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GLOBAL DYNAMICS OF A PREDATOR-PREY MODEL INCORPORATING A CONSTANT PREY REFUGE

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Abstract. In this article, a general predator-prey model incorporating a constant prey refuge with Hassell-Varley type functional response is studied. Sufficient conditions for the stability of the equilibria are obtained. It is shown that the positive equilibrium exists if predator death rate multiplied by a constants is smaller than its growth rate multiplied by capturing rate. Moreover, by constructing a Lyapunov function, it is shown that the positive equilibrium is globally stable.

1. Introduction

In 1980, Freedman [3] proposed a predator-prey model with Holling type II functional response:

$$\begin{gathered} x'(t) = ax(1 - x/K) - bxy/(\beta + x), \\ y'(t) = y(ex/(\beta + x) - D), \\ x(0) > 0, \quad y(0) > 0, \end{gathered} \tag{1.1}$$

where x and y denote the prey and predator populations, respectively at any time t; $a > 0$ represents the intrinsic growth rate of the prey; $K > 0$ is the carrying capacity of the prey in the absence of predator; $b > 0$ is the conversion factor denoting the number of newly born predators for each captured prey; $D > 0$ is the death rate of the predator; $e > 0$ is the intrinsic growth rate of the predator; β represents half saturation constant. The model exhibits the well-known but highly controversial paradox of enrichinent observed by Hairston et al [5] (1960) and by Rosenzweig [15] (1969) which is rarely reported in nature. To address this problem, Arditi and Ginzburg [1] (1989) proposed the following predator-prey model with ratio-dependent type functional response:

$$\begin{gathered} x'(t) = ax(1 - x/K) - bxy/(\beta y + x), \\ y'(t) = y(ex/(\beta y + x) - D), \\ x(0) > 0, \quad y(0) > 0. \end{gathered} \tag{1.2}$$

It is well known system (1.2) can display richer and more plausible dynamics than system (1.1).

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A general predator-prey model with Hassell-Varley type functional response may take the following form (Hsu 2008) [10]:

$$\begin{gathered}
x'(t) = ax(1 - x/K) - bxy/(\beta y^\gamma + x), \\
y'(t) = y(ex/(\beta y^\gamma + x) - D), \\
x(0) > 0, \quad y(0) > 0,
\end{gathered} \tag{1.3}$$

where the constant $\gamma > 0$ is called the Hassel-Varley constant. A unified mechanistic approach was provided by Cosner et al [2] where the functional response in system (1.3) was derived. In a typical predator-prey interaction where predators do not form groups, one can assume that $\gamma = 1$, producing the so-called ratio-dependent predator-prey dynamics. For terrestrial predators that form a fixed number of tight groups, it is often reasonable to assume that $\gamma = 1/2$. For aquatic predators that form a fixed number of tight groups, $\gamma = 1/3$ maybe more appropriate. Since most predators do not form a fixed number of tight groups, it can be argued that for most realistic predator-prey interactions,$\gamma \in [0, 1]$.

Because species compete, evolve and disperse often simply for the purpose of seeking resources to sustain their struggle for their very existence. Their extinctions are often the results of their failure in obtaining the minimum level of resources needed for their subsistence. Thus, prey refuge are widely believed to prevent prey extinction and damp predator-prey oscillations. For example, Gonzalez-Olivares and Ramos-Jiliberto [4] studied the dynamic consequences of the following predator-prey systems with constant number of prey using refuges, which protects of prey m from predation

$$\begin{gathered}
x'(t) = ax(1 - x/K) - \frac{b(x-m)y}{1 + c(x-m)}, \\
y'(t) = -Dy + \frac{be(x-m)y}{1 + c(x-m)},
\end{gathered} \tag{1.4}$$

$m > 0$ is a constant number of prey using refuges, which protects m of prey from predation; $c > 0$ is a constant.

Inspired by [4] and [10], we will consider a more general predator-prey model incorporating a constant prey refuge with Hassell-Varley type functional response.

$$\begin{gathered}
x'(t) = ax(1 - x/K) - \frac{b(x-m)y}{y^\gamma + c(x-m)}, \\
y'(t) = -Dy + \frac{be(x-m)y}{y^\gamma + c(x-m)}, \\
x(0) > m, \quad y(0) > 0.
\end{gathered} \tag{1.5}$$

Mathematically, system (1.1) or (1.2) can be viewed as limiting cases of system (1.3) if one chooses $\gamma = 0$ or 1 in system (1.3). System (1.4) can be viewed as limiting case of system (1.5) if one chooses $\gamma = 0$ in system (1.5). In this paper we take $\gamma \in (0, 1)$.

In this article, we will find sufficient conditions of the stability properties to the equilibria of (1.5). We will show the positive equilibrium exists if predator death rate multiplied by a constant is smaller than its growth rate multiplied by capturing rate. We construct a Lyapunov function to show the global stability of the positive equilibrium.

2. Preliminary analysis

In this section, we present the basic results on the boundedness of positive solutions and the local stabilities of nonnegative equilibria in (1.5).

Let $\Omega_0 = \{(x, y) : x > m,\ y > 0\}$, for practical biological meaning, we simply study system (1.5) in Ω_0.

By the scaling: $t \to at$, $x \to x/m$, $y \to \alpha y$. System (1.5) turns into

$$\begin{gathered} x'(t) = x\Big(1 - \frac{m}{K}x\Big) - \frac{s(x-1)y}{y^\gamma + x - 1} \equiv F(x,y), \\ y'(t) = \delta y\Big(- d + \frac{x-1}{y^\gamma + x - 1}\Big) \equiv G(x,y), \\ x(0) > 1, \quad y(0) > 0, \end{gathered} \tag{2.1}$$

where $s = \frac{b}{a}(cm)^{\frac{1}{\gamma}-1}$, $\delta = \frac{be}{ac}$, $d = \frac{Dc}{be}$. we thus define that $F(1,0) = G(1,0) = 0$. Clearly with this assumption, both F and G are continuous on the closure of Ω, where $\Omega = \{(x,y) | x > 1, y > 0\}$.

The variational matrix of the system (2.1) is

$$A(x,y) = \begin{pmatrix} 1 - \frac{2m}{K}x - \frac{sy}{y^\gamma + x - 1} + \frac{s(x-1)y}{(y^\gamma+x-1)^2} & \frac{-s(x-1)}{(y^\gamma+x-1)^2}[(x-1) + (1-\gamma)y^\gamma] \\ \frac{\delta y^{\gamma+1}}{(y^\gamma+x-1)^2} & \delta(\frac{x-1}{y^\gamma+x-1} - \frac{\gamma(x-1)y^\gamma}{(y^\gamma+x-1)^2} - d) \end{pmatrix}.$$

Proposition 2.1. *Let $(x(t), y(t))$ be any solution of (2.1) with $(x(0), y(0)) \in \Omega$. Then*

$$\limsup_{t\to\infty} (x(t) + \frac{s}{\delta}y(t)) \le \frac{(1 + d\delta)^2 K}{4dm\delta}.$$

Proof. It follows immediately from the existence and uniqueness of solutions for ordinary differential equations with initial conditions that the solution is positive on its domain of definition. Let $V(t) = x(t) + \frac{s}{\delta}y(t)$ and differentiating V once yields

$$V'(t) = -\frac{m}{K}x^2 + (1 + d\delta)x - d\delta V(t) \le \frac{(1 + d\delta)^2}{4m/K} - d\delta V.$$

Hence we have

$$0 < V(t) \le \frac{(1 + d\delta)^2 K}{4dm\delta} + (V(0) - \frac{(1 + d\delta)^2}{4d\delta m/K})e^{-dt\delta}.$$

This gives the desired result. $\square$

System (2.1) has three equilibria. They are $E_0 = (0, 0)$ which is not in Ω, $E_1 = (\frac{K}{m}, 0)$ and $E_* = (x_*, y_*)$, where $x_* > 1$, $y_* > 0$ and

$$\begin{gathered} x_*\left(1 - \frac{m}{K}x_*\right) - \frac{s(x_*-1)y_*}{y_*^\gamma + x_* - 1} = 0, \\ \frac{x_* - 1}{y_*^\gamma + x_* - 1} = d, \end{gathered}$$

if $d \in (0, 1)$.

At E_1, we have

$$A(\frac{K}{m}, 0) = \begin{pmatrix} -1 & s \\ 0 & \delta(1-d) \end{pmatrix}.$$

For the rest of this article, we always assume that $0 < d < 1$. With this assumption, it is easy to know that E_1 is a saddle point. At E_*, we have

$$
\begin{aligned}
&A(x_*, y_*)\\
&= \begin{pmatrix} 1 - \frac{2m}{K}x_* - \frac{sy_*}{y_*^\gamma + x_* - 1} + \frac{s(x_*-1)y_*}{(y_*^\gamma + x_* - 1)^2} & \frac{-s(x_*-1)}{(y_*^\gamma + x_* - 1)^2}[(x_* - 1) + (1-\gamma)y_*^\gamma] \\ \frac{\delta y_*^{\gamma+1}}{(y_*^\gamma + x_* - 1)^2} & -\frac{\delta\gamma(x_*-1)y_*^\gamma}{(y_*^\gamma + x_* - 1)^2} \end{pmatrix},
\end{aligned}
$$

$$
\begin{aligned}
\det A(x_*, y_* &= \frac{-\delta\gamma y_*^\gamma (x_* - 1)(1 - \frac{2m}{K}x_*)}{(y_*^\gamma + x_* - 1)^2} + \frac{s\gamma\delta(x_* - 1)y_*^{\gamma+1}}{(y_*^\gamma + x_* - 1)^3} \\
&\quad + \frac{s\delta(x_* - 1)y_*^{\gamma+1}[(1-\gamma)(x_* - 1) + (1-\gamma)y_*^\gamma]}{(y_*^\gamma + x_* - 1)^4},
\end{aligned}
$$

$$
\operatorname{tr} A(x_*, y_*) = 1 - \frac{2m}{K}x_* - \frac{sy_*}{y_*^\gamma + x_* - 1} + \frac{(x_* - 1)y_*(s - \delta\gamma y_*^{\gamma-1})}{(y_*^\gamma + x_* - 1)^2}.
$$

Hence the stability of E_* is determined by the sign of $\det A(x_*, y_*)$ and $\operatorname{tr} A(x_*, y_*)$.

Proposition 2.2. *For system* (2.1)*, the following statements hold:*

(1) *E_1 is a saddle point;*
(2) *when $\det A(x_*, y_*) > 0$, then E_* is locally asymptotically stable if $\operatorname{tr} A(x_*, y_*) < 0$; E_* is unstable if $\operatorname{tr} A(x_*, y_*) > 0$;*
(3) *when $\det A(x_*, y_*) < 0$, then E_* is a saddle point.*

3. Uniform persistence

The objective of this section is to present conditions ensuring the system (2.1) is uniformly persistent. To this end, we make the change of variables $(x, y) \to (u, z)$ in system (2.1), where $u = \frac{x-1}{y^\gamma}$, $z = y^\sigma$ and σ will be chosen later. This reduces it to the system

$$
\begin{gathered}
u'(t) = g(u) - \varphi_1(u)z^{\sigma_1} - \varphi_2(u)z^{\sigma_2} + (1 - m/K)z^{-1} \equiv f_1(u, z),\\
z'(t) = \psi(u)z \equiv f_2(u, z),\\
u(0) > 0, \quad z(0) > 0,
\end{gathered} \tag{3.1}
$$

where

$$
\begin{gathered}
g(u) = \frac{u}{1+u}[1 + \gamma\delta d - 2m/K + (1 + \gamma\delta d - \gamma\delta - 2m/K)u],\\
\varphi_1(u) = 2m/Ku^2, \quad \varphi_2(u) = \frac{su}{1+u},\\
\psi(u) = \sigma\delta\Big(-d + \frac{u}{1+u}\Big),
\end{gathered}
$$

and $\sigma_1 = \gamma/\sigma$ and $\sigma_2 = (1-\gamma)/\sigma$. Now let $\sigma = \gamma$ if $\gamma \in (0, 1/2)$ and $\sigma = 1 - \gamma$ if $\gamma \in [1/2, 1)$, then

$$
\sigma_1 = \begin{cases} 1 & \text{if } \gamma \in (0, \frac{1}{2}),\\ \gamma/(1-\gamma) & \text{if } \gamma \in [\frac{1}{2}, 1) \end{cases}
$$

and

$$
\sigma_2 = \begin{cases} (1-\gamma)/\gamma & \text{if } \gamma \in (0, 1/2),\\ 1 & \text{if } \gamma \in [1/2, 1). \end{cases}
$$

Hence, $\sigma_i \geq 1, i = 1, 2$ and the vector field (f_1, f_2) is C^1 smooth on the set $\mathbb{R}^2_+$ where $\mathbb{R}^2_+ = \{(u, z) :, u > 0,\ z > 0\}$. Since $0 < d < 1$, we have $\psi(u_*) = 0$ where $u_* = d/(1-d)$ and

$$\psi(u) = \frac{\sigma\delta(1-d)(u-u_*)}{1+u}.$$

Moreover, $g(u) > 0$ on $\mathbb{R}^2_+$ if $\gamma\delta \leq \frac{1-2m/K}{1-d}$ where $1 - 2m/K \geq 0$ and $g(u)$ has exactly one positive zero $u_0 = \frac{-(1+\gamma\delta d - 2M/K)}{1+\gamma\delta d - \gamma\delta - 2m/K}$ if $\gamma\delta > \frac{1-2m/K}{1-d}$. In last case, we have $g(u)(u - u_0) < 0$ for $u \neq u_0$.

From system (3.1), we have that the prey isocline, $z = h(u)$ is implicitly defined by $f_1(u, z) = 0$. Since $\lim_{z\to\infty} f_1(u, z) = -\infty$ and $\frac{\partial f_1}{\partial z}(u, z) < 0$, it follows from the implicit function theorem that $z = h(u)$ is C^1 function defined on $(0, \infty)$ if $\gamma\delta \leq \frac{1-2m/K}{1-d}$ or on $(0, u_0]$ if $\gamma\delta > \frac{1-2m/K}{1-d}$. Moreover,

$$\begin{aligned} h'(u) &= -\frac{\partial f_1(u, h(u))/\partial u}{\partial f_1(u, h(u))/\partial z}, \\ &= \frac{\big(\frac{g(u)}{\varphi_2(u)}\big)' - \big(\frac{\varphi_1(u)}{\varphi_2(u)}\big)' h^{\sigma_1}(u) - \frac{1-m/K}{\varphi_2^2(u)}\varphi_2'(u)h^{-1}(u)}{\big(\frac{\varphi_1(u)}{\varphi_2(u)}\big)\sigma_1 h^{\sigma_1 - 1}(u) + \sigma_2 h^{\sigma_2-1}(u) + \frac{1-m/K}{\varphi_2(u)}h^{-2}(u)}. \end{aligned} \tag{3.2}$$

The qualitative behavior of $z = h(u)$ is given in the following lemma.

Lemma 3.1. (a) *If $\gamma\delta \in (\frac{1-2m/K}{1-d}, \infty)$, then $h(u) > 0 > h'(u)$ for all $u \in [0, u_0]$.*

(b) *If $\gamma\delta \in (0, \frac{1-2m/K}{1-d}]$ and $h(u) > [\frac{K(1+\gamma\delta d - \gamma\delta - 2m/k)}{m}]^{1/\sigma_1}$, then $h(u) > 0 > h'(u)$ for all $u \in (0, \infty)$.*

Proof. From (3.2), we have $h'(u) < 0$ as long as $\gamma\delta \in (\frac{1-2m/K}{1-d}, \infty)$, This proves the assertion (a).

Now let $1 + \gamma\delta d - \gamma\delta - 2m/K \geq 0$, we have

$$\begin{aligned} &h'(u) \\ &= \frac{\frac{1}{s}(1+\gamma\delta d - \gamma\delta - 2\frac{m}{K}) - \frac{m}{sK}(1+2m)h_1^{\sigma}(u) - su^{-2}(1-\frac{m}{K})h^{-1}(u)}{(\frac{\varphi_1(u)}{\varphi_2(u)})\sigma_1 h^{\sigma_1-1}(u) + \sigma_2 h^{\sigma_2-1}(u) + \frac{1-m/K}{\varphi_2(u)}h^{-2}(u)} < 0 \end{aligned}$$

as long as

$$\frac{m}{sK}h^{\sigma_1}(u) > \frac{1}{s(1+\gamma\delta d - \gamma\delta - 2m/K)}.$$

This proves assertion (b). $\square$

System (3.1) has one positive equilibrium $e_* = (u_*, z_*)$ where $z_* = h(u_*)$. The variational matrix of system (3.1) is given by

$$\begin{aligned} &J(u, z) \\ &= \begin{pmatrix} g'(u) - \varphi_1'(u)z^{\sigma_1} - \varphi_2'(u)z^{\sigma_2} & -\sigma_1\varphi_1(u)z^{\sigma_1-1} - \sigma_2\varphi_2(u)z^{\sigma_2-1} - (1-\frac{m}{K})/z^2 \\ \sigma\delta z/(1+u)^2 & \sigma\delta(u/(1+u) - d) \end{pmatrix}. \end{aligned}$$

The stability of equilibrim e_* is determined by the eigenvalues of the matrix $J(e_*)$ and is given in the following lemma.

Lemma 3.2. *For system* (3.1)*, the following statements are true.*

(a) *If $tr(J(e_*)) < 0$, then e_* is locally asymptotically stable;*

(b) *If* $tr(J(e_*)) > 0$*, then* e_* *is an unstable focus or node.*

Remark 3.3. Since $(x_*, y_*) = (u_* z_*^{\frac{\gamma}{\sigma}+1}, z_*^{\frac{1}{\sigma}})$, we have

$$\begin{aligned}\operatorname{tr} A(E_*) &= 1 - 2m/Kx_* - \frac{sy_*}{y_*^\gamma + x_* 1} + \frac{(x_* - 1)y_*(s - \gamma\delta y_*^{\gamma-1})}{(y_*^\gamma + x_* - 1)^2} \\ &= 1 - 2m/K(u_* z_*^{\gamma/\sigma} + 1) - \frac{s z_*^{(1-\gamma)/\sigma}}{(u_* + 1)} + \frac{u_* z_*^{(1-\gamma)/\sigma}(s - \delta\gamma z_*^{(\gamma-1)/\sigma})}{(u_* + 1)^2} \\ &= \operatorname{tr} J(e_*).\end{aligned}$$

So, the locally stability of E_* and e_* are the same.

Lemma 3.4. *System* (3.1) *is uniformly persistent in* $\mathbb{R}_+^2$*.*

Proof. Let $(u(t), z(t))$ be the solution starting at $A = (u_*, M_* + 1)$ where $M_* = [\frac{(1+d\delta)^2 K}{4sdm}]^\sigma$ and Γ be its orbit. Then since $(x(t), y(t)) = (u(t) z^{\frac{\gamma}{\sigma}+1}(t), z^{\frac{1}{\sigma}}(t))$ is a solution of system (2.1) and by Proposition 2.1, we have $\limsup_{t\to\infty} z(t) \le M_*$. Hence $\Gamma \subseteq \mathbb{R}_+ \times (0, M_* + 1)$. The flow analysis gives that Γ must intersect the prey isocline$\{(u, h(u)) | 0 < u < u_*\}$. Let B be the first point that they intersect. There are two possibilities for Γ.

Case 1: $\Gamma \cap \{(u_*, z) | z \in (0, h(u_*))\} \neq \emptyset$**.** Let $C = (u_*, z_1)$ be the first point of $\Gamma \cap \{(u_*, z) | z \in (0, h(u_*))\}$, $D = (\bar{u}, z_1)$ be the intersection of $\{(u, z_1) | u > u_*\}$ and $z = h(u)$. Consider the bounded region $\overline{\Omega}_1$, enclosed by $\Gamma, \overline{CD}, \overline{DE}$ and $\overline{EA}$ where $E = (\bar{u}, M_* + 1)$. Clearly, every trajectory will enter and stay in $\overline{\Omega}_1$ for all t sufficiently large.

Case 2: $\Gamma \cap \{(u_*, z) | z \in (0, h(u_*))\} = \emptyset$**.** This implies $\lim_{t\to\infty}(u(t), z(t)) = e_*$. Let $\overline{\Omega}_2$ be the bounded region enclosed by Γ and $\overline{e_* A}$. Thus every trajectory will either enter $\overline{\Omega}_2$ or tend to e_* as t goes to ∞.

Hence, from the above discussion, we show that system (3.1) is permanent. $\square$

Since every solution of (2.1) takes the form of $(x(t), y(t)) = (u(t) z^{\frac{\gamma}{\sigma}+1}(t), z^{\frac{1}{\sigma}}(t))$, where $(u(t), z(t))$ is some solution of system (3.1). Thus, as a consequence of Lemma 3.4, we have the following theorem for system (2.1).

Theorem 3.5. *System* (2.1) *is uniformly persistent in* Ω*.*

4. Global stability results

To study the global behavior of (2.1), we need following lemma.

Lemma 4.1. *Let* $1 + \gamma\delta d - \gamma\delta - 2m/K \le 0$*, Then the equilibrium* e_* *is globally asymptotically stable for system* (3.1) *in* $\mathbb{R}_+^2$*.*

Proof. To show that e_* is globally asymptotically stable in $\mathbb{R}_+^2$. Consider the following Lyapunov function

$$V(u, z) = z^{-\frac{g(u_*)}{\varphi_2(u_*)}} \exp\Big(\frac{\varphi_1(u_*)}{\varphi_2(u_*)} \frac{z_1^\sigma}{\sigma_1} + \frac{z^{\sigma_2}}{\sigma_2} + \frac{(1 - m/K)z^{-1}}{\varphi_2(u_*)} + \int_{u_*}^u \frac{\psi(\xi)}{\varphi_2(\xi)} d\xi\Big)$$

for $(u, z) \in \mathbb{R}_+^2$. The derivative of V along the solution of (3.1) is

$$\frac{\dot{V}(u, z)}{V(u, z)} = \psi(u)\Big[\frac{g(u)}{\varphi_2(u)} - \frac{g(u_*)}{\varphi_2(u_*)}\Big] - \psi(u) z^{\sigma_1}\Big[\frac{\varphi_1(u)}{\varphi_2(u)} - \frac{\varphi_1(u_*)}{\varphi_2(u_*)}\Big]$$

$$
\begin{aligned}
&+\psi(u)z^{-1}(1-m/K)\Big[\frac{1}{\varphi_2(u)}-\frac{1}{\varphi_2(u_*)}\Big]\\
&=\frac{1}{s}\psi(u)(u-u_*)\Big[1+\gamma\delta d-\gamma\delta-2m/K-m/K(1+u+u_*)z^{\sigma_1}\\
&\quad-(1-m/K)\frac{1-d}{ud}z^{-1}\Big].
\end{aligned}
$$

Clearly, $1+\gamma\delta d-\gamma\delta-2m/K\le 0$ implies $\dot{V}(u,z)\le 0$ for $(u,z)\in\mathbb{R}^2_+$. Hence, the lemma follows from Lyapunov-LaSalle's invariance principle [6]. $\square$

Theorem 4.2. *Let $1+\gamma\delta d-\gamma\delta-2m/K\le 0$, then the equilibrium E_* is globally asymptotically stable for system* (2.1) *in* Ω.

4.1. **Discussion.** To facilitate the discussion section, we summarize our findings. Recall that

$$
s=\frac{b}{a}(cm)^{\frac{1}{\gamma}-1},\quad \delta=\frac{be}{ac},\quad d=\frac{Dc}{be}.
$$

Since $0<d<1$ is equivalent to $Dc<be$. Predator death rate D multiplied by a constants c is smaller than its growth rate e multiplied by capturing rate b. From Theorem 3.5, system (2.1) or equivalently (1.5), is uniformly persistent. This means that neither predator nor prey can die out. Moreover, there is only one positive equilibrium. From (3.2)(8), Lemma 3.1, Lemma 3.2 and Remark 3.3, we have, if $\operatorname{tr} A(E_*)<0$ (>0), then E_* is locally asymptotically stable (unstable). Moreover, if $1+\gamma\delta d-\gamma\delta-2m/K\le 0$, E_* is globally asymptotically stable.

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