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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; (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 [15]. It is a central topic to study the mechanisms driving predator-prey systems in ecology and evolutionary biology [30]. The research results of prey-predator models are helpful to understand the interactions of different species within a fluctuating natural environment [3, 4, 9].

Predator-prey interactions are modified by considering various ecological factors [13, 21]. In the previous models, predators only affect the density of prey population through direct killing [16]. 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

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the prey population, and its influence degree is even greater than that of direct killing [17, 6, 23, 32, 35]. And Zanette et al [35] experimentally showed that there is about 40% reduction in offspring production of the song sparrows due to the fear from predator. Wang et al [30] first introduced the fear factor $F(k, w)$, which accounts the cost of anti-predator defence due to the fear, to a predator-prey system. Their insightful work has drawn many scholars' attention and developed some predator-prey models incorporating the fear effect [31, 25, 20, 19, 28, 29, 36]).

On the other hand, in the natural world, species does not exist alone, and more and more studies show that the competition of resources and space among populations, as well as infectious diseases, affect 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 [11, 8, 10]. Simply speaking, the so-called eco-epidemiological models are demographic models accounting for interactions among different populations in which a disease also spreads [18]. Recently, eco-epidemiological models have drawn much attention from scientists [33, 34, 12, 1, 24, 27, 2, 5, 14]. At the same time, complex dynamics, such as bistability, quasiperiodicity, chaos and so on, has been found in many eco-epidemiological models [1]. Unfortunately, to the best of our knowledge, the study of the dynamics of eco-epidemiological model incorporating fear factor seems rare.

In the present paper, we focus on the dynamics of a predator-prey model with a disease in prey population, and the prey growth rate reduced by the fear from the predator. The rest of this paper is organized as follows: In Section 2, we give the details of the model derivation. In Section 3, we prove the boundedness of the solution of the model. In Section 4, we give the existence and local stability of the equilibria of the model, and furthermore, we show the existence of Hopf bifurcation. In Section 5, we numerically discuss the influence of the cost of fear on the dynamics of the eco-epidemic model. Finally, in Section 6, we conclude the ecological significance of the analytical results.

2 Model derivation

Following [22], 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 sub-classes, 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 is 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 [30], we can obtain:

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

- (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 β . Infected prey population do not recover from the disease.

(v) The predator consumes only the infected prey and does not consume the susceptible prey.

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

Fig. 1 Transfer diagram of model (3) in terms of susceptible and infectious preys and the predator.

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

$$\begin{cases} \frac{du}{dt} = [F(k, w)a]u - du - bu(u + v) - \beta uv, \\ \frac{dv}{dt} = \beta uv - pvw - \delta v, \\ \frac{dw}{dt} = cpvw - \mu w, \end{cases} \quad (1)$$

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 on death rate due to intra-species competition;

β : the contact rate between the susceptible and the infected prey;

p : the attack rate on the infected prey;

δ : the death rate of the infected prey including natural death rate and disease-induced mortality;

c : the conversion coefficient;

μ : 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 behaviour of the prey.

Particularly, for convenience of the analysis, similar to that in [30], we adopt the following form for the fear effect term $F(k, w)$:

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

Then model (1) can be rewritten as follows:

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

3 Existence of the equilibria

Following [7, 26], we can obtain the basic reproduction number $\mathcal{R}_0$ for model (3) as follows:

$$\mathcal{R}_0 = \frac{r\beta}{b\delta}. \quad (4)$$

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 $u_2 = \frac{r}{b\mathcal{R}_0}$, $v_2 = \frac{r^2(\mathcal{R}_0-1)}{b\mathcal{R}_0(\delta\mathcal{R}_0+r)}$ and $\mathcal{R}_0 > 1$.

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:

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

which yields

$$u^* = \frac{r(pw^* + \delta)}{b\delta\mathcal{R}_0}, \quad v^* = \frac{\mu}{cp},$$

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

$$H(z) = m_2(k)z^2 + m_1(k)z + \delta\xi(\mathcal{R}_0) = 0, \quad (5)$$

where

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

$$m_1(k) = \delta(b\delta\mu\mathcal{R}_0^2 + r^2cp + (cdp + b\mu)r\mathcal{R}_0)k + r^2cp^2 > 0,$$

$$\xi(\mathcal{R}_0) = b\delta\mu\mathcal{R}_0^2 - r(rcp - b\mu)\mathcal{R}_0 + r^2cp$$

If $\xi(\mathcal{R}_0) < 0$ (so $rcp > b\mu$), $H(z)$ has a unique positive root:

$$w^* := \frac{-m_1 + \sqrt{m_1^2 - 4\delta m_2 \xi(\mathcal{R}_0)}}{2m_2} = \frac{-2\delta\xi(\mathcal{R}_0)}{m_1 + \sqrt{m_1^2 - 4\delta m_2 \xi(\mathcal{R}_0)}}. \quad (6)$$

And the discussion in details of the sign of $\xi(\mathcal{R}_0)$ is shown in Appendix A.

Set

$$\begin{aligned} b_- &:= \frac{(r+2\delta-2\sqrt{\delta(r+\delta)})pc}{\mu}, \\ b_+ &:= \frac{(r+2\delta+2\sqrt{\delta(r+\delta)})pc}{\mu}, \end{aligned} \quad (7)$$

$$\begin{aligned} \mathcal{R}_0^- &:= \frac{2rcp}{rcp - b\mu + \sqrt{(rcp - b\mu)^2 - 4cpb\delta\mu}}, \\ \mathcal{R}_0^+ &:= \frac{2rcp}{rcp - b\mu - \sqrt{(rcp - b\mu)^2 - 4cpb\delta\mu}}, \end{aligned} \quad (8)$$

then we can obtain the existence of the endemic equilibrium of model (3).

Theorem 1 Assume $rcp > b\mu$. If

$$0 < b < b_- \quad \text{or} \quad b > b_+$$

and

$$1 < \mathcal{R}_0^- < \mathcal{R}_0 < \mathcal{R}_0^+$$

hold, then model (3) has a unique positive equilibrium $E^* = \left(\frac{r(pw^* + \delta)}{b\delta\mathcal{R}_0}, \frac{\mu}{cp}, w^* \right)$, here w^* is defined as in (6).

Remark 1 Simple computation reveals that

$$\frac{dw^*}{dk} = -\frac{w^*(m'_2w^* + m'_1)}{2m_2w^* + m_1} < 0, \quad (9)$$

and

$$\lim_{k \rightarrow 0} w^*(k) = -\frac{\delta\xi(\mathcal{R}_0)}{r^2cp^2}, \quad \lim_{k \rightarrow \infty} w^*(k) = 0, \quad (10)$$

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 increasing. 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 large 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_* as 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

$$\begin{cases} \frac{du}{dt} = u(a - b(u+v) - \beta v - d), \\ \frac{dv}{dt} = v(\beta u - pw - \delta), \\ \frac{dw}{dt} = w(cpv - \mu). \end{cases} \quad (11)$$

It is clear that model (11) has trivial equilibrium $\hat{E}_0 = (0, 0, 0)$, axial equilibrium $\hat{E}_1 = \left(\frac{r}{b}, 0, 0 \right)$, and planar equilibrium $\hat{E}_2 = \left(\frac{r}{b\mathcal{R}_0}, \frac{r^2(\mathcal{R}_0-1)}{b\mathcal{R}_0(\delta\mathcal{R}_0+r)}, 0 \right)$. And if the conditions in Theorem 1 hold, there is a unique interior equilibrium

$$\hat{E}_* = \left(\frac{r^2cp - b\delta\mu\mathcal{R}_0 - rb\mu}{rbc p}, \frac{\mu}{cp}, \frac{\delta(-b\delta\mu\mathcal{R}_0^2 + r(rcp - b\mu)\mathcal{R}_0 - r^2cp)}{r^2cp^2} \right).$$

Comparing the results of the values of equilibria of model (3) with those of model (11), we can see that the fear factor has no influence on the values of the trivial, axial or planar equilibria of model (3). And 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 increasing, but it has no influence on the value of v^* .

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 $E_1 = (\frac{r}{b}, 0, 0)$ is stable, while if $\mathcal{R}_0 > 1$, it is unstable.

Secondly, we will show 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:

- (1) $rcp \leq b\mu$ and $\mathcal{R}_0 > 1$;
- (2) $rcp > b\mu$,
- (2-1) $b_- < b < b_+$ and $\mathcal{R}_0 > 1$;
- (2-2) $0 < b \leq b_-$ or $b \geq b_+$, and $1 < \mathcal{R}_0 \leq \mathcal{R}_0^-$ or $\mathcal{R}_0 \geq \mathcal{R}_0^+$.

(B) Assume that $rcp > b\mu$. If

$$0 < b < b_- \text{ or } b > b_+, \text{ and } 1 < \mathcal{R}_0^- < \mathcal{R}_0 < \mathcal{R}_0^+$$

hold, the planar equilibrium E_2 is unstable.

The proof of Theorem 3 is complex and given in Appendix B.

Thirdly, we will show the stability of the interior equilibrium E^* of model (3).

Theorem 4 Assume that $rcp > b\mu$, $0 < b < b_-$ or $b > b_+$, and $1 < \mathcal{R}_0^- < \mathcal{R}_0 < \mathcal{R}_0^+$ hold. The interior equilibrium E^* of model (3) is locally asymptotically stable if $\Theta_1(k) > 0$, and it is unstable if $\Theta_1(k) < 0$, where $\Theta_1(k)$ is determined as in (15).

Proof The Jacobin matrix of model (3) around $E^* = \left(u^*, \frac{\mu}{cp}, w^* \right)$ is given as

$$J = \begin{pmatrix} -bu^* & -bu^* - \frac{\mathcal{R}_0 b \delta u^*}{r} & -\frac{aku^*}{(1+kw^*)^2} \\ \frac{\mathcal{R}_0 b \delta \mu}{rcp} & \frac{\mathcal{R}_0 b \delta u^*}{r} - pw^* - \delta & -\frac{\mu}{c} \\ 0 & cpw^* & 0 \end{pmatrix}. \quad (12)$$

Hence, the characteristic equation of J is given as

$$\lambda^3 + A_1(k)\lambda^2 + A_2(k)\lambda + A_3(k) = 0, \quad (13)$$

where

$$\begin{aligned} A_1(k) &= \frac{(pw^* + \delta)r}{\delta \mathcal{R}_0} > 0, \\ A_2(k) &= \frac{\mu (pw^* (rcp + b\delta \mathcal{R}_0 + rb) + b\delta^2 \mathcal{R}_0 + rb\delta)}{rcp} > 0, \\ A_3(k) &= \frac{\mu (pw^* + \delta) w^* (rk^2 pw^{*2} + a\delta k \mathcal{R}_0 + 2kpw^* r + pr)}{\delta \mathcal{R}_0 (kw^* + 1)^2} > 0. \end{aligned} \quad (14)$$

Set

$$\Theta(k) := A_1(k)A_2(k) - A_3(k) = \frac{(pw^* + \delta)\mu\Theta_1(k)}{\delta c p \mathcal{R}_0 (kw^* + 1)^2},$$

where

$$\Theta_1(k) := b(r + \delta \mathcal{R}_0)(1 + kw^*)^2(\delta + pw^*) - ac\delta p \mathcal{R}_0 kw^*. \quad (15)$$

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 (13), and $A_i(k) (i = 1, 2, 3)$ are defined as in (14).

Lemma 1 *If $A_i(k) (i = 1, 2, 3)$ are smooth functions of k in an open interval about $k_H \in \mathbb{R}$ such that the characteristic equation (13) has a pair of complex eigen values $\lambda = p_1(k) \pm ip_2(k)$ (with $p_1(k), p_2(k) \in \mathbb{R}$), so they become purely imaginary at $k = k_H$ and $\frac{dp_1(k)}{dk}|_{k=k_H} \neq 0$; and the other eigenvalue is negative at $k = k_H$, then model (3) exhibits a Hopf bifurcation around E^* at $k = k_H$.*

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 If $k = k_H$, the characteristic equation (13) equals

$$\lambda^3 + A_1(k_H)\lambda^2 + A_2(k_H)\lambda + A_3(k_H) = 0. \quad (16)$$

If

$$A_1(k_H)A_2(k_H) = A_3(k_H),$$

then (16) can be factorized as:

$$(\lambda^2 + A_2(k_H))(\lambda + A_1(k_H)) = 0. \quad (17)$$

Easy to obtain that (17) 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 neighbourhood of k_H , the characteristic roots of (17) have the form $\lambda_1 = p_1(k) + ip_2(k)$, $\lambda_2 = p_1(k) - ip_2(k)$ and $\lambda_3 = -p_3(k)$, where $p_i(k) (i = 1, 2, 3)$ are real numbers.

Next, we verify the transversality condition

$$\frac{d}{dk}(\text{Re}(\lambda_i(k)))|_{k=k_H} = \frac{dp_1(k)}{dk}|_{k=k_H} \neq 0, i = 1, 2. \quad (18)$$

Putting $\lambda(k) = p_1(k) + ip_2(k)$ into (13), we have

$$(p_1(k) + ip_2(k))^3 + A_1(p_1(k) + ip_2(k))^2 + A_2(p_1(k) + ip_2(k)) + A_3 = 0. \quad (19)$$

Taking derivative of both sides of (19) with respect to k , we obtain

$$\begin{aligned} & 3(p_1 + ip_2)^2(p_1' + ip_2') + 2A_1(p_1 + ip_2)(p_1' + ip_2') + A_1'(p_1 + ip_2)^2 + A_2(p_1' + ip_2') \\ & + A_2'(p_1 + ip_2) + A_3' = 0, \end{aligned}$$

where $' = \frac{d}{dk}$. Separating the real and complex parts, we have

$$\begin{cases} D_1 p_1' - D_2 p_2' + D_3 = 0, \\ D_2 p_1' + D_1 p_2' + D_4 = 0, \end{cases} \quad (20)$$

where

$$\begin{aligned} D_1 &= 3(p_1^2 - p_2^2) + 2A_1 p_1 + A_2, \quad D_2 = (6p_1 + 2A_1)p_2, \\ D_3 &= A_1'(p_1^2 - p_2^2) + A_2' p_1 + A_3', \quad D_4 = (2A_1' p_1 + A_2')p_2. \end{aligned}$$

It follows from (20) 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 equation (13) has a pair of purely imaginary roots of the form $\pm i\sqrt{A_2}$, that is, $p_1 = 0$, $p_2 = \sqrt{A_2}$ or $-\sqrt{A_2}$. In order to show that the transversality condition (18) holds, we consider whether $D_2 D_4 + D_1 D_3$ is zero at $k = k_H$ in the following two cases.

Case 1: $p_1 = 0, p_2 = \sqrt{A_2}$. We have

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

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 $D_2 D_4 + D_1 D_3 \neq 0$ at $k = k_H$.

Case 2: $p_1 = 0, p_2 = -\sqrt{A_2}$. We have

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

Therefore,

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

Hence, if $p_1 = 0, p_2 = -\sqrt{A_2}$, then $D_2 D_4 + D_1 D_3 \neq 0$ at $k = k_H$.

Based on the results above, we obtain:

$$\frac{d}{dk}(\text{Re}(\lambda_i(k)))|_{k=k_H} = -\frac{D_2 D_4 + D_1 D_3}{D_1^2 + D_2^2}|_{k=k_H} \neq 0$$

and

$$p_3(k_H) = -A_1(k_H) < 0.$$

This ends the proof.

For the sake of understand the complex theoretical results above further, in Fig. 2, we give a bifurcation diagram of model (3) in $\mathcal{R}_0 - k$ 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).

Fig. 2 Bifurcation diagram of model (3) with the parameters set (21).

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 on model (3). As an example, we take the parameters of model (3) as follows:

$$a = 0.5, d = 0.1, b = 0.1, p = 1, \delta = 0.2, c = 0.8, \mu = 0.3, \beta = 0.5. \quad (21)$$

Then we can get:

$$\begin{aligned} r &= 0.4, \mathcal{R}_0 = 10.0, k_H = 0.7615187994, \\ b < b_- &= \frac{(r + 2\delta - 2\sqrt{\delta(r + \delta)})pc}{\mu} = 0.286, \\ \mathcal{R}_0^- &= \frac{2rcp}{rcp - b\mu + \sqrt{(rcp - b\mu)^2 - 4cpb\delta\mu}} = 1.175, \\ \mathcal{R}_0^+ &= \frac{2rcp}{rcp - b\mu - \sqrt{(rcp - b\mu)^2 - 4cpb\delta\mu}} = 18.158. \end{aligned}$$

Thus, the conditions of Theorem 1 are satisfied. In addition, model (3) and model (11) 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).

Firstly, we adopt $k = 0$, without the cost of the fear factor, model (11) has a unique positive equilibrium $\hat{E}_* = (1.75, 0.375, 0.675)$, which is stable (Fig. 3).

Secondly, 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

$$\Theta_1(k) = b(r + \delta\mathcal{R}_0)(1 + kw^*)^2(\delta + pw^*) - ac\delta p\mathcal{R}_0kw^* = 0.06072 > 0,$$

$$A_1(k) = 0.112036, A_2(k) = 0.234094, A_3(k) = 0.021355,$$

$$A_1(k)A_2(k) = 0.02623, A_1(k)A_2(k) - A_3(k) = 0.00487 > 0,$$

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 $\hat{E}_*$ of model (11), which is induced by the cost of fear factor.

Fig. 3 Population dynamics of $u(t)$, $v(t)$ and $w(t)$ of model (11) (without the fear factor).

Fig. 4 Population dynamics of $u(t)$, $v(t)$ and $w(t)$ of model (3) with the level of fear $k = 0.4 < k_H$.

Thirdly, we adopt $k = 0.7615187994 = k_H$ and get:

$$\Theta_1(k) = b(r + \delta \mathcal{R}_0)(1 + kw^*)^2(\delta + pw^*) - ac\delta p \mathcal{R}_0 kw^* = 1 \times 10^{-10} \approx 0,$$

$$A_1(k) = 0.09216, A_2(k) = 0.18191, A_3(k) = 0.01676,$$

$$A_1(k)A_2(k) = 0.01676, A_1(k)A_2(k) - A_3(k) = 0.$$

From Theorem 5, we learn that the cost of the fear factor k can destabilize E^* from a stable spiral sink 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.

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 3-dimensional space.

Fourthly, we adopt $k = 1 > k_H$ and obtain

$$\Theta_1(k) = b(r + \delta \mathcal{R}_0)(1 + kw^*)^2(\delta + pw^*) - ac\delta p \mathcal{R}_0 kw^* = -0.02628 < 0,$$

$$A_1(k) = 0.08431, A_2(k) = 0.16132, A_3(k) = 0.01499,$$

$$A_1(k)A_2(k) = 0.01360, A_1(k)A_2(k) - A_3(k) = -0.00139 < 0,$$

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.

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 3-dimensional space.

Finally, we analyze the effect of high level of fear factor on the population dynamics of model (3). As examples, we adopt three different values of $k = 100, 1000$ and 6000 to show

the influence of the fear factor. The simulation results are shown in Fig. 7, and we can see that as k increasing, the amplitude of w is becoming smaller and smaller (see Figs. 7(a) and 7(b)), and finally goes to extinct (see Fig. 7(c)).

Fig. 7 Time-series plots of model (3) with level of fear factor $k = 100$ (a), 1000 (b) and 6000 (c).

6 Conclusions and discussions

In this paper, we divide the prey population into two sub classes: 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 $k < k_H$, then the coexistence equilibrium E^* of model (3) is stable (see Fig. 4), which is the same as $\hat{E}_*$ of model (11), the case without the fear factor (see Fig. 3). These results agree with those in Refs. [28, 20, 30, 36, 19, 29].
- (b) If $k = k_H$, then 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. [28, 30, 36, 19, 29].
- (c) If $k_H < k < k_*$ (k_* is implicitly determined in Remark 1), then E^* of model (3) is unstable and the system exhibits periodic behavior. These results are similar to those in [19].
- (d) If $k > k_*$, then 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 behaviour of the prey, and the fear factor is induced by the predator w . Biologically speaking, if the fear factor is very large, and the prey will respond to perceived predation risk and show a variety of anti-predator responses (such as changing habitat, forging behaviour, vigilance and physiological changes and so on). 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. And hence, for the coexistence of system (3), k needs to be less than the high risk value of the fear factor k_* , 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:

$$\begin{cases} \frac{du}{dt} = au - bu(u+v) - \beta uv - du, \\ \frac{dv}{dt} = \beta uv - \delta v, \end{cases} \quad (22)$$

which has two boundary equilibria $E_0 = (0,0)$, $E_1 = (\frac{r}{b}, 0)$ and a unique coexistence equilibrium $E^* = (\frac{\delta}{\beta}, \frac{r\beta - \delta b}{\beta(b+\beta)})$. 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 $\frac{\delta}{\beta}$ in E^* as follows:

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

Furthermore, if $r\beta > b\delta$, E^* is stable; while if $r\beta < b\delta$, E^* is unstable. With the parameters set (21), the phase portraits of system (22) are shown in Fig. 8, in which, the boundary points $E_0 = (0,0)$ and $E_1 = (4,0)$ are saddle points, the coexistence equilibrium $E^* = (0.4, 0.6)$ is globally stable.

Fig. 8 Phase portraits of model (22) with parameters (21). $E_0 = (0,0)$ and $E_1 = (4,0)$ are saddle points, $E^* = (0.4, 0.6)$ is a globally stable coexistence point.

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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Conflict of Interest

The authors declare that they have no conflict of interest.

Availability of data and material

Not applicable.

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Appendix A: The sign of $\xi(\mathcal{R}_0)$

Proof Recall

$$\xi(\mathcal{R}_0) := b\delta\mu\mathcal{R}_0^2 - r(rcp - b\mu)\mathcal{R}_0 + r^2cp,$$

so we can discuss the sign of $\xi(\mathcal{R}_0)$ in the following two cases.

Case 1: $rcp \leq b\mu$. In this case, $\xi(\mathcal{R}_0) > 0$.

Case 2: $rcp > b\mu$.

Set

$$\Delta(b) := (rcp - b\mu)^2 - 4cpb\delta\mu = \mu^2b^2 - 2cp\mu(r + 2\delta)b + r^2c^2p^2.$$

Note that $(-2cp\mu(r + 2\delta))^2 - 4\mu^2r^2c^2p^2 = 16c^2\delta\mu^2p^2(r + \delta) > 0$, 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 $\xi(\mathcal{R}_0) > 0$.

Case 2-2: If $b = b_{\pm}$ holds, we have $\Delta(b) = 0$. Thus, when $\mathcal{R}_0 = \frac{2rcp}{rcp - b\mu}$, we have

$\xi(\mathcal{R}_0) = 0$; when $\mathcal{R}_0 \neq \frac{2rcp}{rcp - b\mu}$, we have $\xi(\mathcal{R}_0) > 0$.

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

Then, one can see that $\xi(\mathcal{R}_0)$ has two positive roots $\mathcal{R}_0^-$ and $\mathcal{R}_0^+$, which are defined as in (8). In fact,

$$1 < \frac{2rcp}{rcp - b\mu + \sqrt{(rcp - b\mu)^2 - 4cpb\delta\mu}} = \mathcal{R}_0^-.$$

Hence, if $\mathcal{R}_0 = \mathcal{R}_0^{\pm}$ holds, we have $\xi(\mathcal{R}_0) = 0$; if $1 < \mathcal{R}_0^- < \mathcal{R}_0 < \mathcal{R}_0^+$ holds, we have $\xi(\mathcal{R}_0) < 0$; if $1 < \mathcal{R}_0 < \mathcal{R}_0^-$ or $\mathcal{R}_0 > \mathcal{R}_0^+$ holds, we have $\xi(\mathcal{R}_0) > 0$.

Therefore, we can determine the sign of $\xi(\mathcal{R}_0)$ in three cases as follows:

(1) when $rcp > b\mu$, if $0 < b < b_-$ or $b > b_+$, and $1 < \mathcal{R}_0^- < \mathcal{R}_0 < \mathcal{R}_0^+$ hold, we have $\xi(\mathcal{R}_0) < 0$;

(2) when $rcp > b\mu$, if $0 < b \leq b_-$ or $b \geq b_+$, and $\mathcal{R}_0 = \mathcal{R}_0^{\pm}$, we have $\xi(\mathcal{R}_0) = 0$.

(3) if one of the following inequalities holds:

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

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

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

(ii) $b = b_{\pm}$ and $\mathcal{R}_0 \neq \frac{2rcp}{rcp - b\mu}$;

(iii) $0 < b < b_-$ or $b > b_+$, and $1 < \mathcal{R}_0 < \mathcal{R}_0^-$ or $\mathcal{R}_0 > \mathcal{R}_0^+$,

we have $\xi(\mathcal{R}_0) > 0$.

Appendix B: The Proof of Theorem 3

Proof The Jacobin matrix of model (3) around $E_2 = \left(\frac{r}{b\mathcal{R}_0}, \frac{r^2(\mathcal{R}_0-1)}{b\mathcal{R}_0(\delta\mathcal{R}_0+r)}, 0 \right)$ is given as

$$J_2 = \begin{pmatrix} -\frac{r}{\mathcal{R}_0} & -\frac{r}{\mathcal{R}_0} - \delta & -\frac{akr}{b\mathcal{R}_0} \\ \frac{\delta r(\mathcal{R}_0-1)}{\delta\mathcal{R}_0+r} & 0 & -\frac{pr^2(\mathcal{R}_0-1)}{b\mathcal{R}_0(\delta\mathcal{R}_0+r)} \\ 0 & 0 & -\frac{\xi(\mathcal{R}_0)}{b\mathcal{R}_0(\delta\mathcal{R}_0+r)} \end{pmatrix}.$$

Hence, the characteristic equation of J_2 is given as

$$\left(\lambda^2 \mathcal{R}_0 + r\lambda + r\delta(\mathcal{R}_0-1) \right) (-b\mathcal{R}_0(\delta\mathcal{R}_0+r)\lambda - b\delta\mu\mathcal{R}_0^2 + r(rcp - b\mu)\mathcal{R}_0 - r^2cp) = 0.$$

Set

$$\begin{aligned} \phi(\lambda) &:= -b\mathcal{R}_0(\delta\mathcal{R}_0+r)\lambda - b\delta\mu\mathcal{R}_0^2 + r(rcp - b\mu)\mathcal{R}_0 - r^2cp \\ &= -b\mathcal{R}_0(\delta\mathcal{R}_0+r)\lambda - \xi(\mathcal{R}_0), \end{aligned}$$

then $\phi(\lambda)$ has a unique root $-\frac{\xi(\mathcal{R}_0)}{b\mathcal{R}_0(\delta\mathcal{R}_0+r)}$.

Case 1: When $\xi(\mathcal{R}_0) > 0$, E_2 is stable;

Case 2: When $\xi(\mathcal{R}_0) < 0$, E_2 is unstable;

Case 3: When $\xi(\mathcal{R}_0) = 0$, the root of $\phi(\lambda)$ is zero, which implies that E_2 is a singular point with higher order. In this case, we have

$$\begin{aligned} cpv_2 - \mu &= \frac{cpr^2(\mathcal{R}_0-1)}{b\mathcal{R}_0(\delta\mathcal{R}_0+r)} - \mu \\ &= \frac{b\delta\mu\mathcal{R}_0^2 - r(rcp - b\mu)\mathcal{R}_0 + r^2cp}{b\mathcal{R}_0(\delta\mathcal{R}_0+r)} \\ &= \frac{\xi(\mathcal{R}_0)}{b\mathcal{R}_0(\delta\mathcal{R}_0+r)} \\ &= 0, \end{aligned}$$

which implies that

$$v_2 = \frac{r^2(\mathcal{R}_0-1)}{b\mathcal{R}_0(\delta\mathcal{R}_0+r)} = \frac{\mu}{cp}.$$

Let $u = \bar{u} - \frac{r}{b\mathcal{R}_0}$, $v = \bar{v} - \frac{\mu}{cp}$ and $w = \bar{w}$, then the model (3) becomes

$$\begin{cases} \frac{du}{dt} = -\frac{(bu\mathcal{R}_0+r)(b\delta\mathcal{R}_0v + dkrw + kr^2w + bru + brv)}{rb\mathcal{R}_0}, \\ \frac{dv}{dt} = \frac{(cpv + \mu)(b\delta\mathcal{R}_0u - prw)}{cpr}, \\ \frac{dw}{dt} = cpvw, \end{cases} \quad (23)$$

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 (23) is

$$J_2 = \begin{pmatrix} -\frac{r}{\mathcal{R}_0} & -\frac{b\delta\mathcal{R}_0+br}{b\mathcal{R}_0} & -\frac{dkr+kr^2}{b\mathcal{R}_0} \\ \frac{\mu\mathcal{R}_0b\delta}{cpr} & 0 & -\frac{\mu}{c} \\ 0 & 0 & 0 \end{pmatrix}. \quad (24)$$

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

$$\begin{aligned} u &= \bar{n}_1 w + \bar{n}_2 w^2 + O(w^2), \\ v &= \tilde{n}_1 w + \tilde{n}_2 w^2 + O(w^2). \end{aligned} \quad (25)$$

Then we have

$$\begin{aligned} \frac{du}{dt} &= \bar{n}_1 \frac{dw}{dt} + 2\bar{n}_2 w \frac{dw}{dt} + O(w), \\ \frac{dv}{dt} &= \tilde{n}_1 \frac{dw}{dt} + 2\tilde{n}_2 w \frac{dw}{dt} + O(w) \end{aligned} \quad (26)$$

Substituting (23) and (25) into (26), we can obtain

$$\begin{aligned} &-r(b\delta\mathcal{R}_0\bar{n}_1 + br(\bar{n}_1 + \tilde{n}_1) + kr(d+r))w - b(b\delta\mathcal{R}_0^2\bar{n}_1\tilde{n}_1 + cpr\mathcal{R}_0\bar{n}_1\tilde{n}_1 + br\mathcal{R}_0\bar{n}_1^2 \\ &+ br\mathcal{R}_0\bar{n}_1\tilde{n}_1 + dkr\mathcal{R}_0\bar{n}_1 + kr^2\mathcal{R}_0\bar{n}_1 + \delta r\mathcal{R}_0\tilde{n}_2 + r^2\tilde{n}_2)w^2 + O(w^2) = 0, \\ &(b\delta\mu\mathcal{R}_0\bar{n}_1 - \mu pr)w + (bc\delta p\mathcal{R}_0\bar{n}_1\tilde{n}_1 - c^2p^2r\tilde{n}_1^2 + b\delta\mu\mathcal{R}_0\tilde{n}_2 - cp^2r\tilde{n}_1)w^2 + O(w^2) = 0 \end{aligned} \quad (27)$$

Comparing the coefficients of w and w^2 in (27), we find that

$$\begin{aligned} \bar{n}_1 &= \frac{rp}{\mathcal{R}_0 b \delta}, \quad \bar{n}_2 = \frac{c^2 p^2 r^3 (d\delta k \mathcal{R}_0 + \delta k r \mathcal{R}_0 + pr)^2}{\mathcal{R}_0^3 b^3 \delta^3 (\delta \mathcal{R}_0 + r)^2 \mu}, \quad \tilde{n}_1 = -\frac{(\delta k \mathcal{R}_0 (d+r) + pr)r}{\mathcal{R}_0 b \delta (\delta \mathcal{R}_0 + r)}, \\ \tilde{n}_2 &= \frac{r^2 p^2 c (\delta k \mathcal{R}_0 (d+r) + pr) (b\delta^2 \mu \mathcal{R}_0^3 - cd\delta k r^2 \mathcal{R}_0 - c\delta k r^3 \mathcal{R}_0 + b\delta \mu r \mathcal{R}_0^2 - cpr^3)}{b^3 \mathcal{R}_0^3 \delta^3 (\delta \mathcal{R}_0 + r)^3 \mu}. \end{aligned}$$

Therefore, substituting (25) into (23), we have

$$\frac{dw}{dt} = -cprb^2 \mathcal{R}_0^2 \delta^2 \mu (\delta k \mathcal{R}_0 (d+r) + pr) (\delta \mathcal{R}_0 + r)^2 w^2 + O(w^3), \quad (28)$$

which yield that the origin $(0, 0, 0)$ of system (23) is locally asymptotically stable. Thus, E_2 is locally asymptotically stable when $\xi(\mathcal{R}_0) = 0$.

The proof is completed.