Dynamics of a Predator-prey Model with Delay and Fear Effect*

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Abstract Recent manipulations on vertebrates showed that the fear of predators, caused by prey after they perceived predation risk, could reduce the prey's reproduction greatly. And it's known that predator-prey systems with fear effect exhibit very rich dynamics. On the other hand, incorporating the time delay into predator-prey models could also induce instability and oscillations via Hopf bifurcation. In this paper, we are interested in studying the combined effects of the fear effect and time delay on the dynamics of the classic Lotka-Volterra predator-prey model. It's shown that the time delay can cause the stable equilibrium to become unstable, while the fear effect has a stabilizing effect on the equilibrium. In particular, the model loses stability when the delay varies and then regains its stability when the fear effect is stronger. At last, by using the normal form theory and center manifold argument, we derive explicit formulas which determine the stability and direction of periodic solutions bifurcating from Hopf bifurcation. Numerical simulations are carried to explain the mathematical conclusions.

Keywords Predator-prey interaction, fear effect, delay, combined effect, Hopf bifurcation.

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1. Introduction

Predator-prey interactions play a crucial role in mathematical modeling of ecological processes. Following the work of Lotka and Volterra, there are extensive papers studying the mechanisms of predator-prey systems by observing direct killing of prey by predators. However, from about the early 1990s onwards, many theoretical biologists have argued that indirect effects, caused by costs of prey's behavioral defenses to perceived predation risk, could also alter the prey's reproductive physiology and demography powerfully (see [1, 2, 13]).

Animals will take many kinds of measures, including making fewer forays, enhancing vigilance, and even changing habitats, to cope with the perceived predation risk (for more details, we refer to [2, 17, 18] and [7]). Nevertheless, these antipredator responses could also cause harmful impacts on them. For example, when scared parents forage less, the birth rate is decreased and it will be more tough for the juvenile to survive because of starvation(see, e.g., [1-3]). Similarly, if prev

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migrate from the high-risk habitat to low-risk habitats to escape from predating, they may consume much energy especially when the environment of low-risk habitats are harsh(see [2,16]). In general, such an anti-predator behavior can lower the reproductive rate in long term even though it enhances the probability of survival temporarily.

Except the viewpoints of these theoretical ecologists and evolutionary biologists, direct experimental evidence demonstrating that fear can affect the population of prey was given in 2011. In this year, Zanette et al. conducted an experimental study on wild, free-living song sparrows throughout their breeding season to test whether perceived predation risk could alone affect the number of offspring produced every year. And we can refer to the monograph [25] to obtain the specific experimental details. In this manipulation, females showed a variety of anti-predator responses, such as stopping incubation, foraging less and bringing less food to the nest. Several correlative experimental findings in [4–6, 9, 10, 20, 24] and [19] also suggested that fear of predators could alter prey's demography.

Based on the experimental facts in [27], Wang et al [25] considered a predatorprey model incorporating the cost of the fear into prey's reproduction. Their model is as follows

$$\begin{cases} u'(t) = ur_0 f(k, v) - du - au^2 - g(u)v, \\ v'(t) = v(-m + cg(u)), \end{cases}$$

where u(t) and v(t) denote the densities of prey and predator at time t, respectively, all the parameters are positive, r_0 is the birth rate of prey while d represents the natural death rate of prey, a describes the effect of intra-species competition of prey, c is the conversion rate of prey's biomass to predator's biomass, m is the natural death rate of predator, g(u(t)) represents the functional response between prey and predator, f(k, v) accounts for the cost of anti-predator defense due to perceived predation risk, and k reflects the level of fear which drives anti-predator behaviors of the prey. By the biological meaning of k, v and f(k, v), they assume that

$$\begin{cases} f(0,v) = 1, & f(k,0) = 1, \quad \lim_{k \to +\infty} f(k,v) = 0, \quad \lim_{v \to +\infty} f(k,v) = 0, \\ \frac{\partial f(k,v)}{\partial k} < 0, \quad \frac{\partial f(k,v)}{\partial v} < 0. \end{cases}$$

Their mathematical analysis shows that high levels of fear can stabilize the predator-prey system by excluding the existence of periodic solutions. In addition, relatively low levels of fear can induce periodic solutions via Hopf bifurcation.

However, the model mentioned above only exhibits the change of all populations under ideal conditions. The authors assume that the predator population can convert the consumption into its growth instantaneously, which is obviously not so. In the dynamics of real populations, there are reaction-time lags in the response of predators(see,e.g. [21]), which appear as delays in the numerical response functions. Besides, it has been shown that delay differential equations exhibit much more complicated dynamics than ordinary differential equations in general since a time delay could cause a stable equilibrium to become unstable and cause the populations to fluctuate.

Thus, in this paper, by supposing $f(k, v) = \frac{1}{1+kv}$ and g(u) = pu for the convenience of analysis, we incorporate a constant time delay τ into the above model in

the following way

$$\begin{cases} x'(t) = \frac{r_0 x(t)}{1 + k y(t)} - dx(t) - a x^2(t) - p x(t) y(t), \\ y'(t) = c p x(t - \tau) y(t - \tau) - m y(t), \end{cases}$$
(1.1)

where p is a positive constant.

Then we may wonder whether the time delay can affect the system greatly or how the fear effect and time delay affect our system together. Therefore, the objective of this paper is to study the combined impacts of the time delay and fear effect on the dynamics of predator-prey system. We organise this paper as follows. In the next section, we consider the stability of the equilibria and show that when the delay takes some critical values, Hopf bifurcation occurs by choosing delay $\check{S}O$ as a bifurcation parameter. In Section 3, by using the normal form method and the center manifold theory introduced by [11], we analyse the properties of the bifurcating periodic solutions. In section 4, we shall give some numerical simulations.

2. Stability analysis and Hopf bifurcation

From [25], we know that (1.1) has equilibria $E_0 = (0,0), E_1 = (\frac{r_0-d}{a}, 0)$ under the condition $r_0 > d$, and a unique positive equilibrium $E_2 = (\overline{x}, \overline{y})$ if

$$r_0 > d + \frac{am}{cp} \tag{2.1}$$

holds, where $\overline{x} = \frac{m}{cp}$ and \overline{y} satisfies $\frac{r_0}{1+k\overline{y}} - d - a\overline{x} - p\overline{y} = 0$. In this section, we will consider the stability of the equilibria and Hopf bifurcation of system (1.1).

2.1. Stability of E_0 and E_1

In this section, we are concerned with the stability of E_0 and E_1 of system(1.1), and in what follows, we need the following results from [21].

Lemma 2.1 ([21, Lemma 7]). Considering the transcendental polynomial given by

$$h(\lambda) = \lambda + a - be^{-\lambda\tau}.$$

where a > 0, b > 0, $\tau \ge 0$. For the distribution of the zeros of $h(\lambda)$, we have

- (i) If a < b, then $h(\lambda)$ admits one positive real zero and all other zeros are complex numbers;
- (ii) If a = b, then $\lambda = 0$ is the only real zero of $h(\lambda)$ and all other zeros are complex numbers with negative real parts;
- (iii) If a > b, then $h(\lambda)$ has a unique negative real zero, and all other zeros have negative real parts.

Theorem 2.1. For system (1.1), the trivial equilibrium E_0 is stable if $r_0 < d$ and unstable if $r_0 > d$. The semi-trivial equilibrium E_1 is locally asymptotically stable if (2.1) does not hold and unstable while (2.1) holds.

Proof. Linearizing system (1.1) about E_0 , we obtain the characteristic equation

$$(\lambda + d - r_0)(\lambda + m) = 0, \qquad (2.2)$$

for which the eigenvalues are $\lambda_1 = r_0 - d$ and $\lambda_2 = -m < 0$. Hence, E_0 is stable if $r_0 < d$ and unstable if $r_0 > d$. Similarly, by linearizing system (1.1) about E_1 when $r_0 > d$, we get the characteristic equation as follows

$$(\lambda + r_0 - d)h(\lambda) = 0, \qquad (2.3)$$

where $h(\lambda) = \lambda + m - \frac{cp(r_0-d)}{a}e^{-\lambda\tau}$. Obviously, $\lambda_1 = d - r_0 < 0$ is a real characteristic root, and other roots are zeros of $h(\lambda)$. According to Lemma 2.1, it's easy to know that when $\frac{cp(r_0-d)}{am} < 1$, that is, $r_0 < d + \frac{am}{cp}$, all zeros of $h(\lambda)$ have negative real parts for $\tau \ge 0$. This, together with $\lambda_1 < 0$, suggests that E_1 is locally asymptotically stable. However, when $r_0 > d + \frac{am}{cp}$, $h(\lambda)$ admits a positive zero, which implies E_1 is unstable.

Theorem 2.2. If $d < r_0 < d + \frac{am}{cp}$, the semi-trivial equilibrium E_1 of system (1.1) is globally asymptotically stable. In this case, the predator population will go to extinction.

Proof. By Theorem 2.1, we see that the equilibrium $E_1(\frac{r_0-d}{a}, 0)$ is locally asymptotically stable if $d < r_0 < d + \frac{am}{cp}$. Hence, it is sufficient to show that the equilibrium E_1 is globally attractive.

Following the first equation of (1.1), we can obtain that

$$\begin{aligned} x'(t) &\leq x(t)(\frac{r_0}{1+ky(t)} - d - ax(t)) \\ &\leq x(t)(r_0 - d - ax(t)) \\ &= ax(t)(\frac{r_0 - d}{a} - x(t)), \quad t \geq 0, \end{aligned}$$

which yields

$$\limsup_{t \to +\infty} x(t) \le \frac{r_0 - d}{a}$$

Therefore, for $\varepsilon > 0$ sufficiently small satisfying $cp(\frac{r_0-d}{a}+\varepsilon) < m$, there is a $T_1 > 0$ such that if $t > T_1$, $x(t) \le \frac{r_0 - d}{a} + \varepsilon$. We derive from the second equation of system (1.1) for $t > T_1 + \tau$ that

$$y'(t) \le cp(\frac{r_0-d}{a}+\varepsilon)y(t-\tau) - my(t).$$

Consider the following auxiliary equation

$$v'(t) = cp(\frac{r_0 - d}{a} + \varepsilon)v(t - \tau) - mv(t).$$

Noting that $cp(\frac{r_0-d}{a}+\varepsilon) < m$, it follows that

$$\lim_{t \to +\infty} v(t) = 0.$$

By comparison, we derive that

$$\lim_{t \to +\infty} y(t) = 0.$$

Hence, for any $\varepsilon > 0$ sufficiently small, there exists a $T_2 > T_1 + \tau$ such that if $t > T_2$, $0 < y(t) < \varepsilon.$

It follows from the first equation of system (1.1) that for $t > T_2$,

$$x'(t) \ge x(t)(\frac{r_0}{1+k\varepsilon} - d - p\varepsilon - ax(t)),$$

which yields

$$\liminf_{t \to +\infty} x(t) \ge \frac{r_0 - (d + p\varepsilon)(1 + k\varepsilon)}{a(1 + k\varepsilon)}$$

Since it is true for any $\varepsilon > 0$ sufficiently small, we have

$$\liminf_{t \to +\infty} x(t) = \frac{r_0 - d}{a}$$

Thus, the proof is complete.

2.2. Stability of the positive equilibrium and local Hopf bifurcation

Linearizing system (1.1) at E_2 yields the characteristic equation

$$\lambda^2 + q\lambda + r + (s\lambda + l)e^{-\lambda\tau} = 0, \qquad (2.4)$$

where $q = m + a\overline{x} > 0$, $r = am\overline{x} > 0$, s = -m < 0, $l = -am\overline{x} + cp^2 \overline{x}\overline{y} + \frac{cpkr_0 \overline{x}\overline{y}}{(1+k\overline{y})^2}$. For $\tau = 0$, the characteristic equation becomes

$$\lambda^{2} + (q+s)\lambda + r + l = 0, \qquad (2.5)$$

which has the roots

$$\lambda = \frac{-(q+s) \pm \sqrt{(q+s)^2 - 4(r+l)}}{2}.$$
(2.6)

Observing equation (2.6), we can find that all roots have negative real parts since $q + s = a\overline{x} > 0$ and $r + l = cp^2 \overline{x}\overline{y} + \frac{cpkr_0\overline{x}\overline{y}}{(1+k\overline{y})^2} > 0$. Now for $\tau > 0$, if $\lambda = iw$ is a root of equation (2.4), then we have

$$-w^2 + iqw + r + iswe^{-iw\tau} + le^{-iw\tau} = 0.$$

Separating the real and imaginary parts, we have

$$\begin{cases} sw\sin w\tau + l\cos w\tau = w^2 - r, \\ l\sin w\tau - sw\cos w\tau = qw, \end{cases}$$
(2.7)

which yields

$$w^4 + w^2(q^2 - 2r - s^2) + r^2 - l^2 = 0.$$
 (2.8)

It follows that if $r^2 - l^2 < 0$, equivalently,

$$k > \frac{(2am - cp^2\bar{y})(1 + k\bar{y})^2}{cpr_0\bar{y}},$$
(2.9)

then equation (2.8) has a positive solution

$$w^{2} = \frac{(s^{2} - q^{2} + 2r) + \sqrt{(q^{2} - s^{2} - 2r)^{2} - 4(r^{2} - l^{2})}}{2},$$
 (2.10)

which suggests the characteristic equation (2.4) has a pair of purely imaginary roots. However, if $r \ge l$, equation (2.4) dose not have purely imaginary roots. Summarizing what has been discussed we have the following result.

Theorem 2.3. If (2.9) is reversed, then all roots of equation (2.4) have negative real parts for all $\tau \geq 0$; that is, the equilibrium E_2 is locally asymptotically stable for all $\tau \geq 0$.

From (2.8), we can see that there is a unique positive solution (2.10) if (2.9) holds. Now we calculate the value of τ by substituting (2.10) into system (2.7) and obtain

$$\tau_j = \frac{1}{w} \{\arccos \frac{(l-sq)w^2 - lr}{l^2 + s^2 w^2} + 2j\pi\}, j = 0, 1, 2, 3, \cdots.$$
(2.11)

From the above analysis, we get the following result.

Lemma 2.2. If (2.9) holds, then the equation (2.4) with $\tau = \tau_j$ has a pair of purely imaginary roots $\pm iw$.

Differentiating equation (2.4) with respect to τ , we obtain

$$(2\lambda + q + (s - \tau(s\lambda + l))e^{-\lambda\tau})\frac{d\lambda}{d\tau} = \lambda(s\lambda + l)e^{-\lambda\tau}.$$
(2.12)

Thus,

$$\left(\frac{d\lambda}{d\tau}\right)^{-1} = -\frac{2\lambda + q}{\lambda(\lambda^2 + q\lambda + r)} + \frac{s}{\lambda(s\lambda + l)} - \frac{\tau}{\lambda}.$$
(2.13)

Then we can obtain

$$sign\left\{Re\frac{d\lambda}{d\tau}\right\}_{\tau=\tau_{j}} = sign\left\{Re\frac{d\tau}{d\lambda}\right\}_{\lambda=iw}$$
$$= sign\left\{\frac{w^{4}s^{2} + 2w^{2}l^{2} - 2rl^{2} + q^{2}l^{2} - s^{2}r^{2}}{[q^{2}w^{2} + (r - w^{2})^{2}](w^{2}s^{2} + l^{2})}\right\}.$$
 (2.14)

Substituting the expression of w^2 into equation (2.14) under the condition l-r > 0, we can get the result $sign \left\{ Re \frac{d\lambda}{d\tau} \right\}_{\tau=\tau_j} > 0$. Regrouping our results we have the following theorem.

Theorem 2.4. For system (1.1), we have:

- (i) If (2.9) is reversed, then the positive equilibrium E_2 is locally asymptotically stable for all $\tau \ge 0$;
- (ii) If (2.9) holds, then the positive equilibrium E_2 is locally asymptotically stable for $\tau \in [0, \tau_0)$ and unstable for $\tau > \tau_0$. Hopf bifurcation occurs when $\tau = \tau_0$; that is, a family of periodic solutions bifurcates from E_2 as τ passes through the critical value τ_0 .

Remark 2.1. By making comparison, we are able to discover a fabulous fact. In [25], the positive equilibrium is globally asymptotically stable in the model with linear functional response. However, if we consider the time delay τ in the way as system (1.1), the positive equilibrium is even not locally asymptotically stable when τ is bigger than τ_0 , that is, the time delay can destabilize a stable equilibrium and induce oscillations in the predator-prey model.

3. Direction and stability of the Hopf bifurcation

In this section, we get the conditions which guarantee system (1.1) undergoes the Hopf bifurcation at the positive equilibrium E_2 when $\tau = \tau_j$. In this section, we shall determine the direction, stability and period of the bifurcating periodic solutions by using the norm form and the center manifold theory developed by Hassard et al. [11] . Denote any of these critical values $\tau = \tau_j (j = 0, 1, 2, \cdots)$ by $\tilde{\tau}$. Let $u_1(t) = x(\tau t) - \bar{x}, u_2(t) = y(\tau t) - \bar{y}$ and $\tau = \tilde{\tau} + \mu, \mu \in \mathbb{R}$. Then $\mu = 0$ is the Hopf bifurcation value of system (1.1). Then (1.1) can be written as

$$\begin{cases} u_1'(t) = (\tilde{\tau} + \mu) \left(\frac{r_0(u_1(t) + \overline{x})}{1 + k(u_2(t) + \overline{y})} - d(u_1(t) + \overline{x}) - a(u_1(t) + \overline{x})^2 - p(u_1(t) + \overline{x})(u_2(t) + \overline{y}) \right), \\ u_2'(t) = (\tilde{\tau} + \mu)(cp(u_1(t-1) + \overline{x})(u_2(t-1) + \overline{y}) - m(u_2(t) + \overline{y})). \end{cases}$$

$$(3.1)$$

Hence, we can analyze in the space $D = C([-1,0], R^2)$, which does not depend on the time delay τ . And the system above can be translated into a FDE as

$$u(t) = L_{\mu}(u_t) + F(\mu + u_t).$$
(3.2)

Denote the right side of the first equation of (1.1) as $f^1(x(t-\tau), x(t), y(t-\tau), y(t))$ and the right side of the second equation of (1.1) as $f^2(x(t-\tau), x(t), y(t-\tau), y(t))$, then for any $\varphi = (\varphi_1, \varphi_2) \in D$, let

$$L_{\mu}(\varphi) = (\tilde{\tau} + \mu) \begin{pmatrix} -a\overline{x}\varphi_1(0) - \left(\frac{kr_0\overline{x}}{(1+k\overline{y})^2} + p\overline{x}\right)\varphi_2(0) \\ cp\overline{y}\varphi_1(-1) + cp\overline{x}\varphi_2(-1) - m\varphi_2(0) \end{pmatrix}$$
(3.3)

and

$$F(\mu,\varphi) = (\tilde{\tau}+\mu) \begin{pmatrix} f_{22}^1(\varphi_1(0))^2 + f_{24}^1\varphi_1(0)\varphi_2(0) + f_{44}^1(\varphi_2(0))^2 + \cdots \\ cp\varphi_1(-1)\varphi_2(-1) \end{pmatrix}, \quad (3.4)$$

where

$$\begin{split} f_{22}^{1} &= \left. \frac{\partial^{2} f^{1}(x(t-\tau), x(t), y(t-\tau), y(t))}{\partial x(t)^{2}} \right|_{(\overline{x}, \overline{y})}, \\ f_{24}^{1} &= \left. \frac{\partial^{2} f^{1}(x(t-\tau), x(t), y(t-\tau), y(t))}{\partial x(t) \partial y(t)} \right|_{(\overline{x}, \overline{y})}, \\ f_{44}^{1} &= \left. \frac{\partial^{2} f^{1}(x(t-\tau), x(t), y(t-\tau), y(t))}{\partial y(t)^{2}} \right|_{(\overline{x}, \overline{y})}. \end{split}$$

We consider the following linear equation

$$u(t) = L_{\mu}(u_t).$$
 (3.5)

By the Riese representation theorem, there exists a matrix of which components are bounded variation $\eta(\theta, \mu)$ in $\theta \in [-1, 0]$ such that

$$L_{\mu}\varphi = \int_{-1}^{0} \mathrm{d}\eta(\theta,\mu)\varphi(\theta), \quad \text{for } \varphi \in D.$$

and $\eta(\theta, \mu)$ can be chosen as

$$\eta(\theta,\mu) = \begin{cases} \left(\tilde{\tau}+\mu\right) \begin{pmatrix} -a\overline{x} \ \frac{-kr_0\overline{x}}{(1+k\overline{y})^2} - p\overline{x} \\ 0 & -m \end{pmatrix}, \ \theta = 0, \\ 0, & \theta \in (-1,0), \\ \left(\tilde{\tau}+\mu\right) \begin{pmatrix} 0 & 0 \\ -cp\overline{y} - cp\overline{x} \end{pmatrix}, & \theta = -1. \end{cases}$$
(3.6)

For any $\varphi \in C^1([-1,0], \mathbb{R}^2)$, define

$$A(\mu)\varphi = \begin{cases} \frac{\mathrm{d}\varphi(\theta)}{\mathrm{d}\theta}, & \theta \in [-1,0), \\ \int_{-1}^{0} \mathrm{d}\eta(\xi,\mu)\varphi(\xi), \, \theta = 0, \end{cases}$$
$$R(\mu)\varphi = \begin{cases} 0, & \theta \in [-1,0), \\ F(\mu,\varphi), \, \theta = 0. \end{cases}$$

Then system (3.1) can be written as

$$\dot{u}_t = A(\mu)u_t + R(\mu)u_t, \tag{3.7}$$

where $u_t(\theta) = u(t+\theta)$ for $\theta \in [-1,0]$. For $\psi \in C^1([0,1], (R^2)^*)$, define

$$A^*\psi = \begin{cases} -\frac{\mathrm{d}\psi(s)}{\mathrm{d}s}, & s \in (0,1]\\ \int_{-1}^0 \psi(-\theta)\mathrm{d}\eta^T(\theta,0), & s = 0, \end{cases}$$

and a bilinear inner product

$$\langle \psi(s), \varphi(\theta) \rangle = \bar{\psi}(0)\varphi(0) - \int_{-1}^{0} \int_{\xi=0}^{\theta} \bar{\psi}(\xi-\theta) \mathrm{d}\eta(\theta,0)\varphi(\xi) \mathrm{d}\xi.$$
(3.8)

Then A(0) and A^* are adjoint operators.

By the analysis in the last section, we get that $\pm i\tilde{\tau}w$ are eigenvalues of A(0). Hence, they are also eigenvalues of A^* . Supposing that $q(\theta)$ is the eigenvector of A(0) corresponding to $i\tilde{\tau}\omega$ and $q^*(s)$ is the eigenvector of A^* corresponding to $-i\tilde{\tau}\omega$, then it is easy to calculate $q(\theta) = (1, \gamma)^T e^{i\theta\omega\tilde{\tau}}$ and $q^*(s) = H(\gamma^*, 1)e^{is\omega\tilde{\tau}}$, where $\gamma = \frac{-(a\bar{x}+iw)(1+k\bar{y})^2}{kr_0\bar{x}+(1+k\bar{y})^2p\bar{x}}$, $\gamma^* = \frac{cp\bar{y}e^{iw\tilde{\tau}}}{a\bar{x}-iw}$. Since

$$\langle q^*(s), q(\theta) \rangle = \bar{H} \left\{ (\bar{\gamma^*}, 1)(1, \gamma)^T - \int_{-1}^0 \int_{\xi=0}^\theta (\bar{\gamma^*}, 1) e^{-i(\xi-\theta)\omega\tilde{\tau}} \mathrm{d}\eta(\theta, 0)(1, \gamma)^T e^{i\xi\omega\tilde{\tau}} \mathrm{d}\xi \right\}$$

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$$= \bar{H}[\bar{\gamma^*} + \gamma + (cp\bar{y} + \gamma cp\bar{x})\tilde{\tau}e^{-iw\tilde{\tau}}]$$

= 1,

we can choose ${\cal H}$ as

$$H = \frac{1}{\bar{\gamma} + \gamma^* + (cp\overline{y} + \bar{\gamma}cp\overline{x})\tilde{\tau}e^{iw\tilde{\tau}}}.$$
(3.9)

Using the same notations as in Hassard et al.[32], We first compute the coordinates to describe the center manifold D_0 at $\mu = 0$. Let u_t be the solution of equation (3.1) when $\mu = 0$. Denote

$$z(t) = \langle q^*, u_t \rangle, \quad W(t, \theta) = u_t(\theta) - z(t)q(\theta) - \bar{z}(t)\bar{q}(\theta), \tag{3.10}$$

then on the center manifold D_0 , we have

$$W(t,\theta) = W(z(t), \bar{z}(t), \theta),$$

where

$$W(z, \bar{z}, \theta) \triangleq W_{20}(\theta) \frac{z^2}{2} + W_{11}(\theta) z \bar{z} + W_{02}(\theta) \frac{\bar{z}^2}{2} + \cdots,$$

z and \bar{z} are local coordinates for center manifold D_0 in the direction of q^* and $\bar{q^*}$. Note that W is real if u_t is real. We only consider real solutions. For the solution $u_t \in D_0$ of (3.1), since $\mu = 0$, we have

$$\dot{z(t)} = i\tilde{\tau}\omega z + \langle q^*(\theta), F(0, zq(\theta) + \bar{z}\bar{q}(\theta) + W(z, \bar{z}, \theta)) \rangle$$

$$\triangleq i\tilde{\tau}\omega z + \bar{q^*}(0)F_0,$$

that is,

$$\dot{z}(t) = i\omega\tilde{\tau}z(t) + g(z(t), \bar{z(t)}), \qquad (3.11)$$

where

$$g(z,\bar{z}) = \bar{q^*}(0)F_0(z,\bar{z}) = g_{20}\frac{z^2}{2} + g_{11}z\bar{z} + g_{02}\frac{\bar{z}^2}{2} + g_{21}\frac{z^2\bar{z}}{2}\cdots$$
 (3.12)

It follows from (3.10) that

$$u_t(\theta) = (u_{1t}(\theta), u_{2t}(\theta))^T$$

= $W(t, \theta) + zq(\theta) + \bar{z}\bar{q}(\theta)$
= $W_{20}(\theta)\frac{z^2}{2} + W_{11}(\theta)z\bar{z} + W_{02}(\theta)\frac{\bar{z}^2}{2} + (1, \gamma)^T e^{iw\tilde{\tau}\theta}z + (1, \bar{\gamma})^T e^{-iw\tilde{\tau}\theta}\bar{z} + \cdots$

This, together with (3.4), suggests that

$$\begin{split} g(z,\bar{z}) &= \bar{q^*}(0)F_0(z,\bar{z}) \\ &= \tilde{\tau}\bar{H}(\bar{\gamma^*},1) \begin{pmatrix} -2au_{1t}^2(0) - (\frac{kr_0}{(1+k\bar{y})^2} + p)u_{1t}(0)u_{2t}(0) + \frac{2kr_0\bar{x}}{(1+k\bar{y})^3}u_{2t}^2(0) \\ &cpu_{1t}(-1)u_{2t}(-1) \\ & \\ &\triangleq \tilde{\tau}\bar{H}(\bar{\gamma^*},1) \begin{pmatrix} -2au_{1t}^2(0) - \beta u_{1t}(0)u_{2t}(0) + \delta u_{2t}^2(0) \\ &cpu_{1t}(-1)u_{2t}(-1) \end{pmatrix} \end{split}$$

$$\begin{split} &= \tilde{\tau}\bar{H}\left\{-2au_{1t}^{2}(0)\bar{\gamma^{*}} - \beta u_{1t}(0)u_{2t}(0)\bar{\gamma^{*}} + \delta u_{2t}^{2}(0)\bar{\gamma^{*}} + cpu_{1t}(-1)u_{2t}(-1)\right\} \\ &= \tilde{\tau}\bar{H}\left\{\left[-2a\bar{\gamma^{*}} - \beta\bar{\gamma^{*}}\gamma + \delta\bar{\gamma^{*}}\gamma^{2} + cp\gamma e^{-2iw\tilde{\tau}}\right]z^{2} \\ &+ \left[-4a\bar{\gamma^{*}} - \beta\bar{\gamma^{*}}(\gamma + \bar{\gamma}) + 2\delta\bar{\gamma^{*}}\gamma\bar{\gamma} + cp(\bar{\gamma} + \gamma)\right]z\bar{z} \\ &+ \left[-2a\bar{\gamma^{*}} - \beta\bar{\gamma^{*}}\bar{\gamma} + \delta\bar{\gamma^{*}}\bar{\gamma}^{2} + cp\bar{\gamma}e^{2iw\tilde{\tau}}\right]\bar{z}^{2} \\ &+ \left[-2a\bar{\gamma^{*}}\left(W_{20}^{(1)}(0) + 2W_{11}^{(1)}(0)\right) \\ &- \beta\bar{\gamma^{*}}\left(W_{11}^{(2)}(0) + \frac{1}{2}W_{20}^{(2)}(0) + \frac{1}{2}W_{20}^{(1)}(0)\bar{\gamma} + W_{11}^{(1)}(0)\gamma\right) \\ &+ cp\left((W_{11}^{(2)}(-1) + W_{11}^{(1)}(-1)\gamma)e^{-iw\tilde{\tau}} + \frac{1}{2}(W_{20}^{(2)}(-1) + W_{20}^{(1)}(-1)\bar{\gamma})e^{iw\tilde{\tau}}\right) \\ &+ \delta\bar{\gamma^{*}}\left(2W_{11}^{(2)}(0)\gamma + W_{20}^{(2)}(0)\bar{\gamma}\right)\right]z^{2}\bar{z} + \cdots\right\}. \end{split}$$

Comparing the coefficients with (3.12), we get

$$\begin{split} g_{20} &= 2\tilde{\tau}\bar{H}(-2a\bar{\gamma^*} - \beta\bar{\gamma^*}\gamma + \delta\bar{\gamma^*}\gamma^2 + cp\gamma e^{-2iw\tilde{\tau}}),\\ g_{11} &= \tilde{\tau}\bar{H}(-4a\bar{\gamma^*} - \beta\bar{\gamma^*}(\gamma + \bar{\gamma}) + 2\delta\bar{\gamma^*}\gamma\bar{\gamma} + cp(\bar{\gamma} + \gamma)),\\ g_{02} &= 2\tilde{\tau}\bar{H}(-2a\bar{\gamma^*} - \beta\bar{\gamma^*}\bar{\gamma} + \delta\bar{\gamma^*}(\bar{\gamma})^2 + cp\bar{\gamma}e^{2iw\tilde{\tau}}),\\ g_{21} &= 2\tilde{\tau}\bar{H}\bigg[(-2a\bar{\gamma^*} - \frac{1}{2}\beta\bar{\gamma^*}\bar{\gamma})W_{20}^{(1)}(0) + (-4a\bar{\gamma^*} - \beta\bar{\gamma^*}\gamma)W_{11}^{(1)}(0) \\ &\quad + (-\frac{1}{2}\beta\bar{\gamma^*} + \delta\bar{\gamma^*}\bar{\gamma})W_{20}^{(2)}(0) + (2\delta\bar{\gamma^*}\gamma - \beta\bar{\gamma^*})W_{11}^{(2)}(0) \\ &\quad + \frac{1}{2}cp(W_{20}^{(1)}(-1) + W_{20}^{(2)}(-1))e^{iw\tilde{\tau}} + cp(\gamma W_{11}^{(1)}(-1) + W_{11}^{(2)}(-1))e^{-iw\tilde{\tau}}\bigg]. \end{split}$$

Then we still need to compute $W_{20}(\theta)$ and $W_{11}(\theta)$ since they are included in g_{21} . From (3.7) and (3.10), we have

$$\dot{W} = \dot{u}_t - \dot{z}q - \dot{\bar{z}}\bar{q} = \begin{cases} AW - gq(\theta) - \bar{g}\bar{q}(\theta), & \theta \in [-1,0), \\ AW - gq(0) - \bar{g}\bar{q}(0) + F_0, \theta = 0. \end{cases}$$
(3.13)

Besides, on the center manifold ${\cal D}_0$ near the origin, we obtain

$$\begin{split} \dot{W} &= W_{z}\dot{z} + W_{\bar{z}}\dot{z} \\ &= [W_{20}(\theta)z + W_{11}(\theta)\bar{z}]\dot{z} + [W_{11}(\theta)z + W_{02}(\theta)\bar{z}]\dot{z} + \cdots \\ &= [W_{20}(\theta)z + W_{11}(\theta)\bar{z}]\left(i\omega\tilde{\tau}z + g(z,\bar{z})\right) \\ &+ [W_{11}(\theta)z + W_{02}(\theta)\bar{z}]\left(-i\omega\tilde{\tau}\bar{z} + \bar{g}(z,\bar{z})\right) + \cdots . \end{split}$$

This, together with (3.13), implies that

$$(2i\omega\tilde{\tau}I - A)W_{20}(\theta) = \begin{cases} -g_{20}q(\theta) - \bar{g}_{02}\bar{q}(\theta), & \theta \in [-1,0) \\ -g_{20}q(0) - \bar{g}_{02}\bar{q}(0) + F_{z^2}, \, \theta = 0 \end{cases}$$
(3.14)

and

$$AW_{11}(\theta) = \begin{cases} -g_{11}q(\theta) - \bar{g}_{11}\bar{q}(\theta), & \theta \in [-1,0) \\ -g_{11}q(0) - \bar{g}_{11}\bar{q}(0) + F_{z\bar{z}}, \, \theta = 0. \end{cases}$$
(3.15)

According to (3.14) and the definition of A_0 , when $\theta \in [-1, 0)$, we obtain

$$W_{20}'(\theta) = 2i\omega\tilde{\tau}W_{20}(\theta) + g_{20}q(\theta) + \bar{g}_{02}\bar{q}(\theta),$$

of which the solution is

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$$W_{20}(\theta) = \frac{ig_{20}}{\omega\tilde{\tau}}q(0)e^{i\omega\tilde{\tau}\theta} + \frac{i\bar{g}_{02}}{3\omega\tilde{\tau}}\bar{q}(0)e^{-i\omega\tilde{\tau}\theta} + E_1e^{2i\omega\tilde{\tau}\theta}.$$
(3.16)

And when $\theta = 0$, we have

$$\int_{-1}^{0} \mathrm{d}_{\theta} \eta(\theta, 0) W_{20}(\theta) = 2i\omega \tilde{\tau} W_{20}(0) + g_{20}q(0) + \bar{g}_{02}\bar{q}(0) - F_{z^2}.$$
(3.17)

Substituting (3.16) into (3.17), and noticing $\left(i\omega\tilde{\tau}I - \int_{-1}^{0} e^{i\omega\tilde{\tau}\theta} d_{\theta}\eta(\theta,0)\right)q(0) = 0$, we can derive that

$$E_{1} = \left[2i\omega\tilde{\tau}I - \int_{-1}^{0} e^{2i\omega\tilde{\tau}\theta} d_{\theta}\eta(\theta, 0)\right]^{-1} F_{z^{2}}$$
$$= (\tilde{\tau})^{-1} \left(\begin{array}{c} 2i\omega + a\overline{x} & -\frac{kr_{0}\overline{x}}{(1+k\overline{y})^{2}} + p\overline{x} \\ -cp\overline{y}e^{-2iw\tilde{\tau}} & 2iw + m - cp\overline{x}e^{-2iw\tilde{\tau}} \end{array} \right)^{-1} \times \left(\begin{array}{c} -2a - \beta\gamma + \delta\gamma^{2} \\ cp\gamma e^{-2iw\tilde{\tau}} \end{array} \right).$$

Similarly, as discussed above , when $\theta \in [-1,0),$ we have

$$W'_{11}(\theta) = g_{11}q(\theta) + \bar{g}_{11}\bar{q}(\theta).$$

It is easy to calculate the solution as follows,

$$W_{11}(\theta) = -\frac{ig_{11}}{\omega\tilde{\tau}}q(0)e^{i\omega\tilde{\tau}\theta} + \frac{i\bar{g}_{11}}{\omega\tilde{\tau}}\bar{q}(0)e^{-i\omega\tilde{\tau}\theta} + E_2, \qquad (3.18)$$

and $W_{11}(\theta)$ satisfies

$$\int_{-1}^{0} \mathrm{d}_{\theta} \eta(\theta, 0) W_{11}(\theta) = g_{11} q(0) + \bar{g}_{11} \bar{q}(0) - F_{z\bar{z}}.$$
(3.19)

when $\theta = 0$. Then

$$E_{2} = -\left[\int_{-1}^{0} d_{\theta}\eta(\theta, 0)\right]^{-1} F_{z\bar{z}}$$
$$= (\tilde{\tau})^{-1} \begin{pmatrix} a\bar{x} & \frac{kr_{0}\bar{x}}{(1+k\bar{y})^{2}} + p\bar{x} \\ -cp\bar{y} & m - cp\bar{x} \end{pmatrix}^{-1} \times \begin{pmatrix} -4a - \beta(\gamma + \bar{\gamma}) + 2\delta\gamma\bar{\gamma} \\ cp(\gamma + \bar{\gamma}) \end{pmatrix}$$

can be calculated.

Now, we can compute the values of $W_{20}(\theta)$ and $W_{11}(\theta)$, and get the following values:

$$c_{1}(0) = \frac{i}{2\omega\tilde{\tau}} \left[g_{11}g_{20} - 2|g_{11}|^{2} - \frac{|g_{02}|^{2}}{3} \right] + \frac{g_{21}}{2}$$
$$\mu_{2} = -\frac{\operatorname{Re}(c_{1}(0))}{\operatorname{Re}(\lambda'(\tilde{\tau}))},$$
$$\beta_{2} = 2\operatorname{Re}(c_{1}(0)),$$
$$T_{2} = -\frac{\operatorname{Im}(c_{1}(0)) + \mu_{2}\operatorname{Im}(\lambda'(\tilde{\tau}))}{\omega\tilde{\tau}},$$

which determine the properties of bifurcating periodic solutions at the critical value $\tilde{\tau}$, i.e., μ_2 determines the directions of the Hopf bifurcation: if $\mu_2 > 0(<0)$, then Hopf bifurcation is supercritical (subcritical) and the bifurcating periodic solutions exist for $\tau > \tilde{\tau}(\tau < \tilde{\tau})$; β_2 determines the stability of the bifurcating periodic solutions: the bifurcating periodic solutions in the center manifold are stable(unstable) if $\beta_2 < 0(\beta_2 > 0)$; and T_2 determines the period of bifurcating periodic solutions: the period increases (decreases) if $T_2 > 0(<0)$. Furthermore, according to what has been analysed above, we obtain the following theorem about the direction of the Hopf bifurcation.

Theorem 3.1. For system (1.1), suppose that (2.9) holds, then the Hopf bifurcations occur at E_2 when $\tau = \tau_j$. Moreover, if $Re(c_1(0)) < 0$ ($Re(c_1(0)) > 0$), the Hopf bifurcations are supercritical (subcritical), and the bifurcating periodic solutions in the center manifold are stable(unstable).

0.3 ٥. 0.3 0.35 0.25 0.3 0.25 0.2 0.2 0.15 0.15 0.1 L 0.1 0.6 × 0.6 0.8 1.2 x (b) (a)

4. Numerical simulations

Figure 1. (a) The equilibrium $(\bar{x}, \bar{y}) = (0.500, 0.2355)$ is locally asymptotically stable when $\tau = 0$. Here x(0) = 0.32, y(0) = 0.15. (b) There is a bifurcating periodic solution for $\tau = 5.28$.

In this section, to better demonstrate the analytical results about the effects of the time delay and the fear of predators, we will give some numerical simulations for the system (1.1) by using the software Matlab R2014a.

As an example, by making parameters are $r_0 = 0.14, k = 8, d = 0.02, a = 0.01, p = 0.1, c = 0.4, m = 0.02$, we firstly consider the system

$$\begin{cases} x'(t) = \frac{0.14x(t)}{1+8y(t)} - 0.02x(t) - 0.01(x(t))^2 - 0.1x(t)y(t), \\ y'(t) = 0.04x(t-\tau)y(t-\tau) - 0.02y(t). \end{cases}$$
(4.1)

There is a positive equilibrium $(\bar{x}, \bar{y}) = (0.500, 0.2355)$. Case I. $\tau = 0$. In this



Figure 2. Behavior of the prey and predator populations for k = 8, $\tau = 6$.

case, the numerical simulation (see Fig.1(a)) shows that the predator and prey's populations spiral toward the equilibrium (0.500, 0.2355).

Case II. $\tau \neq 0$. We are interested in the combined effect of the delay τ and the fear effect k on the dynamics of the model. By Theorem 2.4, There is a critical value $\tau_0 = 5.2706$, the equilibrium (\bar{x}, \bar{y}) is stable when $\tau < 5.2706$; Hopf bifurcation occurs when $\tau = 5.2706$; and the equilibrium becomes unstable and a bifurcating periodic solution exists when $\tau > 5.2706$ (see Fig.1(b)).

We can also vary the value of k to see how it affects the dynamics. For example, choose $\tau = 6$ (a value at which the positive equilibrium is unstable), both the prey and predator's populations oscillate about the equilibrium values when k = 8 (see Fig.2);

However, when k = 60 (a value which is bigger enough), both the prey and predator's populations converge to the equilibrium values (See Fig.3).Therefore, the system regains its stability when the fear effect is increased. This indicates that the fear effect k has an effect of stabilizing the equilibrium of the model.

5. Summary and discussion

In this paper, we have studied a predator-prey system with time delay and fear effect caused by the prey after they perceived the predation risk. In our model, the linear functional response function has been considered and we have got some interesting results.

It has been shown that when the time delay does not exist, the unique positive equilibrium is locally asymptotically stable, that is, the cost of fear does not affect the dynamical behaviors of the system (1.1). However, compared with the model



Figure 3. Behavior of the prey and predator populations for $k = 60, \tau = 6$.

in [25], if the time delay exists, it can not only destroy the global stability of the positive equilibrium, but also can induce instability and oscillations via Hopf bifurcation in our model, and then by using the normal form theory and center manifold argument, we have derived explicit formulas which determine the stability and the direction of periodic solutions bifurcating from Hopf bifurcation; Moreover, fear of predators has the effect of stabilizing the positive equilibrium, and then our model regains its stability when the fear level is increased.

There still be a tremendous amount of work to do in this area. For example, it would be interesting to see what the behaviors of system (1.1) would be when the spatial dispersal is considered into the interaction. Besides, system (1.1) with the harvesting strategy could also be observed. We leave these for future research projects.

References

- S. Creel, D. Christianson, Relationships between direct predation and risk effects, Trends Ecol Evolut, 2008, 23(4), 194–201.
- [2] W. Cresswell, Predation in bird populations, J. Ornithol, 2011, 152(1), 251–263.
- [3] M. Clinchy, M. J. Sheriff, L. Y. Zanette, Predator-induced stress and the ecology of fear, Funct Ecol, 2013, 27(1), 56–65.
- [4] S. Creel, D. Christianson, S. Liley, J. A. Winnie, Predation risk affects reproductive physiology and demography of elk, Science, 2007, 315(5814), 960-šC960.
- [5] S. Eggers, M. Griesser, J. Ekman, Predator-induced plasticity in nest visitation rates in the Siberian jay(Perisoreus infaustus), Behav Ecol, 2005, 16(1), 309– 315.
- [6] S. Eggers, M. Griesser, M. Nystrand, J. Ekman, Predation risk induces changes in nest-site selection and clutch size in the Siberian jay, Proc R Soc B Biol Sci, 2006, 273(1587), 701–706.
- [7] J. J. Fontaine, T. E. Martin, Parent birds assess nest predation risk and adjust their reproductive strategies, Ecol Lett, 2006, 9(4), 428–434.

- [8] C. K. Ghalambor, S. I. Peluc, T. E. Martin, *Plasticity of parental care under the risk of predation: how much should parents reduce care?* BiolLett, 2013, 9(4), 20130154.
- [9] F. Hua, R. J. Fletcher, K. E. Sieving, R. M. Dorazio, Too risky to settle: avian community structure changes in response to perceived predation risk on adults and offspring, Proceedings of the Royal Society B: Biological Sciences, 2013, 280(1764), 20130762.
- [10] F. Hua, K. E. Sieving, R. J. Fletcher, C. A. Wright, Increased perception of predation risk to adults and offspring alters avian reproductive strategy and performance, Behav Ecol, 2014, 25(3), 509–519.
- [11] B. D. Hassard, N. D. Kazarinoff, Y. H. Wan, Theory and applications of Hopf bifurcation, Cambridge Univ. Press, Cambridge, 1981.
- [12] J. Hale, S. V. Lunel, Introduction to Functional Differential Equations, vol 99. Springer, Berlin, 1993.
- [13] S. L. Lima, Nonlethal effects in the ecology of predatoršCprey interactions, Bioscience, 1998, 48(1), 25–34.
- [14] A. Martin, S. Ruan, Predator-prey models with delay and harvesting, J. Math. Biol., 2001, 43, 247–267.
- [15] J. D. Meiss, *Differential dynamical systems*, vol 14. SIAM, Philadelphia, 2007.
- [16] J. L. Orrock, R. J. Fletcher, An island-wide predator manipulation reveals immediate and long-lasting matching of risk by prey, Proc R Soc B Biol Sci, 2014, 281(1784), 20140391.
- [17] E. L. Preisser, D.I. Bolnick, The many faces of fear: comparing the path ways and impacts of noncon- sumptive predator effects on prey populations, PloS One, 2008, 3(6), e2465.
- [18] N. Pettorelli, T. Coulson, S. M.Durant, J. M.Gaillard, Predation, individual variability and vertebrate population dynamics, Oecologia, 2011, 167(2), 305– 314.
- [19] S. D. Peacor, B. L. Peckarsky, G. C. Trussell, J. R. Vonesh, Costs of predatorinduced phenotypic plasticity: a graphical model for predicting the contribution of nonconsumptive and consumptive effects of predators on prey, Oecologia, 2013, 171(1), 1–10.
- [20] M. J. Sheriff, C. J. Krebs, R. Boonstra, The sensitive hare: sublethal effects of predator stress on reproduction in snowshoe hares, J Anim Ecol, 2009, 78(6), 1249–1258.
- [21] H. Shu, X. Hu, L. Wang, W. James, Delay induced stability switch, multitype bistability and chaos in an intraguild predation model, J. Math. Biol., 2015, 71, 1269–1298.
- [22] G. Seo, D. L. DeAngelis, A predatoršCprey model with a Holling type I functional response including a predator mutual interference, J Nonlinear Sci, 2011, 21(6), 811–833.
- [23] Y. Song, J. Wei, Local Hopf bifurcation and global periodic solutions in a delayed predatr-prey system, J. Math. Anal. Appl., 2005, 301, 1–21.
- [24] A. J. Wirsing, W. J. Ripple, A comparison of shark and wolf research reveals similar behavioural responses by prey, Front Ecol Environ, 2011, 9(6), 335–341.

- [25] X.Wang, L. Y.Zanette, X. Zou, Modelling the fear effect in predator-prey interactions, J Math Biol., 2016, 73, 1179–1204.
- [26] X. Wang, X. Zou, Modeling the fear effect in Predator-prey interactions with adaptive avoidance of predators, Bull Math Biol., 2017, 79, 1325–1359.
- [27] L. Y. Zanette, A. F. White, M. C. Allen, M. Clinchy, Perceived predation risk reduces the number of offspring songbirds produce per year, Science, 2011, 334(6061), 1398–1401.