

Stability Analysis of a Mutual Interference Predator-prey Model with the Fear Effect

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Abstract

In this paper, we consider a predator-prey system incorporating mutual interference into predator and the fear effect into prey. By using theories on exceptional directions and normal sectors, we show that both the two boundary equilibria are saddle points and the interior equilibrium is globally stable. Compared to the corresponding predator-prey model without mutual interference, we find that the mutual interference can stabilize the predator-prey system.

Key Words: Predator-prey, Fear Effect, Mutual Interference, Global Stability

1. Introduction

The traditional predator-prey systems assume that predators can lead to the reduction of the prey population only through direct killing [1–10]. In [11], they introduced two game-solution concepts, that is the static solution and the dynamical solution. In [12], the authors investigate the dynamics of a predator-prey system under an assumption that both preys and predators use game theory-based strategies to maximize their per capita population growth rates. In the past decade, many biologists have experimentally demonstrated that the predator-prey system reflects not merely direct killing by predators but also the fear of predators (see [13] for example). In the natural world, the fear of predators can stimulate prey to avoid direct killing by a variety of anti-predator responses such as changes in foraging behaviours, habitat usage and physiology, which may cause a long-term decrease in prey population. For example, in the absence of direct killing, Zanette et al. [14] found that the song sparrows surrounded by predator sounds produce 40% less offspring than the others hearing no-predator sounds. Also, there are much evidence show that fear can affect populations such as evidence in snowshoe hares

[15] or in birds [16]. Based on this fact, recently, Wang et al. [17] considered the predator-prey system with adaptive avoidance of predators and the fear effect, and studied its long-term dynamics. Wang et al. [18] considered the following predator-prey system incorporating the cost of fear into prey reproduction

$$\begin{aligned} \dot{x}(t) &= axf(k, y) - dx - bx^2 - mxy \\ \dot{y}(t) &= nmxy - ey \end{aligned} \quad (1)$$

where x and y denote the densities of prey species and predator species at time t , respectively; a is the birth rate of prey; d and e denote the natural death rates of prey and predator, respectively; b represents the death rate due to intra-species competition; m is the capture rate and n is the food conversion rate of predator. [14–16] showed that the prey production is indirectly influenced by the fear effect. Hence $f(k, y)$ is the cost of anti-predator defence due to fear [18], and by the biological meanings of k , y and $f(k, y)$, it is reasonable to assume that

$$\begin{aligned} f(0, y) = 1, \quad f(k, 0) = 1, \quad \lim_{k \rightarrow +\infty} f(k, y) = 0 \\ \lim_{y \rightarrow +\infty} f(k, y) = 0, \quad \frac{\partial f(k, y)}{\partial k} < 0, \quad \frac{\partial f(k, y)}{\partial y} < 0 \end{aligned}$$

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Therefore, the value $f(k, y)$ may be $\frac{1}{1+ky}$ or e^{-ky} or others [18]. System (1) has a trivial equilibrium $E_1(0, 0)$, and a boundary equilibrium $E_2\left(\frac{a-d}{b}, 0\right)$ if $a > d$. In addition, there exists a unique co-existence equilibrium $E^*(x^*, y^*)$ of model (1) if $a > d + \frac{be}{nm}$, where $x^* = \frac{e}{nm}$ and y^* satisfies $af(k, y^*) - d - bx^* - my^* = 0$. Furthermore, the following theorem was obtained in [18]:

Theorem A. (i) If $a < d$, then the trivial equilibrium E_1 of system (1) is globally asymptotically stable;
 (ii) if $d < a < d + \frac{be}{nm}$, then the boundary equilibrium E_2 of system (1) is globally asymptotically stable;
 (iii) if $a > d + \frac{be}{nm}$, then the unique positive equilibrium E^* of system (1) is globally asymptotically stable.

On the other hand, the predator interference was proposed by Hassell in 1971, due to the fact that predators tend to leave each other when they encountered, which can interfere with the effect of trapping predators. From the experiments, Hassell introduced the concept of mutual interference constant θ ($0 < \theta \leq 1$) into a Volterra model [19]. For more works in this direction, one could refer to [20–24] and the references cited therein.

Motivated by the above papers, the main purpose of this paper is to study system (1) with mutual interference. More precisely, we study the stability of the following model

$$\begin{aligned} \dot{x}(t) &= axf(k, y) - dx - bx^2 - mxy^\theta \\ \dot{y}(t) &= nmxy^\theta - ey \end{aligned} \tag{2}$$

where a, k, d, b, n, m, e are positive constants, whose biological meanings are the same as those in system (1); θ with $0 < \theta \leq 1$ is the mutual interference constant, and system (2) is reduced to model (1) when $\theta = 1$. Hence, we only consider $0 < \theta < 1$ in the rest of this paper.

The organization of this paper is as follows: the local and global stability property of equilibria of system (2) are discussed in the next section. In section 3, the influence of fear effect and a briefly discussion are given.

2. Main Results

Let $R_+^2 = \{(x, y): x \geq 0, y \geq 0\}$. For biological meaning, we only discuss model (2) in R_+^2 . It is easy to derive that there exists a trivial equilibrium $E_1(0, 0)$, and a boundary equilibria $E_2\left(\frac{a-d}{b}, 0\right)$ if $a > d$. Further, we study the existence of a unique positive interior equilibrium by analyzing the properties of predator isocline and prey isocline as follows:

(1) The prey isocline is $l_1: af(k, y) - d - bx - my^\theta = 0$.

Let $a > d$. If $y = 0$, then $x = \frac{a-d}{b} \triangleq x_0 > 0$. If $x = 0$,

we obtain $H(y) = af(k, y) - d - my^\theta$, obviously $H(0) = a - d > 0$ and $H'(y) = af'_y(k, y) - m\theta y^{\theta-1} < 0$ ($y \neq 0$), thus there exists a $y_0 > 0$ such that $H(y_0) = 0$. Notice that $x_0 > 0, y_0 > 0$ and $\frac{dy}{dx} = \frac{b}{af'_y(k, y) - m\theta y^{\theta-1}} <$

0. Therefore, l_1 monotonically decreases with respect to x , which starts from the point $(0, y_0)$ in the y -axis to the point $(x_0, 0)$ in the positive x -axis.

(2) The predator isocline is $l_2: -e + nmxy^{\theta-1} = 0$. Obviously, the point $(0, 0)$ lies on this isocline, $\frac{dy}{dx} =$

$\frac{y}{(1-\theta)x} > 0$ and $\frac{d^2y}{dx^2} = \frac{\theta y}{(1-\theta)^2 x^2} > 0$. Therefore, l_2

is a concave curve, which passes through $(0, 0)$ and monotonically increases as x increases.

The above analysis shows that l_1 and l_2 have a unique interior intersection point in the first quadrant. Hence, model (2) admits a unique interior positive equilibrium $E^*(x^*, y^*)$. Here, x^* and y^* satisfy the equations: $P(x^*, y^*) = 0, Q(x^*, y^*) = 0$, with $P(x, y) \triangleq axf(k, y) - dx - bx^2 - mxy^\theta$ and $Q(x, y) \triangleq nmxy^\theta - ey$.

Lemma 2.1 If $a > d$, then $E_1(0, 0)$ and $E_2\left(\frac{a-d}{b}, 0\right)$ are saddle points, and $E^*(x^*, y^*)$ is a locally stable node or focus.

Proof. (1) For $E_1(0, 0)$, we have:

$$\frac{\partial P(0, 0)}{\partial x} = \lim_{x \rightarrow 0} \frac{P(x, 0) - P(0, 0)}{x} = a - d,$$

$$\frac{\partial P(0, 0)}{\partial y} = \lim_{y \rightarrow 0} \frac{P(0, y) - P(0, 0)}{y} = 0,$$

$$\frac{\partial Q(0, 0)}{\partial x} = \lim_{x \rightarrow 0} \frac{Q(x, 0) - Q(0, 0)}{x} = 0,$$

$$\frac{\partial Q(0, 0)}{\partial y} = \lim_{y \rightarrow 0} \frac{P(0, y) - P(0, 0)}{y} = -e.$$

Hence the equilibrium point E_1 has two eigenvalues: $\lambda_1 = a - d$ and $\lambda_2 = -e$, that is $E_1(0, 0)$ is a saddle point.

(2) We analyze E_2 by applying the theories on exceptional directions and normal sectors in [25]. Firstly, we rewrite model (2) as

$$\frac{dx}{dt} = ax[1 + yf'_y(k, 0) + o(y)] - dx - bx^2 - mxy^\theta$$

$$\frac{dy}{dt} = nmxy^\theta - ey$$
(3)

Noting that $x = 0$ and $y = 0$ are orbits of model (2), $y = 0$ starts along the x-axis into $E_2\left(\frac{a-d}{b}, 0\right)$. For $0 < \theta < 1$,

we denote $\theta = \frac{1}{u}$, then $u > 1$. Taking the following scalings: $y = \bar{y}^u, x = \bar{x}, dt = \bar{y}^u d\tau$ and rewrite x, y, τ as \bar{x}, \bar{y}, τ , respectively, then model (3) takes the following form

$$\frac{d\bar{x}}{d\tau} = a\bar{x}\bar{y}^u + a\bar{x}\bar{y}^{2u}f'_y(k, 0) - d\bar{x}\bar{y}^u - b\bar{x}^2\bar{y}^u$$

$$- m\bar{x}\bar{y}^{u+1} + a\bar{x}\bar{y}^u(o(\bar{y}^u))$$
(4)

$$\frac{d\bar{y}}{d\tau} = \frac{1}{u}(nm\bar{x}\bar{y}^2 - e\bar{y}^{u+1})$$

Thus the equilibrium $E_2\left(\frac{a-d}{b}, 0\right)$ is a high order singular point. Furthermore, taking the following scalings: $\bar{x} = x - \frac{a-d}{b}, \bar{y} = y$ and rewriting \bar{x}, \bar{y} , as x, y , respectively, model (4) takes the following form

$$\frac{dx}{dt} = -(a-d)xy^u + axy^{2u}f'_y(k, 0) + \frac{a(a-d)}{b}y^{2u}f'_y(k, 0) - bx^2y^u$$

$$- mxy^{u+1} - \frac{m(a-d)}{b}y^{u+1} + a\left(x + \frac{a-d}{b}\right)y^u(o(y^u))$$

$$\frac{dy}{dt} = \frac{nm(a-d)}{bu}y^2 + \frac{nm}{u}xy^2 - \frac{e}{u}y^{u+1}$$
(5)

Let $x = r \cos \varphi$ and $y = r \sin \varphi$, then model (5) can be

rewritten as an equation of polar coordinates: $r \frac{d\varphi}{dr} = \frac{F(\varphi) + o(1)}{G(\varphi) + o(1)}$, where $F(\varphi) = \frac{nm(a-d)}{bu}$ and $G(\varphi) = \frac{nm(a-d)}{bu} \sin^3 \varphi$. Clearly, $\varphi_1 = \frac{\pi}{2}$ and $\varphi_2 = \frac{3\pi}{2}$ are exceptional directions. Note that $F'\left(\frac{\pi}{2}\right) < 0, G\left(\frac{\pi}{2}\right) > 0,$

$F'\left(\frac{3\pi}{2}\right) > 0$ and $G\left(\frac{3\pi}{2}\right) < 0$, then the normal sectors of φ_1 and φ_2 are of second type and there is a unique orbit starting along the exceptional direction $\varphi_1 = \frac{\pi}{2} \left(\varphi_2 = \frac{3\pi}{2} \right)$ into the equilibrium $(0, 0)$ of system (5), that is, there is a unique orbit of system (2) in R_+^2 starting along the line $x = \frac{a-d}{b}$ into E_2 . In addition, due to $\left. \frac{dx}{dt} \right|_{x=\frac{a-d}{b}} \leq$

$(ax - dx - bx^2 - mxy^\theta) \Big|_{x=\frac{a-d}{b}} = -mxy^\theta < 0$, the orbit of system (2) passes the line $x = \frac{a-d}{b}$ from right to left.

Thus the equilibrium E_2 is a saddle point.

(3) For $E^*(x^*, y^*)$, the Jacobian matrix of system (2) at the equilibrium point E^* is

$$J(E^*) = \begin{pmatrix} -bx^* & ax^*f'_y(k, y^*) - \frac{e\theta}{n} \\ nm(y^*)^\theta & -e(1-\theta) \end{pmatrix}$$

Clearly, $\det(J(E^*)) = bx^*e(1 - \theta) + nm(y^*)^\theta \left(\frac{e\theta}{n} - ax^*f'_y(k, y^*) \right) > 0$ and $\text{tr}(J(E^*)) = -bx^* -$

$e(1 - \theta) < 0$. Hence, E^* is a locally stable node or focus. The proof is complete.

Theorem 2.1 (i) If $a \leq d$, then the trivial equilibrium $E_1(0, 0)$ is globally asymptotically stable;
 (ii) if $a > d$, then the positive equilibrium $E^*(x^*, y^*)$ is globally asymptotically stable.

Proof. (i) Let $x(t)$ be a positive solution of system (2). From the first equation of system (2), it follows that $\frac{dx}{dt} \leq (a-d)x - bx^2 - mxy^\theta$, then $a \leq d$ implies $\lim_{t \rightarrow +\infty} x(t) = 0$. According to the comparison theorem, we have $\lim_{t \rightarrow +\infty} y(t) = 0$. Hence, $E_1(0, 0)$ is globally asymptotically stable.

(ii) Now, we first prove that every solution of system (2) starting in R_+^2 is uniformly bounded. Letting $V(x, y) = x + \frac{y}{n}$, and calculating the derivative of $V(x, y)$ with respect t (2), we obtain $\dot{V}(x, y) = axf(k, y) - dx - bx^2 - \frac{ey}{n} \leq (a - d)x - bx^2 - \frac{ey}{n}$. Further, there is $\dot{V} + eV \leq \frac{(a - d + e)^2}{4b} \triangleq L$, then $0 < V(x, y) \leq \frac{L}{e}$ as $t \rightarrow +\infty$, that is, solutions of system (2) stay in $\Omega = \{(x, y) \in R_+^2 : x + \frac{y}{n} \leq \frac{L}{e} + \varepsilon, \forall \varepsilon > 0\}$.

In Lemma 2.1, the unique interior equilibrium $E^*(x^*, y^*)$ is locally asymptotically stable if $a > d$. To prove $E^*(x^*, y^*)$ is globally asymptotically stable in area Ω we need to consider the Dulac function $u(x, y) = x^{-1}y^{-1}$, then $\frac{\partial(uP)}{\partial x} + \frac{\partial(uQ)}{\partial y} = -by^{-1}$. Therefore, by the Dulac theorem, there is no closed orbit in area Ω . Hence, $E^*(x^*, y^*)$ is globally asymptotically stable. The proof is complete.

3. Discussion

We first discuss the influence of fear effect on the predator and prey densities. Denote $F(x^*, y^*, k) = af(k, y^*) - d - bx^* - m(y^*)^\theta = 0$ and $G(x^*, y^*, k) = nm x^*(y^*)^{\theta-1} - e = 0$. By simple computation, we have

$$J = \frac{\partial(F, G)}{\partial(x^*, y^*)} = \begin{vmatrix} F_{x^*} & F_{y^*} \\ G_{x^*} & G_{y^*} \end{vmatrix} = \begin{vmatrix} -b & af'_y(k, y^*) - \theta m(y^*)^{\theta-1} \\ nm(y^*)^{\theta-1} & -(1-\theta)nm x^*(y^*)^{\theta-2} \end{vmatrix} > 0,$$

$$J_1 = \frac{\partial(F, G)}{\partial(k, y^*)} = -af'_k(k, y^*)(1-\theta)nm x^*(y^*)^{\theta-2} > 0,$$

$$J_2 = \frac{\partial(F, G)}{\partial(x^*, k)} = -af'_k(k, y^*)nm(y^*)^{\theta-1} > 0,$$

for all $\theta \in (0, 1)$. Then $\frac{dx^*}{dk} = -\frac{J_1}{J} < 0$, $\frac{dy^*}{dk} = -\frac{J_2}{J} < 0$.

Hence, with the increase of fear level k , the value of E^* decreases, that is, both predator and prey densities decrease (see Figures 1(a), 1(b)).

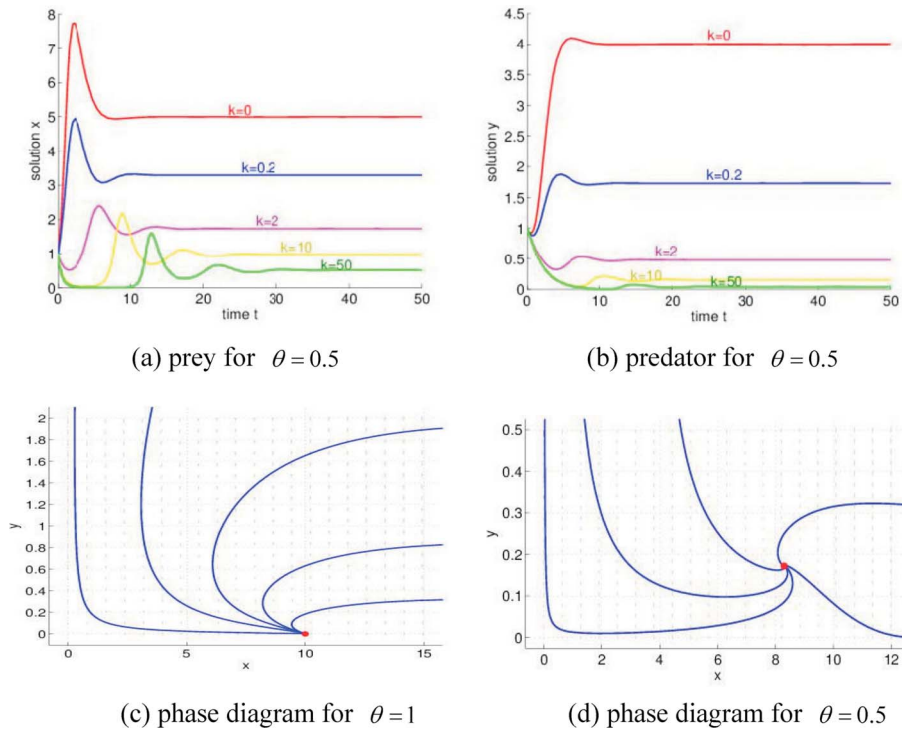


Figure 1. Dynamic behaviors of system (2).

Let $f(k, y) = \frac{1}{1 + ky}$ [18], and consider the following

example to verify the feasibility of our main result. In (2), let $k = b = n = 0.2$, $d = e = 2$ and $m = 0.5$, then $a > d$ and $d + \frac{be}{nm} = 14$. If $a = 4$, $\theta = 1$, that is, model (2) is re-

duced to model (1). It follows from Theorem A that $E_1(10, 0)$ is globally asymptotically stable (see Figure 1(c)), that is, for system (2) without predator mutual interference, the predator is extinct. If $a = 4$, $\theta = 0.5$. It follows from Theorem 2.1 that $E^*(8.2973, 0.1721)$ is globally asymptotically stable (see Figure 1(d)), which means that both predator species and prey species coexist for model (2) with predator mutual interference. Therefore the mutual interference can promote the stability of system (2). If $a = 3$, by increasing the value of θ , the prey is increasing and the predator is decreasing to zero (see Figure 2(a)). If $a = 15$, the prey is decreasing and the predator is increasing with increasing the value of θ (see Figure 2(b)).

We list the main results for system (2) in Table 1, where the results for $\theta = 1$ are obtained in [18]. Comparing our result with those in [18], we find that when $a > d + \frac{be}{nm}$, the introduction of predator mutual inference does not change the stability of the system. However, when $d < a < d + \frac{be}{nm}$, Table 1 shows that the predator of system (2) without mutual interference is extinct, but when considering system (2) with mutual interference, the extinction of the predator is significantly changed. Thus mutual interference can stabilize the predator-prey sys-

Table 1. Equilibria of system (2)

$\theta = 1$	$d < a < d + \frac{be}{nm}$	E_1 GAS
	$d + \frac{be}{nm} < a$	E^* GAS
$0 < \theta < 1$	$a > d$	E^* GAS

tem. On the other hand, we show that the value of E^* of system (2) decreases with the increase of fear level k . We conclude that fear effect can reduce the population of the predator-prey system, which is in accord with [14].

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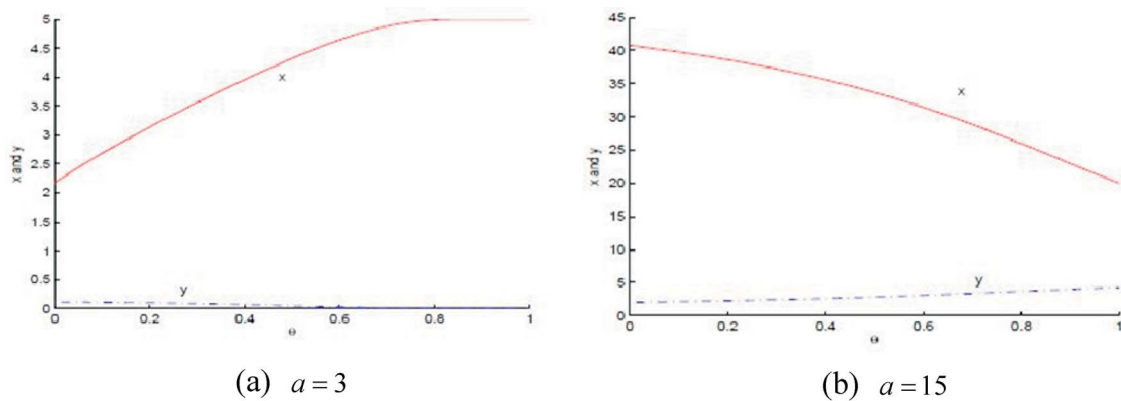


Figure 2. Bifurcation diagram of system (2) with θ as the bifurcation parameter.

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