The Influence of Density Dependent Death Rate of Predator Species to the Lotka-Volterra Predator Prey System with Fear Effect

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Abstract: - A Lotka-Volterra predator prey system incorporating fear effect of the prey species and density dependent death rate of predator species is proposed and studied in this paper. Local and global stability property of the equilibria are investigated. Our study shows that the density dependent death rate of predator species has no influence to the persistent or extinction property of the system. However, with the increasing of the density dependent death rate, the final density of the predator species is decreasing and the final density of the prey species is increasing. Hence, the increasing of the the density dependent death rate enhance the possibility of the extinction of the predator specie. Numeric simulations show that too high density dependent death rate and too high fear effect of prey species may lead to the extinction of the predator species.

Key-Words: Lotka-Volterra predator prey model; Stability; Fear effect; Density dependent death rate

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1 Introduction

The aim of this paper is to investigate the dynamic behaviors of the following Lotka-Volterra predator prey system incorporating fear effect of the prey and the density dependent death rate of predator species

$$\begin{aligned} \frac{du}{dt} &= \frac{r_0 u}{1+kv} - du - au^2 - puv, \\ \frac{dv}{dt} &= cpuv - mv - ev^2, \end{aligned} \tag{1.1}$$

where u and v are the density of prey species and the predator species at time t, respectively. r_0 is the birth rate of the prey species, d is the death rate of the prey species, a is the density dependent death rate of the prey species, $m + ev$ is the death rate of the predator species, obviously, it is density dependent; p denotes the strength of interspecific between prey and predator; c is the conversion efficiency of ingested prey into new predators; k is the level of fear, which is due to anti-predator behaviours of the prey.

Recently, Wang, Zanette and Zou[1] proposed the following Lotka-Volterra predator prey system incorporating fear effect of the prey

$$\begin{aligned} \frac{du}{dt} &= r_0 u f(k,v) - du - au^2 - puv, \\ \frac{dv}{dt} &= cpuv - mv. \end{aligned} \tag{1.2}$$

The system admits three nonnegative equilibrium, $E_0(0,0)$, $E_1(\frac{r_0-d}{a},0)$ and $E_2(\overline{u},\overline{v})$, where $\overline{u}=\frac{m}{cp}$, and $\overline{v}$ satisfies

$$r_0 f(k,\overline{v}) - d - a\overline{u} - p\overline{v} = 0. \tag{1.3}$$

Concerned with the global stability property of the system (1.2), the authors obtained the following result.

Theorem A. *Assume that $r_0 < d$, then E_0 is globally asymptotically stable; The boundary equilibrium E_1 is globally asymptotically stable if $r_0 \in (d, d+\frac{am}{cp})$, and the unique positive equilibrium E_2 is globally asymptotically stable if $r_0 > d + \frac{am}{cp}$.*

It brings to our attention that in system (1.2), the authors did not consider the influence of the intra-competition of the predator species, though such an assumption were adopt by many scholars ([1]-[22]) and it seems reasonable. We should also pay attention to the other case. In the lack of food situation, competitive of food resource will become urgent, and those predators that less food maybe driven to extinction, this leads to the increasing of the death rate of predator species. Hence, many scholars ([23]-[33]) also proposed the predator prey system with density dependent death rate of predator species. It bring to our attention that, to this day, though there are many papers ([1]-[11]) investigated the dynamic behaviors of the predator prey system incorporating the fear effect of prey species, there are still no scholars consider the influence of the density dependent death rate to the system (1.2). This motivated us to propose the system (1.1).

The aim of this paper is to investigate the dynamic behaviors of the system (1.1), and to find out the influence of the density dependent death rate of predator species.

The rest of the paper is arranged as follows. We will investigate the local and global stability property of the equilibria of the system (1.1) in Section 2 and 3, respectively, and then discuss the influence of density dependent death rate of predator species in Section 4. By applying the existence theorem for implicit function, we discuss the influence of the fear effect and the density dependent death rate of the predator species. Numeric simulations are presented in Section 5 to show the feasibility of the main results. We end this paper with a brief discussion.

2 The existence and local stability of the equilibria

Concerned with the existence of the equilibria of system (1.1), we have the following result.

Theorem 2.1. *System (1.1) always admits the trivial boundary equilibrium $E_0(0,0)$ and if $r_0 > d$ holds, the predator free equilibrium $E_1\Big(\dfrac{r_0-d}{a},0\Big)$ exists. Also, there exists a unique positive equilibrium $E_2(u^*,v^*)$, if*

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

holds, where $u^* = \dfrac{ev^*+m}{cp}$ and v^* is the unique positive solution of the equation

$$A_1v^2 + A_2v + A_3 = 0, \tag{2.2}$$

where

$$\begin{aligned} A_1 &= ckp^2 + aek, \\ A_2 &= cdkp + akm + cp^2 + ae, \\ A_3 &= dcp - r_0\,cp + am. \end{aligned} \tag{2.3}$$

Remark 2.1. By introducing the density dependent rate of the predator species, system (1.1) also admits a prey free equilibrium $E_3(0,-\dfrac{m}{e})$, since $-\dfrac{m}{e} < 0$, E_3 is lack of biological meaning, and we will not investigate it.

Proof of Theorem 2.1. The equilibria of system (1.1) satisfy the equation

$$\begin{aligned} \frac{r_0u}{1+kv} - du - au^2 - puv &= 0, \\ cpuv - mv - ev^2 &= 0. \end{aligned} \tag{2.4}$$

From the second equation of (2.4), one has $v = 0$ or $u = \dfrac{ev+m}{cp}$. Substituting $v = 0$ to the first equation of (2.4) leads to

$$r_0u - du - au^2 = 0. \tag{2.5}$$

Equation (2.5) has solutions $u_1 = 0$ and $u_2 = \dfrac{r_0-d}{a}$. Hence, system (1.1) admits the trivial equilibrium $E_0(0,0)$, and if $r_0 > d$ holds, the predator free equilibrium $E_1\Big(\dfrac{r_0-d}{a},0\Big)$ exists.

Next, substituting $u = \dfrac{ev+m}{cp}$ to the first equation of (2.4) and simplifying it leads to

$$A_1v^2 + A_2v + A_3 = 0. \tag{2.6}$$

Under the assumption of (2.1), one could easily see that $A_3 < 0$, hence, (2.6) admits a unique positive solution v^*, consequently, system (1.1) admits a unique positive equilibrium $E_2(u^*,v^*)$.

The first equation of (2.4) has a solution $u = 0$, substituting this to second equation of (2.4) leads to

$$-mv - d_1v^2 = 0. \tag{2.7}$$

Hence, system (1.1) admits the prey free equilibrium $E_3(0,-\dfrac{m}{d_1})$. Since $-\dfrac{m}{d_1} < 0$, E_3 has no biological meaning, and we will not investigate the stability property of this equilibrium.

This ends the proof of Theorem 2.1.

Theorem 2.2. *The trivial equilibrium $E_0(0,0)$ is locally asymptotically stable if*

$$r_0 < d \tag{2.8}$$

holds; If

$$d < r_0 < d + \frac{am}{cp} \tag{2.9}$$

holds, the predator free equilibrium $E_1\Big(\dfrac{r_0-d}{a},0\Big)$ is locally asymptotically stable; The positive equilibrium $E_3(u^*,v^*)$ is locally asymptotically stable if

$$r_0 > d + \frac{am}{cp} \tag{2.10}$$

holds, i.e, the positive equilibrium is locally asymptotically stable as long as it exists.

Proof. The Jacobian matrix of the system (1.1) is calculated as

$$J = \begin{pmatrix} J_{11} & J_{12} \\ J_{21} & J_{22} \end{pmatrix}, \tag{2.11}$$

where

$$\begin{aligned} J_{11} &= \frac{r_0}{kv+1} - d - 2\,au - pv, \\ J_{12} &= -\frac{r_0\,uk}{(kv+1)^2} - pu, \\ J_{21} &= cpu - 2\,ev - m, \\ J_{22} &= cpu - m - 2d_1v. \end{aligned} \tag{2.12}$$

Then the Jacobian matrix of the system (1.1) about the trivial equilibrium $E_0(0,0)$ is

$$J(E_0(0,0)) = \begin{pmatrix} r_0 - d & 0 \\ 0 & -m \end{pmatrix}. \tag{2.13}$$

Under the assumption (2.8) holds, the eigenvalues of $J(E_0)$ are $\lambda_1 = r_0 - d < 0$, $\lambda_2 = -m < 0$. Thus, the trivial equilibrium $E_0(0,0)$ is locally asymptotically stable.

It follows from (2.3) that the Jacobian matrix of the system (1.1) about the predator free equilibrium $E_1\Big(\dfrac{r_0-d}{a},0\Big)$ is

$$J\Big(E_1(\frac{r_0-d}{a},0)\Big) = \begin{pmatrix} -(r_0-d) & -(r_0k+p)\dfrac{r_0-d}{a} \\ 0 & cp\dfrac{r_0-d}{a} - m \end{pmatrix}. \tag{2.14}$$

Under the assumption (2.9) holds, the eigenvalues of $J(E_1)$ are $\lambda_1 = -(r_0-d) < 0$, $\lambda_2 = cp\frac{r_0-d}{a} - m < 0$. Thus, $E_1(\frac{r_0-d}{a},0)$ is locally asymptotically stable.

The Jacobian matrix of the system (1.1) about the positive equilibrium $E_2(u^*,v^*)$ is

$$J(E_2(u^*,v^*)) = \begin{pmatrix} -au^* & -\dfrac{r_0u^*k}{(kv^*+1)^2} - pu^* \\ cpv^* & -ev^* \end{pmatrix}. \tag{2.15}$$

Then we have

$$\begin{aligned} & DetJ(E_2(u^*,v^*)) \\ = \;& aeu^*v^* + cpv^*u^*\Big(\frac{r_0k}{(kv^*+1)^2} + p\Big) \\ > \;& 0 \end{aligned}$$

and

$$TrJ(E_2(u^*,v^*)) = -au^* - ev^* < 0.$$

So that both eigenvalues of $J(E_2(u^*,v^*))$ have negative real parts, consequently, $E_2(u^*,v^*)$ is locally asymptotically stable.

This ends the proof of Theorem 2.2.

3 Global asymptotical stability

Concerned with the global stability property of the equilibria of system (1.1), we have the following result.

Theorem 3.1. *Assume that $r_0 < d$, then trivial equilibrium E_0 is globally asymptotically stable; The predator free equilibrium E_1 is globally asymptotically stable if $r_0 \in (d, d + \dfrac{am}{cp})$, and the unique positive equilibrium E_2 is globally asymptotically stable if $r_0 > d + \dfrac{am}{cp}$.*

Proof. We first show that the system admits no limit cycle in the first quadrant. Let's consider the Dulac function $B(u,v) = \dfrac{1}{uv}$, then

$$\begin{aligned} & \frac{\partial(PB)}{\partial u} + \frac{\partial(QB)}{\partial v} \\ = \;& \frac{1}{uv}\Big(\frac{r_0}{kv+1} - d - 2\,au - pv\Big) \\ & -\frac{1}{u^2v}\Big(\frac{r_0\,u}{kv+1} - du - au^2 - puv\Big) \\ & +\frac{cpu - 2\,ev - m}{uv} - \frac{cpuv - ev^2 - mv}{uv^2} \\ = \;& -\frac{au+ev}{uv} < 0, \end{aligned} \tag{3.1}$$

where $P(u,v), Q(u,v)$ represent the two functions on the right hand side of system (1.1). By Dulac Theorem[34], there is no closed orbit in the first quadrant.

(1) When $r_0 < d$, the system admits only one nonnegative equilibrium $E_0(0,0)$, this, together with the fact that the system has no periodic orbit in R_2^+, implies that every positive solution will approach E_0, that is, E_0 is globally asymptotically stable;

(2) When $d < r_0 < d + \dfrac{am}{cp}$, the system admits two equilibrium E_0 and E_1. Noting that in this case, E_0 is unstable, and E_1 is locally asymptotically stable, also, the system has no periodic orbit in R_2^+ hence, every positive solution will approach E_1, that is, E_1 is globally asymptotically stable;

(3) When $r_0 > d + \dfrac{am}{cp}$, the system admits three equilibria E_0, E_1 and E_2, since in this case, only E_2 is locally asymptotically stable, while E_0 and E_1 are both unstable. This, together with the fact that the system has no periodic orbit in R_2^+ implying that every positive solution will approach E_2, that is, E_2 is globally asymptotically stable;

The proof of Theorem 3.1 is finished.

Remark 3.1. Compared with Theorem 3.1 and Theorem A, one could see that the dynamic behaviors of system (1.1) is similar to the dynamic behaviors of system (1.2). The density dependent death rate of predator species has no influence to the persistent and extinction property of the system.

4 The influence of parameters k and e

Following we will discuss the influence of fear effect and the density dependent death rate of predator species.

Denote

$$\begin{aligned} F(u^*,v^*,k,e) &= \frac{r_0}{1+kv^*}-d \\ &\quad -au^*-pv^*, \qquad (4.1) \\ G(u^*,v^*,k,e) &= cpu^*-m-ev^*. \end{aligned}$$

Then the positive equilibrium $E_2(u^*,v^*)$ satisfies

$$\begin{cases} F(u^*,v^*,k,e) = 0, \\ G(u^*,v^*,k,e) = 0. \end{cases} \qquad (4.2)$$

By simple computation, we have

$$\begin{aligned} J &= \frac{D(F,G)}{D(u^*,v^*)} = \begin{vmatrix} F_{u^*} & F_{v^*} \\ G_{u^*} & G_{v^*} \end{vmatrix} \\ &= \begin{vmatrix} -a & -\frac{r_0k}{(1+kv^*)^2}-p \\ cp & -e \end{vmatrix} \\ &= ae+cp\Big(\frac{r_0k}{(1+kv^*)^2}+p\Big)>0 \end{aligned}$$

for all $u^*>0, v^*>0, k>0, e>0$. Thus, the equations (4.2) satisfy the conditions of the existence theorem for implicit functions, then the equations (4.2) determine two implicit functions of

$$u^*=u^*(k,e),\ \ v^*=v^*(k,e)$$

for all $k>0, e>0$. Also,

$$\frac{\partial u^*}{\partial k}=-\frac{1}{J}\frac{D(F,G)}{D(k,v^*)},\ \ \frac{\partial v^*}{\partial k}=-\frac{1}{J}\frac{D(F,G)}{D(u^*,k)},$$

$$\frac{\partial u^*}{\partial e}=-\frac{1}{J}\frac{D(F,G)}{D(e,v^*)},\ \ \frac{\partial v^*}{\partial e}=-\frac{1}{J}\frac{D(F,G)}{D(u^*,e)}.$$

Since

$$\begin{aligned} &\frac{D(F,G)}{D(k,v^*)} \\ &= \begin{vmatrix} -\frac{r_0v^*}{(1+kv^*)^2} & -\frac{r_0k}{(1+kv^*)^2}-p \\ 0 & -e \end{vmatrix} \\ &= \frac{er_0v^*}{(1+kv^*)^2}>0, \\ &\frac{D(F,G)}{D(u^*,k)} \\ &= \begin{vmatrix} -a & -\frac{r_0v^*}{(1+kv^*)^2} \\ cp & 0 \end{vmatrix} \\ &= \frac{cpr_0v^*}{(1+kv^*)^2}>0, \\ &\frac{D(F,G)}{D(e,v^*)} \\ &= \begin{vmatrix} 0 & -\frac{r_0k}{(1+kv^*)^2}-p \\ -v^* & -e \end{vmatrix} \\ &= -v^*\Big(\frac{r_0k}{(1+kv^*)^2}+p\Big)<0, \\ &\frac{D(F,G)}{D(u^*,e)} \\ &= \begin{vmatrix} -a & 0 \\ cp & -v^* \end{vmatrix} \\ &= av^*>0. \end{aligned}$$

Hence, we have

(1) $\frac{\partial u^*}{\partial k}<0$, that is, the prey density u^* is a decreasing function of k;

(2) $\frac{\partial v^*}{\partial k}<0$, that is, the predator density v^* is a decreasing function of k;

(3) $\frac{\partial u^*}{\partial e}>0$, that is, the prey density u^* is a increasing function of e;

(4) $\frac{\partial v^*}{\partial e}<0$, that is, the predator density v^* is a decreasing function of e.

5 Numeric simulation

We will introduce two examples to show the feasibility of the main results.

Example 5.1. Let's consider the following model

$$\begin{aligned} \frac{du}{dt} &= \frac{4u}{1+kv} - u - u^2 - 2uv, \\ \frac{dv}{dt} &= uv - v - ev^2. \end{aligned} \tag{5.1}$$

Here, corresponding to system (1.1), we take $r_0 = 4, d = a = m = 1, p = 2, c = 0.5.$ then one could see that

$$r_0 = 4 > 2 = d + \frac{am}{cp}. \tag{5.2}$$

Hence, it follows from Theorem 3.1 that for all $k \in [0, +\infty)$ and $e \in [0, +\infty)$, system (5.1) admits a unique positive equilibrium, which is globally asymptotically stable. Numeric simulation (Fig. 1) also supports this assertion.

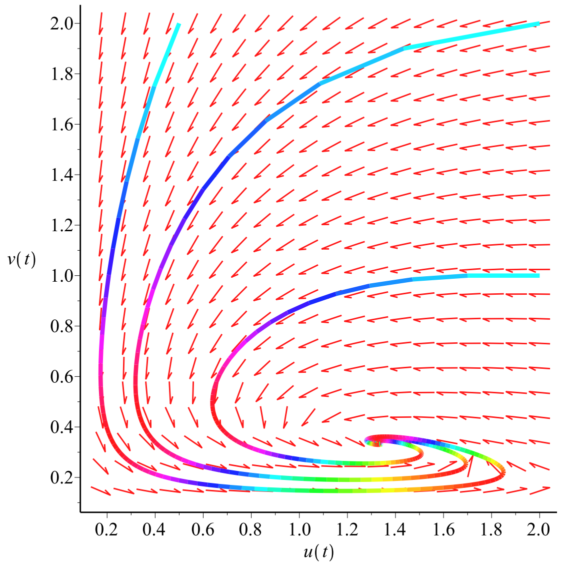

Figure 1: Dynamic behaviors of the system (5.1), the initial condition $(u(0), v(0)) = (2, 2)$, $(2, 1)$, $(2, 0.2)$ and $(2, 0.5)$, respectively.

Now, let's further take $e = 1$ in system (5.1), then we could obtain the positive equilibrium

$$\begin{aligned} u^*(k) &= 1 + v^*(k), \\ v^*(k) &= \frac{-2k - 3 + \sqrt{4k^2 + 36k + 9}}{6k}. \end{aligned} \tag{5.3}$$

Fig. 2 shows that $u^*(k)$ and $v^*(k)$ both are the decreasing function of k.

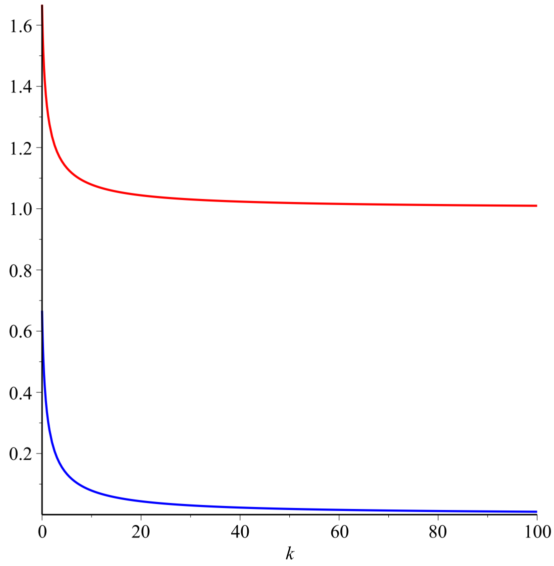

Figure 2: Relationship of u^* and k and v^* and k, the red one is $u^*(k)$, the blue one is $v^*(k)$.

Also, by simple computation, we have

$$\begin{aligned} & \lim_{k \to +\infty} v^*(k) \\ = & \lim_{k \to +\infty} \frac{-2k - 3 + \sqrt{4k^2 + 36k + 9}}{6k} \\ = & \lim_{k \to +\infty} \frac{-2 - \frac{3}{k} + 2\sqrt{1 + \frac{9}{k} + \frac{9}{4k^2}}}{6} \\ = & \lim_{k \to +\infty} \frac{-2 - \frac{3}{k} + 2\left(1 + \frac{1}{2} \cdot \frac{9}{k} + \frac{1}{2} \cdot \frac{9}{4k^2}\right)}{6} \\ = & \ 0, \\ & \lim_{k \to +\infty} u^*(k) \\ = & \lim_{e \to +\infty} \left(1 + v^*(k)\right) = 1. \end{aligned} \tag{5.4}$$

Now, let's further take $k = 1$ in system (5.1), then we could obtain the positive equilibrium

$$\begin{aligned} u^*(e) &= 1 + \tfrac{e}{2} v^*(e), \\ v^*(e) &= \tfrac{1}{2} \frac{-e - 4 + \sqrt{e^2 + 16e + 32}}{e + 2}. \end{aligned} \tag{5.5}$$

Fig. 3 shows that $u^*(e)$ is the increasing function of

e and $v^*(e)$ is the decreasing function of k.

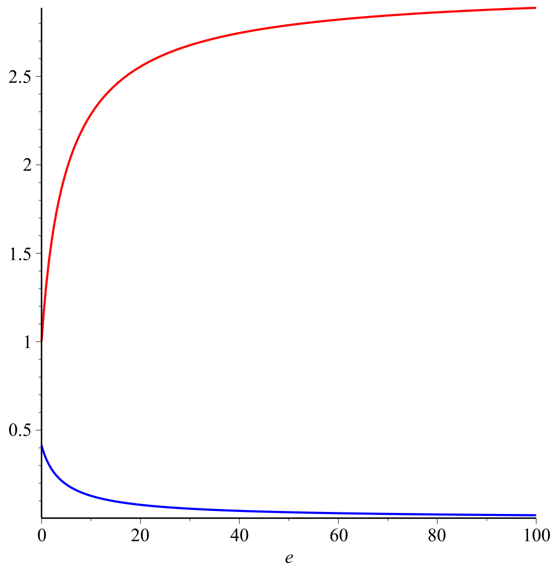

Figure 3: Relationship of u^* and e and v^* and e, the red one is $u^*(e)$, the blue one is $v^*(e)$.

Also, by simple computation, we have

$$\begin{aligned} & \lim_{e\to+\infty} v^*(e) \\ = \ & \frac{1}{2}\lim_{e\to+\infty} \frac{-e-4+\sqrt{e^2+16e+32}}{e+2} \\ = \ & \frac{1}{2}\lim_{e\to+\infty} \frac{-1-\frac{4}{e}+\sqrt{1+\frac{16}{e}+\frac{32}{e^2}}}{1+\frac{2}{e}} \\ = \ & \frac{1}{2}\lim_{e\to+\infty} \frac{-1-\frac{4}{e}+1+\frac{1}{2}\left(\frac{16}{e}+\frac{32}{e^2}\right)}{1+\frac{2}{e}} \\ = \ & 0, \end{aligned} \tag{5.6}$$

$$\begin{aligned} & \lim_{e\to+\infty} u^*(e) \\ = \ & 1+\frac{1}{2}\lim_{e\to+\infty} e\frac{-e-4+\sqrt{e^2+16e+32}}{e+2} \\ = \ & 1+\frac{1}{2}\lim_{e\to+\infty} \frac{-1-\frac{4}{e}+\sqrt{1+\frac{16}{e}+\frac{32}{e^2}}}{\frac{1}{e}\left(1+\frac{2}{e}\right)} \\ = \ & 1+\frac{1}{2}\lim_{e\to+\infty} \frac{-1-\frac{4}{e}+1+\frac{1}{2}\left(\frac{16}{e}+\frac{32}{e^2}\right)}{\frac{1}{e}\left(1+\frac{2}{e}\right)} \\ = \ & 3. \end{aligned} \tag{5.7}$$

Numeric simulations in accordance with the theoretical analysis in Section 4.

6 Conclusion

Wang, Zanette and Zou[1] proposed a Lotka-Volterra predator prey system incorporating the fear effect of prey species, i.e., system (1.2). Their result (Theorem A) indicates that the fear effect has no influence to the existence and stability of the equilibria. Stimulated by the fact that the predator species may also have nonlinear intra competition, and this may lead to the density dependent death rate, we propose the system (1.1), where both the fear effect and the density dependent death rate are considered.

It seems interesting that the density dependent death rate has no influence to the persistent or extinction of the system, since Theorem 3.1 shows that under the same assumption of Theorem A, system (1.1) admits the same dynamic behaviors as that of the system (1.2). However, by applying the existence theorem for implicit functions, we could show that u^* and v^* both are the decreasing function of the k, that is, with the increasing of the fear effect, the final density of predator and prey species decreasing. We also show that u^* is the increasing function of e and v^* is the decreasing function of the e, which means that the density dependent death rate of the predator species have negative effect on the final density of the predator species, and with the decreasing of the predator species, the density of prey species become increasing, since the chance of the prey species to be harvested becomes decreasing.

We mention her that despite the density dependent death rate and fear effect have no influence to the persistent property of the system, which seems similar to that of the system (1.2). However, as was shown in Example 5.2, $v^*(k)$ is the decreasing function of k, and $v^*(k) \to 0$ as $k \to 0$. Hence, with the increasing of the fear effect, the final density of predator species approach to zero, which means the extinction of the predator species. The reason for this maybe due to the fact that increasing the fear effect may lead to the decreasing of the density of prey species, and this finally leads to the lack of the food for maintain developing of the predator species. Example 5.2 also shows that $v^*(e) \to 0$ as $e \to +\infty$, and $u^*(e) \to \overline{u}$, where $\overline{u} = \dfrac{r_0 - d}{a}$, hence, with the level of the density dependent death rate of predator species increasing, the final density of predator species approach to zero, which means the extinction of the predator species.

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Qun Zhu carried out the simulation.
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Conflict of Interest

The authors have no conflict of interest to declare that is relevant to the content of this article.