Complex dynamics in an eco-epidemiological model with the cost of anti-predator behaviors

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Abstract In this paper, we investigate the complex dynamics of a predator–prey model with disease in the prey, which is characterized by the reduction of prey growth rate due to the anti-predator behavior. The value of this study lies in two aspects: Mathematically, it provides the existence and the stability of the equilibria and gives the existence of Hopf bifurcation. And epidemiologically, we find that the influence of the fear factor is complex: (i) The level of the population density decreases with the increasing of the fear factor; (ii) the cost of fear can destabilize the stability and benefit the emergency of the periodic behavior; and (iii) the high level of fear can induce the extinction of the predator. These results may enrich the dynamics of the eco-epidemiological systems.

Keywords Fear factor · Eco-epidemiological model · Hopf bifurcation · Extinction

1 Introduction

The dynamic relationship between predators and their prey is one of the dominant themes in theoretical ecology due to its universal existence and importance [17]. It is a central topic to study the mechanisms driving predator–prey systems in ecology and evolutionary biology [35]. The research results of prey–predator models are helpful to understand the interactions of different species within a fluctuating natural environment [4, 5, 10].

Predator–prey interactions are modified by considering various ecological factors [15, 26]. In the previous models, predators only affect the density of prey population through direct killing [18]. A new view is that the presence of predators can also change the behavior and physiological characteristics of the prey to a certain extent, so as to affect the amount of the prey population, and its influence degree is even greater than that of direct killing [7, 20, 28, 37, 40]. And Zanette et al. [40] experimentally showed that there is about 40% reduction in offspring production of the song sparrows due to the fear from predators. Wang et al. [35] first introduced the fear factor $F(k, w)$, which accounts for the cost of anti-predator defense due to the fear on a predator–prey system. Their insightful work has drawn many scholars’ attention and developed some predator–prey models incorporating the fear effect [24, 25, 30, 33, 34, 36, 41].

On the other hand, in the natural world, species do not exist alone, and more and more studies show that the competition of resources and space among populations, as well as infectious diseases, affects population growth. Therefore, the combination of the
predator–prey model and the epidemic model, i.e., eco-epidemiological model, has a very high research ability [9,11,12]. Simply speaking, the so-called eco-epidemiological models are demographic models accounting for interactions among different populations in which a disease also spreads [21]. Recently, eco-epidemiological models have drawn much attention of scientists [2,3,6,13,16,29,32,38,39]. At the same time, complex dynamics, such as bistability, quasiperiodicity and chaos, has been found in many eco-epidemiological models [2]. But little attention has been paid so far to the study of the dynamics of eco-epidemiological model incorporating fear factor. And there comes a question: How does the fear factor affect the persistence and extinction of the predator–prey system?

The main goal of this article is to investigate how the fear factor affects the predation dynamics through studying the stability of the equilibria and Hopf bifurcation of the model.

The rest of this paper is organized as follows: In Sect. 2, we give the details of the model derivation. In Sect. 3, we provide the existence of the equilibria of the model. In Sect. 4, we give the local stability of the equilibria and the existence of Hopf bifurcation. In Sect. 5, we numerically discuss the influence of the cost of fear on the dynamics of the eco-epidemic model. Finally, in Sect. 6, we conclude the ecological significance of the analytical results.

2 Model derivation

Following [27], we construct an eco-epidemic model of one predator and one prey with a disease in prey population incorporating the fear factor from the predator. First of all, we give some assumptions as follows:

(i) Only the prey population is infected by an infectious disease.

(ii) In the presence of disease, total prey population is divided into two subclasses, namely susceptible prey population \( u \) and infected prey population \( v \).

(iii) In the absence of predation, the infected prey population dies before having capability of reproducing. Consider the simple birth–death process of the prey \( u(t) \) modeled by

\[
\frac{du}{dt} = au - du,
\]

where \( a \) is the birth rate and \( d \) the natural death rate. For the positive growth of the prey, we assume \( r := a - d > 0 \). And by introducing the cost of fear according to [35], we obtain:

\[
\frac{du}{dt} = [F(k,w)a]u - du.
\]

In addition, the susceptible prey population feels the population pressure of both susceptible and infected prey population, i.e., intraspecific and interspecific competition.

(iv) The disease in prey population is transmitted vertically from susceptible to infected prey population according to law of mass action at constant rate of infection \( \beta \). Infected prey population do not recover from the disease.

(v) The predator consumes only the infected prey and does not consume the susceptible prey. This is in accordance with the fact that the infected prey are less active and can be caught easily [38], or the experimental observations that some fish (trematode \textit{Euhaplorchis californiensis}) infect the brain of killifish (\textit{Fundulus parvipinnis}), and since upper surface contains more oxygen, infected fish come closer to water surface and are eaten by piscivorous birds strikingly about 31 times on average that of non-parasitized fish [1,14,19]. In addition, Peterson and Page [23] observed that wolf often attacks successfully on the moose infected by \textit{Echinococcus granulosus}.

Based on the assumptions above, the model structure is shown in the transfer diagram of Fig. 1.

And the model can be presented by the following set of ordinary differential equations:

\[
\begin{align*}
\frac{du}{dt} &= [F(k,w)a]u - du - bu(u + v) - \beta uv, \\
\frac{dv}{dt} &= \beta uv - pvw - \delta v, \\
\frac{dw}{dt} &= cpvw - \mu w,
\end{align*}
\]

with initial conditions
\[
u(0) \geq 0, \quad v(0) \geq 0, \quad w(0) \geq 0,
\]

where \( u(t) \), \( v(t) \) and \( w(t) \) are the density of the uninfected (susceptible) prey, the infected prey and the
predator at time $t$, respectively. All parameters are positive constants and

- $a$: the birth rate of the susceptible prey;
- $d$: the natural death rate of the susceptible prey;
- $b$: the density dependent death rate due to intra-species competition;
- $\beta$: the contact rate between the susceptible and the infected prey;
- $p$: the attack rate on the infected prey;
- $\delta$: the death rate of the infected prey including natural death rate and disease-induced mortality;
- $c$: the conversion coefficient;
- $\mu$: the natural death rate of the predator;
- $F(k, w)$: the fear factor. Here, the parameter $k$ represents the level of fear which drives anti-predator behavior of the prey.

Particularly, for convenience of the analysis, similar to that in [35], we adopt the following form for the fear effect term $F(k, w)$:

$$F(k, w) := \frac{1}{1 + kw},$$ (2)

Then, model (1) can be rewritten as follows:

$$\begin{align*}
\frac{du}{dt} &= \frac{a}{1 + kw}u - du - bu(u + v) - \beta uv, \\
\frac{dv}{dt} &= \beta uv - pvw - \delta v, \\
\frac{dw}{dt} &= cpvw - \mu w.
\end{align*}$$ (3)

3 Existence of the equilibria

Following [8,31], we obtain the basic reproduction number $R_0$ for model (3) as follows:

$$R_0 = \frac{r \beta}{b \delta}. $$ (4)

Easy to verify that model (3) has the following trivial and semi-trivial equilibria:

(1) Trivial equilibrium: $E_0 = (0, 0, 0)$;
(2) Axial equilibrium: $E_1 = (\frac{r}{b}, 0, 0)$;
(3) Planar equilibrium: $E_2 = (u_2, v_2, 0)$, here $u_2 = \frac{r}{b R_0}, v_2 = \frac{r^2 (R_0 - 1)}{b \delta R_0 + r}$ and $R_0 > 1$.

Next, we mainly study the existence of the positive equilibrium $E^* = (u^*, v^*, w^*)$ of model (3). Any positive equilibrium $(u^*, v^*, w^*)$ of model (3) satisfies:

$$\begin{align*}
au^* \left(1 + kw^*\right) - bu^* (u^* + v^*) - \beta uu^*v^* - du^* &= 0, \\
\beta uu^*v^* - pv^*w^* - \delta v^* &= 0, \\
cpv^*w^* - \mu w^* &= 0,
\end{align*}$$

which yields

$$u^* = \frac{r (pw^* + \delta)}{b \delta R_0}, \quad v^* = \frac{\mu}{cp},$$

and $w^* = w^*(k)$ is the positive root of the following equation:

$$H(w) = m_2(k)w^2 + m_1(k)w + \delta \xi (R_0) = 0,$$ (5)

where

$$m_2(k) = r^2 c k p^2 > 0,$$

$$m_1(k) = \delta \left(b \delta \mu R_0^2 + r^2 cp + (cdp + b \mu) r R_0\right).$$
Simple computation reveals that which indicates that $w^*$ is a strictly decreasing function with respect to $k$. That is, the value of the predator equilibrium $w^*$ decreases as $k$ increases. And from (10), we know that there exists a $k_*$ such that

$$w^*(k_*) < 1 \times 10^{-4} \approx 0,$$

i.e., if the level of the fear $k$ is larger than $k_*$, the value of the predator $w^*$ will tend to 0, and $w(t)$ will almost go to extinction. And we can call $k_*$ the high risk value of the fear factor.

**Remark 2** In the case without the fear factor, i.e., $k = 0$, model (3) can be rewritten as

$$\begin{align*}
\frac{du}{dt} &= u (a - b(u + v) - \beta v - d), \\
\frac{dv}{dt} &= v (\beta u - pw - \delta), \\
\frac{dw}{dt} &= w (cpv - \mu).
\end{align*}$$

(12)

It is clear that model (12) has trivial equilibrium $\hat{E}_0 = (0, 0, 0)$, axial equilibrium $\hat{E}_1 = (\xi, 0, 0)$ and planar equilibrium $\hat{E}_2 = \left( \frac{r}{bR_0}, \frac{r^2}{bR_0(\delta R_0 + r)}, 0 \right)$. And if the conditions in Theorem 1 hold, there is a unique interior equilibrium

$$\hat{E}_* = \left( \frac{r^2 cp - bR_0 - rb \mu}{rbcp}, \frac{\mu}{cp}, \frac{\delta(-bR_0 + r(cep - bR_0 - r^2 cp))}{r^2 cp^2} \right).$$

Comparing the results of the values of equilibria of model (3) with those of model (12), we can see that the fear factor has no influence on the values of the trivial, axial or planar equilibria of model (3). What’s more, the cost of fear $k$ does not affect the existence of the interior equilibrium $E_*$ of model (3), and it can decrease the values of $u^*$ and $w^*$ as $k$ increases, but it has no influence on the value of $v^*$ directly.

## 4 Stability analysis of the equilibria

### 4.1 Local stability

Firstly, we directly give the results of stability of trivial and axial equilibria $E_0$ and $E_1$ as follows. The proof is standard, and hence, we omit it here.
Theorem 2 For model (3),
(i) The trivial equilibrium $E_0 = (0, 0, 0)$ is unstable;
(ii) If $\mathcal{R}_0 < 1$, the axial equilibrium $E_1 = \left( \frac{r}{b}, 0, 0 \right)$ is stable; while if $\mathcal{R}_0 > 1$, it is unstable.

Secondly, we present the stability of the planar equilibrium $E_2$ of model (3).

Theorem 3 For model (3), (A) The planar equilibrium $E_2 = \left( \frac{r}{b \mathcal{R}_0}, \frac{r^2 (\mathcal{R}_0 - 1)}{b \mathcal{R}_0 (\delta \mathcal{R}_0 + r)}, 0 \right)$ is stable, if one of the following inequalities holds:

\[ A_1(k) = \frac{(pw^* + \delta) r}{\delta \mathcal{R}_0} > 0, \]
\[ A_2(k) = \frac{\mu \left( pw^* (r c p + b \delta \mathcal{R}_0 + rb) + b \delta^2 \mathcal{R}_0 + rb \delta \right)}{rc p} > 0, \]
\[ A_3(k) = \frac{\mu (pw^* + \delta) w^* \left( rk^2 pw^*^2 + a \delta k \mathcal{R}_0 + 2 k pw^* r + pr \right)}{\delta \mathcal{R}_0 (kw^* + 1)^2} > 0. \]

Hence, the characteristic equation of $J$ is given as

\[ \lambda^3 + A_1(k) \lambda^2 + A_2(k) \lambda + A_3(k) = 0, \]

where

\[ J = \begin{pmatrix} -bu^* & -bu^* - \frac{\mathcal{R}_0 \delta u^*}{r} & -a k u^* \\ \frac{\mathcal{R}_0 \delta u^*}{r} & -pw^* - \delta & -\frac{\mu}{c} \\ 0 & cp w^* & 0 \end{pmatrix}. \]

Thus, by the Routh–Hurwitz criterion, we can arrive at the conclusion.

4.2 Hopf bifurcation

In this subsection, we take $k$ as the bifurcation parameter. The characteristic equation of model (3) at $E^* = (u^*, v^*, w^*)$ is (15), and $A_i(k) (i = 1, 2, 3)$ are defined as in (16). There exists a positive constant $K_H$ such that $\Theta_1(k) = 0$, where $\Theta_1(k)$ is defined as in (13).

Theorem 5 Model (3) possesses a Hopf bifurcation around $E^* = (u^*, v^*, w^*)$ when $k$ passes through $k_H$ provided $A_1(k_H) A_2(k_H) = A_3(k_H)$.

Proof Following [22], one can know that the Hopf bifurcation occurs if and only if $A_i(k) (i = 1, 2, 3)$ are smooth functions of $k$ in an open interval about $k_H \in \mathbb{R}$, and the characteristic Eq. (15) has:

(I) a pair of complex eigenvalues $\lambda = p_1(k) \pm ip_2(k)$ (with $p_1(k), p_2(k) \in \mathbb{R}$), so that they become purely imaginary at $k = k_H$ and $\frac{dp_1(k)}{dk} |_{k=k_H} \neq 0$;

(II) the other eigenvalue is negative at $k = k_H$. 

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If \( k = k_H \), the characteristic Eq. (15) equals

\[
\lambda^3 + A_1(k_H)\lambda^2 + A_2(k_H)\lambda + A_3(k_H) = 0, \quad (17)
\]

then, (17) can be factorized as:

\[
(\lambda^2 + A_2(k_H))(\lambda + A_1(k_H)) = 0. \quad (18)
\]

It is easy to obtain that (18) has three roots: \( \lambda_1 = i\sqrt{A_2(k_H)} \), \( \lambda_2 = -i\sqrt{A_2(k_H)} \) and \( \lambda_3 = -A_1(k_H) \). What’s more, \( A_i \) (\( i = 1, 2, 3 \)) are smooth functions of \( k \). Thus, if \( k \) lies in a neighborhood of \( k_H \), the characteristic roots have the form \( \lambda_1 = p_1(k) + i p_2(k) \), \( \lambda_2 = p_1(k) - i p_2(k) \) and \( \lambda_3 = -p_3(k) \), where \( p_i(k) \) (\( i = 1, 2, 3 \)) are real numbers.

Next, we verify the transversality condition

\[
\frac{d}{dk} \text{Re}(\lambda_i(k)) \bigg|_{k=k_H} = \frac{d p_1(k)}{d k} \bigg|_{k=k_H} \neq 0, \quad i = 1, 2. \quad (19)
\]

Putting \( \lambda(k) = p_1(k) + i p_2(k) \) into (15), we have

\[
(p_1(k) + i p_2(k))^3 + A_1(p_1(k) + i p_2(k))^2 \\
+ A_2(p_1(k) + i p_2(k)) + A_3 = 0. \quad (20)
\]

Taking derivative of both sides of (20) with respect to \( k \), we obtain
where \( \prime = \frac{d}{dx} \). Separating the real and imaginary parts, we have

\[
\begin{aligned}
D_1 p_1' - D_2 p_2' + D_3 &= 0, \\
D_2 p_1' + D_1 p_2' + D_4 &= 0,
\end{aligned}
\]

(21)

where

\[
D_1 = 3(p_1^2 - p_2^2) + 2A_1 p_1 + A_2, \quad D_2 = (6p_1 + 2A_1)p_2, \\
D_3 = A_1^2(p_1^2 - p_2^2) + A_1' p_1 + A_3, \quad D_4 = (2A_1' p_1 + A_2')p_2.
\]

It follows from (21) that

\[
p_1' = -\frac{D_2 D_4 + D_1 D_3}{D_1^2 + D_2^2}.
\]

We know that when the Hopf bifurcation occurs, the characteristic Eq. (15) has a pair of purely imaginary roots at \( k = k_H \) in the following two cases.

**Case 1** \( p_1 = 0, p_2 = \sqrt{A_2} \).

We have

\[
D_1 = -2A_2, \quad D_2 = 2A_1 \sqrt{A_2}, \quad D_3 = -A_1' A_2 + A_3', \quad D_4 = A_2' \sqrt{A_2}.
\]

Therefore,

\[
D_2 D_4 + D_1 D_3 = 2A_2 (A_1 A_2' + A_1' A_2 - A_3') = 2A_2 \Theta'(k).
\]

Hence, if \( p_1 = 0, p_2 = \sqrt{A_2} \), then \( D_2 D_4 + D_1 D_3 = 2A_2 \Theta'(k_H) \) at \( k = k_H \).

**Case 2** \( p_1 = 0, p_2 = -\sqrt{A_2} \).

We have

\[
D_1 = -2A_2, \quad D_2 = -2A_1 \sqrt{A_2}, \\
D_3 = -A_1' A_2 + A_3', \quad D_4 = -A_2' \sqrt{A_2}.
\]

Therefore,

\[
D_2 D_4 + D_1 D_3 = 2A_2 \Theta'(k).
\]

Hence, if \( p_1 = 0, p_2 = -\sqrt{A_2} \), then \( D_2 D_4 + D_1 D_3 = 2A_2 \Theta'(k_H) \) at \( k = k_H \).

Note that

\[
\Theta'(k) \bigg|_{k=k_H} = \frac{dw^*}{dk} \Theta_1(k) \bigg|_{k=k_H} + \frac{(pw^* + \delta) \mu \frac{d\theta_1}{dk}(k)}{\delta \mathcal{R}_0 c (1 + k w^*)^2} \bigg|_{k=k_H} \\
- \frac{(pw^* + \delta) \mu \Theta_1(k) \left( w^* + k \frac{dw^*}{dk} \right)}{\delta \mathcal{R}_0 c p (1 + k w^*)^2} \bigg|_{k=k_H} = \frac{(pw^* + \delta) \mu \frac{d\theta_1}{dk}(k)}{\delta \mathcal{R}_0 c p (1 + k w^*)^2} \bigg|_{k=k_H} \\
= \frac{(pw^* + \delta) \mu}{\delta \mathcal{R}_0 c p (1 + k w^*)^2} \left[ \frac{2 b (\delta \mathcal{R}_0 + r) (1 + k w^*) (\delta + p w^*) \left( w^* + k \frac{dw^*}{dk} \right)}{2 b (\delta \mathcal{R}_0 + r) (1 + k w^*)^2 p \frac{dw^*}{dk} - a c \delta p \mathcal{R}_0 w^* - a c \delta p \mathcal{R}_0 k \frac{dw^*}{dk}} \bigg|_{k=k_H} \\
+ b (\delta \mathcal{R}_0 + r) (1 + k w^*)^2 p \frac{dw^*}{dk} - a c \delta p \mathcal{R}_0 w^* - a c \delta p \mathcal{R}_0 k \frac{dw^*}{dk} \bigg] \bigg|_{k=k_H} \\
= \frac{(pw^* + \delta) \mu}{\delta \mathcal{R}_0 c (1 + k w^*)^2 (r + \delta \mathcal{R}_0) (1 + k w^*) \Psi} \bigg|_{k=k_H},
\]

where

\[
\Psi = \left( 2 b k (\delta + p w^*) - \frac{\delta b (1 + k w^*)}{w^*} \right) \frac{dw^*}{dk} \\
- \frac{b}{k} (\delta + p w^*) + b (\delta + p w^*) w^*.
\]
From (9), one can obtain that

\[ \psi = -pb (1 + kw^*) \left( w^*b \delta^2 k_\mu R_0^2 + w^* c p \delta k \mu R_0 + w^* b \delta k_\mu r R_0 + r^2 c p^2 w^* + c \delta p r^2 \right) \left( b \delta^2 k_\mu R_0^2 + c p \delta k \mu R_0 + b \delta k_\mu r R_0 + 2 r^2 c p^2 w^* + c \delta k \mu r R_0 + r^2 c p^2 \right) k < 0, \]

which implies that

\[ \Theta'(k) \big|_{k=k_H} \neq 0. \]

Based on the results above, we obtain:

\[ \frac{dp_1(k)}{dk} \bigg|_{k=k_H} = - \frac{D_2 D_4 + D_1 D_3}{D_1^2 + D_2^2} \bigg|_{k=k_H} \neq 0 \]

and

\[ \lambda_3 = -A_1(k_H) < 0. \]

Therefore, conditions (I) and (II) are satisfied and this completes the proof. \( \square \)

For the sake of understanding the complex theoretical results above further, in Fig. 2, we give a bifurcation diagram of model (3) in \( R_0 - k \) parameter space. One can see that the fear factor can destabilize the coexistence equilibrium \( E^* \) of model (3) and will benefit the occurrence of limit cycle oscillation. More precisely, if \( k < k_H \), below the Hopf bifurcation, \( E^* \) is always stable (see Theorem 4); if \( k = k_H \), model (3) undergoes a Hopf bifurcation (see Theorem 5) and there is a limit cycle around \( E^* \), while if \( k > k_H \), \( E^* \) is unstable (see Theorem 4).

### 5 Numerical simulations

In this section, we verify the correctness of the theoretical results by numerical simulation. What’s more, we mainly focus on the impact of the level of fear factor \( k \) in model (3). As an example, we take the parameters of model (3) as follows:

\[ a = 0.5, \ b = 0.1, \ p = 1, \ \delta = 0.2, \]
\[ c = 0.8, \ \mu = 0.3, \ \beta = 0.5. \]  \( (22) \)

Then, we get:

\[ r = 0.4, \ \ R_0 = 10.0, \ k_0 = 0.7615187994, \]
\[ b < b_\infty = \frac{(r + 2\delta - 2\sqrt{\delta(r + \delta)})pc}{\mu} = 0.286, \]
\[ R_0 = \frac{2rcp}{rcp - b\mu + \sqrt{(rcp - b\mu)^2 - 4cpb\delta\mu}} = 1.175. \]

Thus, the conditions of Theorem 1 are satisfied. In addition, model (3) and model (12) have the same boundary equilibria: trivial equilibrium \( \hat{E}_0 = (0, 0, 0) \), axial equilibrium \( \hat{E}_1 = (4, 0, 0) \) and planar equilibrium \( \hat{E}_2 = (0.4, 0.6, 0). \)

Next, we take some different values of \( k \) to understand the impact of the fear factor on the resulting dynamics of the system (3).

**Example 1** We adopt \( k = 0 \); without the cost of the fear factor, model (12) has a unique positive equilibrium \( \hat{E}_2 = (1.75, 0.375, 0.675) \), which is stable (Fig. 3).

**Example 2** We adopt \( k = 0.4 < k_H \); with the cost of the fear factor, model (3) has a unique positive equilibrium \( E^* = (1.120, 0.375, 0.360) \). In this case, we obtain

\[ \Theta_1(k) = b(r + \delta R_0)(1 + kw^*)^2(\delta + pw^*) - ac\delta p R_0 k w^* = 0.06072 > 0, \]
\[ A_1(k) = 0.112036, \ A_2(k) = 0.234094, \]
\[ A_3(k) = 0.021355, \]
\[ A_1(k) A_2(k) = 0.02623, \ A_1(k) A_2(k) = 0.00487 > 0, \]

which means that \( E^* \) is locally asymptotically stable (see Fig. 4). In addition, the dynamics is similar to that in Fig. 3, and the difference between these two cases is that the value of \( E^* \) of model (3) is smaller than \( \hat{E}_2 \) of model (12), which is induced by the cost of fear factor.

**Example 3** We adopt \( k = 0.7615187994 = k_H \) and get:

\[ \Theta_1(k) = b(r + \delta R_0)(1 + kw^*)^2(\delta + pw^*) - ac\delta p R_0 k w^* = 1 \times 10^{-10} \approx 0, \]
\[ A_1(k) = 0.09216, \ A_2(k) = 0.18191, \]
\[ A_3(k) = 0.01676, \ A_1(k) A_2(k) = 0.01676, \]
\[ A_1(k) A_2(k) - A_3(k) = 0. \]

From Theorem 5, we learn that the cost of the fear factor \( k \) can destabilize \( E^* \) from a stable spiral sink
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Fig. 5 Population dynamics of $u(t)$, $v(t)$ and $w(t)$ of model (3) with the level of fear factor $k = 0.7615187994 = k_H$. a Time-series plots; b phase portraits in three-dimensional space

Fig. 6 Population dynamics of $u(t)$, $v(t)$ and $w(t)$ of model (3) with the level of fear factor $k = 1 > k_H$. a Time-series plots; b phase portraits in three-dimensional space

point to an unstable spiral source one, and model (3) undergoes a Hopf bifurcation and there is a limit cycle around $E^* = (0.922, 0.375, 0.261)$. In other words, the system exhibits periodic phenomenon. The numerical results are shown in Fig. 5. Comparing Fig. 4 with Fig. 5, one can see that there are two different implications induced by the fear factor $k$: The first is the decrease of values of $u^*$ and $w^*$ of $E^*$, and the second is that the stability of $E^*$ converts from stable into unstable.

Example 4 We adopt $k = 1 > k_H$ and obtain

$$
\Theta_1(k) = b(r + \delta R_0)(1 + k w^*)^2(\delta + pw^*) - ac \delta p R_0 k w^* = -0.02628 < 0,
$$
$$
A_1(k) = 0.08431, \quad A_2(k) = 0.16132,
$$
$$
A_3(k) = 0.01499,
$$
$$
A_1(k) A_2(k) = 0.01360, \quad A_1(k) A_2(k) - A_3(k) = -0.00139 < 0,
$$

which means that $E^*$ is unstable and model (3) exhibits periodic phenomenon. The numerical results can be found in Fig. 6, similar to that in Fig. 5. The difference between them is the decrease of value of $E^*$ from $(0.922, 0.375, 0.261)$ to $(0.843, 0.375, 0.222)$, which is induced by the influence of the fear factor.

Example 5 We analyze the effect of high level of fear factor on the population dynamics of model (3). As examples, we adopt four different values of $k = 10$, $100$, $1000$ and $50000$ to show the influence of the fear factor. The simulation results are shown in Fig. 7; where as $k$ increases, the amplitude of $w(t)$ is becoming smaller and smaller (see Fig. 7(a), 7(b) and 7(c)). And when $k = 50000$, $0 < w(t) < 1 \times 10^{-4} \approx 0$, according to (11), we can claim that the value of the predator $w(t)$ will tend to 0, and $w(t)$ will almost go to extinction (see Fig. 7(d)). In addition, at the same time, $u(t)$ and $v(t)$ oscillate periodically.

6 Conclusions and discussion

In this paper, we divide the prey population into two subclasses: the susceptible and the infected. To study the influence of the fear factor on the population
dynamics, we establish an eco-epidemiological model incorporating the cost of fear in the susceptible prey induced by the predator. Mathematically, we give the conditions for existence (see Theorem 1) and local asymptotic stability (see Theorems 2, 3 and 4) of the equilibria of model (3). In addition, we show that the fear factor can destabilize the stability of $E^*$ and the model exhibits the Hopf bifurcation (see Theorem 5). Biologically, we summarize our main findings as follows.

(a) If the level of fear factor $k < k_H$, the coexistence equilibrium $E^*$ of model (3) is stable (see Fig. 4), which is the same as $\hat{E}_s$ of model (12), the case without the fear factor (see Fig. 3). These results agree with those in Refs. [24,25,33–35,41].

(b) If $k = k_H$, the fear effect can destabilize $E^*$ and will benefit the occurrence of periodic oscillation (see Fig. 5). In other words, the system has periodic behavior and the model undergoes a limit cycle. These results agree with those in Refs. [24,33–35,41].

(c) If $k_H < k < k_s$ ($k_s$ is implicitly determined in Remark 1), $E^*$ of model (3) is unstable and the system exhibits periodic behavior. These results are similar to those in [24].

(d) If $k > k_s$, the solutions of model (3) will tend to $E_2 = (u^*, v^*, 0)$, i.e., the predator $w$ will go to extinction, and the fear factor can prevent the occurrence of the limit cycle oscillation and increase the extinction of the system. This can be seen as a population example of “kill 1000 enemies with 800 soldiers killed” extended from “Sun Tzu’s Art of War,” one of the earliest military works in the world. As we know, $k$ reflects the level of fear factor which drives anti-predator behavior of the prey, and the fear factor is induced by the predator $w$. Biologically speaking, if the fear factor is very large, the prey will respond to perceived predation risk and show a variety of anti-predator responses (such as changing habitat, forging behavior, vigilance and physiological changes). When the anti-predator response is the key factor in the predator–prey system, there is not enough prey for the predator, which leads to the extinction of the predator. Hence, for the coexistence of system (3), $k$ needs to be less than the high risk value of the fear factor $k_s$; otherwise, the predator $w(t)$ will almost go extinct, and the prey population will be permanent (see Remark 1). In the meantime, model (3) degenerates to the following limit epidemic model:

$$
\begin{align*}
\frac{du}{dt} &= au - bu(u + v) - \beta uv - du, \\
\frac{dv}{dt} &= \beta uv - \delta v,
\end{align*}
$$

which has two boundary equilibria $E_0 = (0, 0)$, $E_1 = (4, 0)$ and a unique coexistence equilibrium $E^* = (\frac{\delta}{b}, \frac{r\beta - \delta - b}{b(\delta + \beta)}).$ Consider Theorem 1 and Remark 1 again, and we know that the value of $u^*(k)$ in $E^*$ of model (3) is related to the value of $\frac{\delta}{b}$ in $E^*$ as follows:

$$
\lim_{k \to \infty} u^*(k) = \frac{\delta}{b}.
$$

Furthermore, if $r\beta > b\delta$, $E^*$ is stable, while if $r\beta < b\delta$, $E^*$ is unstable. With the parameters set (22), the phase portraits of system (23) are shown in Fig. 8, in which the boundary points $E_0 = (0, 0)$ and $E_1 = (4, 0)$ are saddle points, and the coexistence equilibrium $E^* = (0.4, 0.6)$ is globally stable.

To the best of our knowledge, the extinction of the predator $w$ in eco-epidemiological model (3) induced by the fear factor seems to be the first reported case.
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Declaration

Conflict of Interest The authors declare that they have no conflict of interest.

Appendix A: The sign of $\xi(\lambda_0)$

Proof Recall

$$\xi(\lambda_0) := b\delta \mu \lambda_0^2 - r(rcp - b\mu)\lambda_0 + r^2 cp,$$

so we can discuss the sign of $\xi(\lambda_0)$ in the following two cases.

Case 1 $rcp \leq b\mu$. In this case, $\xi(\lambda_0) > 0$.

Case 2 $rcp > b\mu$.

Set

$$\Delta(b) := (rcp - b\mu)^2 - 4cpb\delta\mu$$

$$= \mu^2 b^2 - 2cp\mu(r + 2\delta)b + r^2 c^2 p^2.$$ 

Note that $(-2cp\mu(r + 2\delta))^2 - 4\mu^2 c^2 p^2 > 0$, then $\Delta(b)$ has two positive roots $b_-$ and $b_+$, which are defined as in (7).

Case 2-1 If $b_- < b < b_+$ holds, we have $\Delta(b) < 0$, which implies that $\xi(\lambda_0) > 0$.

Case 2-2 If $b = b_+$ holds, we have $\Delta(b) = 0$. Thus, when $\lambda_0 = \frac{2rcp}{rcp - b\mu}$, we have $\xi(\lambda_0) = 0$; when $\lambda_0 \neq \frac{2rcp}{rcp - b\mu}$, we have $\xi(\lambda_0) > 0$.

Case 2-3 If $0 < b < b_-$ or $b > b_+$ holds, we have $\Delta(b) > 0$.

Then, one can see that $\xi(\lambda_0)$ has two positive roots $\lambda_0^-$ and $\lambda_0^+$, which are defined as in (8). In fact,

$$1 < \frac{2rcp}{rcp - b\mu + \sqrt{(rcp - b\mu)^2 - 4cpb\delta\mu}} = \lambda_0^- .$$

Hence, if $\lambda_0 = \lambda_0^+$ holds, we have $\xi(\lambda_0) = 0$; if $1 < \lambda_0^- < \lambda_0^+ < \lambda_0^+$ holds, we have $\xi(\lambda_0) < 0$; and if $1 < \lambda_0^- < \lambda_0^+ < \lambda_0^+$ holds, we have $\xi(\lambda_0) > 0$.

Therefore, we can determine the sign of $\xi(\lambda_0)$ in three cases as follows:

(1) when $rcp > b\mu$, if $0 < b < b_-$ or $b > b_+$, and $1 < \lambda_0^- < \lambda_0^+ < \lambda_0^+$, we have $\lambda_0^- < \lambda_0^+$; or $\lambda_0 > \lambda_0^+$, we have $\lambda_0^- = \lambda_0^+$.

(3-1) $rcp < b\mu$;

(3-2) $rcp > b\mu$,

(i) $b_- < b < b_+$;

(ii) $b = b_+$ and $\lambda_0 \neq \frac{2rcp}{rcp - b\mu}$;

(iii) $0 < b < b_-$ or $b > b_+$, and $1 < \lambda_0^- < \lambda_0^+$

or $\lambda_0 > \lambda_0^+$, we have $\xi(\lambda_0) < 0$.

Appendix B: The Proof of Theorem 3

Proof The Jacobian matrix of model (3) around $E_2 = \left( \frac{r}{b\lambda_0}, \frac{r^2(\lambda_0 - 1)}{b\lambda_0(\lambda_0 + r)}, 0 \right)$ is given as

$$J_2 = \left( \begin{array}{ccc} \frac{-r}{b\lambda_0} & \frac{-r}{b\lambda_0} & \frac{-akr}{b\lambda_0} \\ \frac{\delta r(\lambda_0 - 1)}{b\lambda_0(\lambda_0 + r)} & 0 & \frac{-pr^2(\lambda_0 - 1)}{b\lambda_0(\lambda_0 + r)} \\ 0 & 0 & \frac{\xi(\lambda_0)}{b\lambda_0(\lambda_0 + r)} \end{array} \right).$$

Hence, the characteristic equation of $J_2$ is given as

$$\left( \lambda^2 \lambda_0 + r\lambda - r(\lambda_0 - 1) \right)(-b\lambda_0(\delta\lambda_0 + r)\lambda - b\delta\mu \lambda_0^2 + r(rcp - b\mu)\lambda_0 - r^2 cp) = 0.$$
Set
\[ \phi(\lambda) := -b\delta R_0(\delta R_0 + r_0)\lambda - b\delta \mu R_0^2 + r(\delta R_0 - b\mu)R_0 - r^2cp \]
\[ = -b\delta R_0(\delta R_0 + r_0)\lambda - \xi(R_0), \]
then \( \phi(\lambda) \) has a unique root \( -\frac{\xi(R_0)}{b\delta R_0(\delta R_0 + r_0)} \).

Case 1 When \( \xi(R_0) > 0, E_2 \) is stable;
Case 2 When \( \xi(R_0) < 0, E_2 \) is unstable;
Case 3 When \( \xi(R_0) = 0, \) the root of \( \phi(\lambda) \) is zero, which implies that \( E_2 \) is a singular point with higher order. In this case, we have

\[ cpv_2 - \mu = \frac{cpr^2(\delta R_0 - 1)}{b\delta R_0(\delta R_0 + r_0)} - \frac{\mu}{cp} \]
\[ = \frac{b\delta \mu R_0^2 - r(\delta R_0 - b\mu)R_0 + r^2cp}{b\delta R_0(\delta R_0 + r_0)} \]
\[ = \frac{\xi(R_0)}{b\delta R_0(\delta R_0 + r_0)} \]
\[ = 0, \]
which implies that

\[ v_2 = \frac{r^2(\delta R_0 - 1)}{b\delta R_0(\delta R_0 + r_0)} = \frac{\mu}{cp}. \]

Let \( u = \bar{u} - \frac{r_0}{b\delta R_0}, v = \bar{v} - \frac{\mu}{cp} \) and \( w = \bar{w}, \) then the model (3) becomes

\[
\begin{align*}
\frac{du}{dt} &= -(bu + r_0)(b\delta R_0 u + dkr w + kr^2 w + bru + brv), \\
\frac{dv}{dt} &= (cp + \mu)(b\delta R_0 u - pr w), \\
\frac{dw}{dt} &= cpvw,
\end{align*}
\]

where we substitute \( u, v, w \) for \( \bar{u}, \bar{v}, \bar{w}, \) Hence, the planar equilibrium \( E_2 \) moves to \((0, 0, 0)\). The Jacobian matrix at \((0, 0, 0)\) of (24) is

\[ J_2 = \begin{pmatrix} -\mu & -b\delta b\delta R_0 & -dkr + kr^2 \\ \frac{\mu}{cp} & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}. \]

Thus, the center manifold is a curve tangent to the \( w \)-axis. In order to obtain the approximative expression of the center manifold, we set

\[ u = \bar{n}_1 w + \bar{n}_2 w^2 + O(w^2), \]
\[ v = \bar{n}_1 w + \bar{n}_2 w^2 + O(w^2). \]

Then, we have

\[ \frac{du}{dt} = \bar{n}_1 \frac{dw}{dt} + 2\bar{n}_2 w \frac{dw}{dt} + O(w), \]
\[ \frac{dv}{dt} = \bar{n}_1 \frac{dw}{dt} + 2\bar{n}_2 w \frac{dw}{dt} + O(w) \]
\[ \frac{dw}{dt} = \bar{n}_1 \frac{dw}{dt} + 2\bar{n}_2 w \frac{dw}{dt} + O(w) \]

Substituting (24) and (26) into (27), we can obtain

\[ -r(b\delta R_0 \bar{n}_1 + br(\bar{n}_1 + \bar{n}_2) + kr(d + r))w \]
\[ -b(b\delta R_0^2 \bar{n}_1 + cpr R_0 \bar{n}_1 \bar{n}_2) \]
\[ + br R_0 \bar{n}_1 \]
\[ + kr^2 R_0 \bar{n}_1 + \delta \bar{R} \bar{n}_2 \]
\[ + r^2 \bar{n}_2 + r^2 \bar{n}_2 w^2 + O(w^2) = 0, \]
\[ (b\delta \mu R_0 \bar{n}_1 - \mu p r)w \]

Comparing the coefficients of \( w \) and \( w^2 \) in (28), we find that

\[ +(bc\delta p R_0 \bar{n}_1 \bar{n}_2 - c^2 p^2 \bar{n}_1^2) \]
\[ + b\delta \mu R_0 \bar{n}_2 - cp^2 \bar{n}_1 \bar{n}_2^2 + O(w^2) = 0. \]
\[
\tilde{n}_1 = \frac{rp}{R_0 b \delta},
\]
\[
\tilde{n}_2 = \frac{c^2 p^2 r^2 (d \delta k R_0 + \delta k r R_0 + pr)^2}{R_0^3 b^3 \delta^3 (\delta R_0 + r)^2 \mu},
\]
\[
\tilde{n}_1 = \frac{-(\delta k R_0 (d + r) + pr)r}{R_0 b \delta (\delta R_0 + r)},
\]
\[
\tilde{n}_2 = \frac{r^2 p^2 c (\delta k R_0 (d + r) + pr) (b \delta^2 \mu R_0^3 - c d \delta k r R_0 - c \delta k r^2 R_0 + b \delta \mu r R_0^2 - c p r)}{b^3 R_0^3 \delta^3 (\delta R_0 + r)^3 \mu}.
\]

Therefore, substituting (26) into (24), we have

\[
\frac{dw}{dr} = -c p r b^2 R_0^2 \delta^2 \mu (\delta R_0 (d + r) + pr) (\delta R_0 + r)^2 w^2 + O(w^3),
\]

which yield that the origin \((0, 0, 0)\) of system (24) is locally asymptotically stable. Thus, \(E_2\) is locally asymptotically stable when \(\xi(R_0) = 0\).

The proof is completed. \(\square\)

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