} > 0$, the system has no stable equilibrium for all $\tau > 0$. In such a case, periodic behavior is the outcome. This is demonstrated in Fig. 9. Indeed, we not only observe the periodic

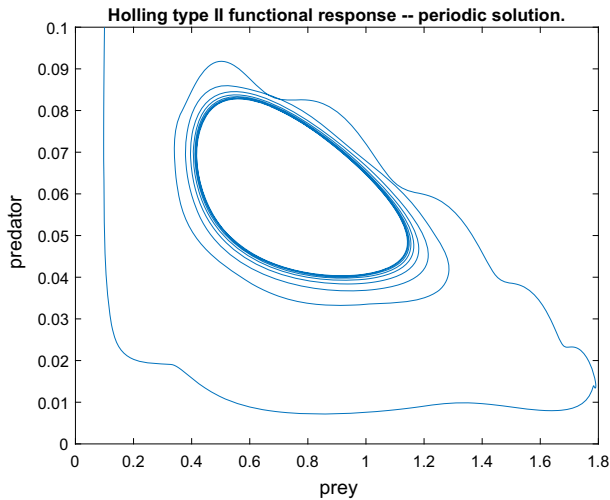


Fig. 7 Periodic orbits when $k = 1$ and $\tau = 120$

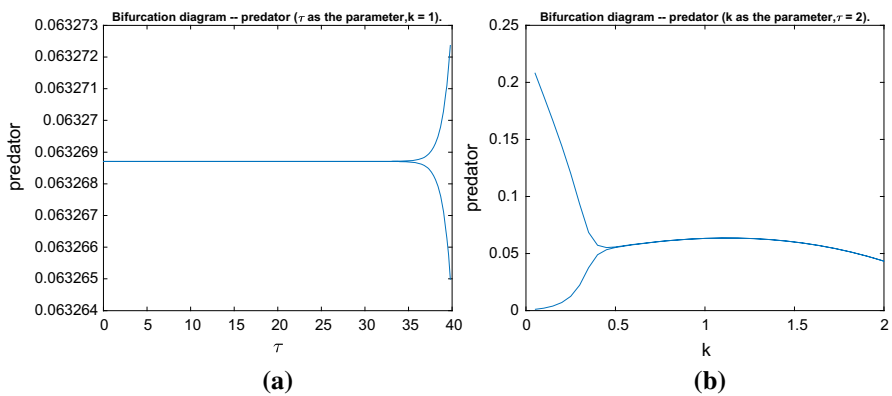


Fig. 8 Bifurcation diagram for **a** fix $k = 1$, choose τ as the bifurcation parameter. **b** Fix $\tau = 2$, choose k as the bifurcation parameter

behaviors, but also find that the magnitude of the sustained oscillations (periodic solutions) is enlarged by $\tau > 0$.

5 Conclusion and Discussion

Recent field studies on the fear effect in predator–prey interactions have triggered the need to modify existing predator–prey models that do not consider the fear effect. In a recent work Wang et al. (2016), the authors incorporated an anti-predation mechanism into an ODE model to account for the fear effect which leads to a cost in reproduction; analyzing the model, they have obtained some results on the effect of such an anti-predation response. In this paper, based on the fact that in addition to cost, there is also

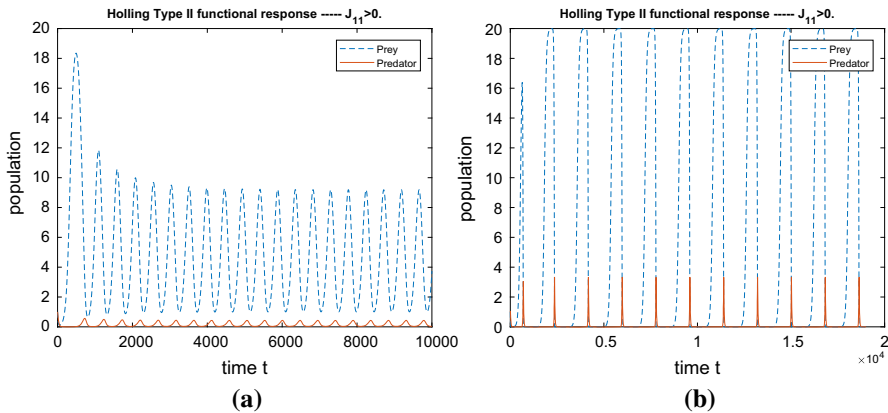


Fig. 9 By setting $k = 3.4$, $J_{11} = 0.00084875902838911633 > 0$. **a** Solutions approach to a periodic solution for $\tau = 0$ (periodic solutions for the ODE). **b** Periodic behaviors are preserved for $\tau > 0$ and are actually magnified by $\tau > 0$

a benefit for an anti-predication response; and meanwhile, there is also a time delay in biomass transfer from prey to predator after predation, we have further modified the model studied in Wang et al. (2016) to explore the joint effects of both biomass transfer delay and the fear effect.

Following Wang et al. (2016), we have considered two types of functional responses: Holling Type I and Holling Type II. In both cases, we have obtained and stated our main results *more explicitly* in terms of some parameters such as r_0 and d , but they can be translated into statements in terms of the two main parameters k and τ . Such a translation will lead to loss of some explicitness, but this can be easily achieved numerically, as demonstrated in Sect. 4. For example, when Holling Type I (linear) functional response is adopted, Theorem 3.1 can be restated in terms of k and τ as below:

Theorem 5.1 *For the predator–prey system (3.1) with linear functional response under condition $r_0 > d$, there may exist two critical values of the anti-predation level k that $0 < \hat{k} < k^*$, such that,*

- (i) *When $k > k^*$, $E_u = \left(\frac{r_0-d}{a}, 0\right)$ is globally asymptotically stable. When $k < k^*$, $E_u = \left(\frac{r_0-d}{a}, 0\right)$ is unstable and there occurs a unique coexistence equilibrium E^+ .*
- (ii) *When $k^* > k > \hat{k}$, the unique coexistence equilibrium $E^+ = (\bar{u}, \bar{v})$ is locally asymptotically stable for all $\tau > 0$. If $0 < k < \hat{k}$, there is a $\tau_0 > 0$ such that $E^+ = (\bar{u}, \bar{v})$ is locally asymptotically stable when $0 < \tau < \tau_0$ and unstable when $\tau > \tau_0$; furthermore, there is a Hopf bifurcation about E^+ at $\tau = \tau_0$.*

When Holling type II functional response is adopted, Theorem 3.4 can be restated in terms of k and τ as below.

Theorem 5.2 *Consider the predator–prey system (3.24) with Holling type II functional response under condition $r_0 > d$.*

- (i) There exists a critical value $k^* > 0$ such that for $k > k^*$, $E_u = \left(\frac{r_0-d}{a}, 0\right)$ is globally asymptotically stable. When $k < k^*$, $E_u = \left(\frac{r_0-d}{a}, 0\right)$ is unstable and there occurs a unique coexistence equilibrium $E^+ = (\bar{u}, \bar{v})$.
- (ii) When $k < k^*$ and $J_{11} < 0$, there exists another critical value $0 < \hat{k} < k^*$ such that
- (ii)-1 if $\hat{k} < k < k^*$, the unique coexistence equilibrium E^+ is locally asymptotically stable for all $\tau > 0$;
- (ii)-2 if $0 < k < \hat{k}$, there is a $\tau_0 > 0$ such that E^+ is locally asymptotically stable only when $0 < \tau < \tau_0$ and it becomes unstable when $\tau > \tau_0$; furthermore, there is a Hopf bifurcation about E^+ at $\tau = \tau_0$.
- (iii) When $k < k^*$ and $J_{11} > 0$, a periodic solution occurs even if $\tau = 0$, and it does not vanish for all $\tau > 0$.

We point out that the critical values k^* and \hat{k} in the above translated theorems are defined implicitly by equations in Theorem 3.4-(ii) corresponding to the thresholds for the inequalities there, which in general cannot be solved explicitly. However, as demonstrated in Sect. 4, given the values of other parameters, they can be numerically calculated.

From the above theorems, we find that the anti-predation strategy k and the digestion delay τ play important roles in both models. As long as r_0 (the natural growth rate of prey) is greater than d (the natural death rate of prey), the trivial equilibrium solution is unstable and the populations of the predator and prey are determined by k and τ , in terms of the critical values k^* , \hat{k} and τ_0 , as classified in the theorems. Note that τ_0 depends on k , as illustrated in Fig. 10 for both functional responses considered for the given set of parameter values in (4.3). Also from the equations that determine the critical values k^* ($r_0 = d + am/c\rho(k)$ in Theorem 3.1 and (3.29) in Theorem 3.4), we can see the impact of the incorporated benefit factor $\rho(k)$ as a function of the anti-predation response level k . This shows the *trade-off effect* of cost and benefit of the response k , and is *in strong contrast* to the corresponding models considered in Wang et al. (2016), where *no benefit* was considered ($\rho(k) = 1$) and hence small k favors the prey population since k only leads to a cost of reducing the reproduction of the prey. Also, in the ODE model in Wang et al. (2016) with Holling Type I functional response, there is no periodic solution for any values of the parameter set; however, with the digestion delay incorporated, periodic phenomenon becomes possible.

We also point out an important difference of the model with Holling Type II functional response from that with Holling Type I functional response. For the former, when $k < k^*$, delay caused oscillations can occur only in the case when $J_{11} < 0$; and when $J_{11} > 0$, there is also a periodic solution but that is not caused by the delay τ . This indicates that the sign change of J_{11} from negative to positive also leads to Hopf bifurcation, and this is in agreement with the periodic solution observed in the ODE model with Holling Type II functional response in Wang et al. (2016). Accordingly, one can also explore the sign change numerically by the formula defining J_{11} and the equations in (3.25) that determine the coexistence equilibrium $E^+ = (\bar{u}, \bar{v})$.

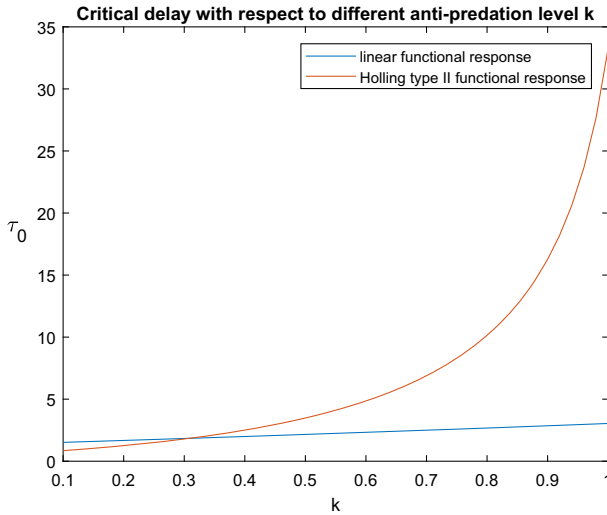


Fig. 10 Critical value of time delay for fixed anti-predation level k for both functional responses

The differences between the two functional responses considered in our model are illustrated in Sect. 4 by using the same set of parameter values. It has been seen that for a given $\tau > 0$, the critical value k^* in Holling type II model is much less than that in the model with linear functional response (2.636363636 vs 15 in our numeric results). This seems to suggest that anti-predation strategy is more sensitive to the population of predator with Holling Type II functional response than with Holling Type I. Similarly, for a given k , the critical delay τ_0 in Holling type II model is much greater than that in the model with linear functional response (see Fig. 10). Thus, the results are actually specific to the particular choice of the functional response function. This is not surprising to predator-prey modellers as it has been widely known that different kinds of predation between species have different characteristics and hence, needs to use different functional responses to capture the main feature. Exploring the joint impacts of anti-predation response and biomass transfer delay on the population dynamics with other types of functional responses remains an interesting and worthwhile topic for future research. We point out that in both cases, we have only explored the Hopf bifurcation at the first critical value τ_0 for the delay parameter. This is because this value is most important, serving as a threshold for the stability of the positive equilibrium E^+ and carrying information about the consequence of E^+ becoming unstable. Investigation of the bifurcations at the subsequent critical values τ_n , $n = 1, 2, \dots$ is more involving, demanding theory and methods on global bifurcation and hence could be very lengthy. Therefore, we decide not to explore in this paper.

We have chosen the ODE model (1.2) from Wang et al. (2016) as the basic model into which a benefit coming from the anti-predation response and a delay in biomass transfer are incorporated. Note that this basic model uses the *logistic growth* for the prey population and assumes that the predator is a *specialist*. Other types of growth for prey population and the predation by generalist predators are also important topics

to investigate, when the fear effect and the biomass transfer delay are incorporated. We remark that, also based on (1.2), Das and Samanta (2018) incorporated an extra food source for the predator and added a white noise to the death rates of the prey and predator and they analyzed the resulting stochastic model. Mondal et al. (2018) further considered a digestion delay in addition to the cost of fear, white noise in the death rates, and extra food for the predator; however, the benefit of the anti-predation response was not considered.

References

- Abrams, P.A., Ginzburg, L.R.: The nature of predation: Prey dependent, ratio dependent or neither? *Trends Ecol. Evol.* **15**, 337–341 (2000)
- Arditi, R., Ginzburg, L.R.: Coupling in predator–prey dynamics: ratio dependence. *J. Theor. Biol.* **139**, 311–326 (1989)
- Castillo-Chavez, C., Thieme, H.R.: Asymptotically autonomous epidemic models. In: Arino, O., et al. (eds.) *Mathematical Population Dynamics: Analysis of Heterogeneity, I. Theory of Epidemics*, pp. 33–50. Wuerz, Winnipeg (1995)
- Creel, S., Christianson, D.: Relationships between direct predation and risk effects. *Trends Ecol. Evol.* **23**, 194–201 (2008)
- Cresswell, W.: Predation in bird populations. *J. Ornithol.* **152**, 251–263 (2011)
- Cushing, J.M.: *Integro-Differential Equations and Delay Models in Population Dynamics*. Lecture Notes in Biomathematics, vol. 20. Springer, Berlin (1977)
- Das, A., Samanta, G.P.: Modeling the fear effect on a stochastic prey–predator system with additional food for the predator. *J. Phys. A Math. Theor.* **51**, 465601 (2018)
- Hale, J.K., Lunel, S.M.V.: *Introduction to Functional Differential Equations*. Springer, New York (1993)
- Hayes, N.D.: Roots of the transcendental equations associated with a certain differential-difference equation. *J. Lond. Math. Soc.* **25**, 226–232 (1950)
- Holling, C.S.: The functional response of predator to prey density and its role in mimicry and population regulation. *Mem. Entomol. Soc. Can.* **45**, 1–60 (1965)
- Jeschke, J.M., Kopp, M., Tollrian, R.: Predator function responses: discriminating between handling and digesting prey. *Ecol. Monogr.* **72**(1), 95–112 (2002)
- Li, F., Li, H.: Hopf bifurcation of a predator–prey model with time delay and stage structure for the prey. *Math. Comput. Model.* **55**, 672–679 (2012)
- Lima, S.L.: Nonlethal effects in the ecology of predator–prey interactions. *Bioscience* **48**, 25–34 (1998)
- Lima, S.L.: Predators and the breeding bird: behavioural and reproductive flexibility under the risk of predation. *Biol. Rev.* **84**, 85–113 (2009)
- Lotka, A.J.: Analytical note on certain rhythmic relations in organic systems. *Proc. Natl. Acad. Sci. U.S.A.* **6**, 410–415 (1920)
- Lotka, A.J.: *Elements of Physical Biology*. Williams and Wilkins, Philadelphia (1925)
- Mondal, S., Maiti, A., Samanta, G.P.: Effects of fear and additional food in a delayed predator–prey model. *Biophys. Rev. Lett.* **13**, 157–177 (2018)
- Rosenzweig, M.L., MacArthur, R.H.: Graphical representation and stability conditions of predator–prey interactions. *Am. Nat.* **97**, 209–223 (1963)
- Skalski, G.T., Gilliam, J.F.: Functional responses with predator interference: viable alternatives to the Holling type II model. *Ecology* **82**, 3083–3092 (2001)
- Smith, H.: *Monotone Dynamical Systems: An Introduction to the Theory of Competitive and Cooperative Systems*. Mathematical Surveys and Monographs, vol. 41. American Mathematical Society, Providence (1995)
- Smith, H.: *An Introduction to Delay Differential Equations with Applications to the Life Sciences*. Springer, New York (2010)
- Volterra, V.: Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. *Mem. Acad. Lincei Roma* **2**, 31–113 (1926)
- Volterra, V.: Variations and fluctuations of the number of individuals in animal species living together. In: Chapman, R.N. (ed.) *Animal Ecology*. McGraw-Hill, New York (1931)

- Wang, X., Zou, X.: Modeling the fear effect in predator–prey interactions with adaptive avoidance of predators. *Bull. Math. Biol.* **79**, 1325–1359 (2017)
- Wang, X., Zou, X.: Pattern formation of a predator–prey model with the cost of anti-predator behaviours. *Math. Biosci. Eng.* **15**, 775–805 (2018)
- Wang, X., Zanette, L.Y., Zou, X.: Modelling the fear effect in predator–prey interactions. *J. Math. Biol.* **73**, 1179–1204 (2016)
- Wangersky, P.J., Cunningham, W.J.: Time lag in prey–predator population models. *Ecology* **38**, 136–139 (1957)
- Xu, R.: Global dynamics of a predator-prey model with time delay and stage structure for the prey. *Nonlinear Anal. RWA* **12**, 2151–2162 (2011)
- Zanette, L.Y., White, A.F., Allen, M.C., Clinchy, M.: Perceived predation risk reduces the number of offspring songbirds produce per year. *Science* **334**(6061), 1398–1401 (2011)

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