GLOBAL DYNAMICS OF A PREDATOR-PREY MODEL WITH HASSELL-VARLEY TYPE FUNCTIONAL RESPONSE

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Abstract. Predator-prey models with Hassell-Varley type functional response are appropriate for interactions where predators form groups and have applications in biological control. Here we present a systematic global qualitative analysis to a general predator-prey model with Hassell-Varley type functional response. We show that the predator free equilibrium is a global attractor only when the predator death rate is greater than its growth ability. The positive equilibrium exists if the above relation reverses. In cases of practical interest, we show that the local stability of the positive steady state implies its global stability with respect to positive solutions. For terrestrial predators that form a fixed number of tight groups, we show that the existence of an unstable positive equilibrium in the predator-prey model implies the existence of an unique nontrivial positive limit cycle.

1. **Introduction.** Predator-prey models are arguably the most fundamental building blocks of the any bio- and ecosystems as all biomasses are grown out of their resource masses. 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. Depending on their specific settings of applications, predator-prey models can take the forms of resource-consumer, plant-herbivore, parasite-host, tumor cells (virus)-immune system, susceptible-infectious interactions, etc. They deal with the general loss-win interactions and hence may have applications outside of ecosystems. When seemingly competitive interactions

are carefully examined, they are often in fact some forms of predator-prey interaction in disguise.

The most popular predator-prey model is the one with Michaelis-Menten type (or Holling type II) functional response (Freedman 1980):

$$\begin{cases} x'(t) &=& ax(1 - x/K) - cxy/(m + x) \\ y'(t) &=& y(fx/(m + x) - D) \\ x(0) > 0, \ y(0) > 0 \end{cases} \tag{1}$$

where x, y stand for prey and predator density, respectively. The constants a, K, c, m, f, D are positive that stand for prey intrinsic growth rate, carrying capacity, capturing rate, half saturation constant, maximal predator growth rate, predator death rate, respectively. This model exhibits the well-known but highly controversial "paradox of enrichment" observed by Hairston et al (1960) and by Rosenzweig (1969) which is rarely reported in nature. To address this problem and respond to the need of a simple deterministic model that producing the often observed extinction of prey species in island ecosystems (Ebert 2000, Fan et al. 2005), Arditi and Ginzburg (1989) proposed the following predator-prey model with ratio-dependent type functional response:

$$\begin{cases} x'(t) &=& ax(1 - x/K) - cxy/(my + x) \\ y'(t) &=& y(fx/(my + x) - D) \\ x(0) > 0, \ y(0) > 0. \end{cases} \tag{2}$$

It is well known (Kuang and Beretta (1998), Jost et al. (1999), Hsu et al. (2001), Xiao and Ruan (2001), Berezovskaya et al. (2001)) that the system (1.2) can display richer and more plausible dynamics than that of system (1).

It was known that the functional response can depend on predator density in other ways. One of the more widely known one is due to Hassell and Varley (1969). A general predator-prey model with Hassell-Varley type functional response may take the following form

$$\begin{cases} x'(t) &=& ax(1 - x/K) - cxy/(my^\gamma + x) \equiv F(x, y), \\ y'(t) &=& y(-D + fx/(my^\gamma + x)) \equiv G(x, y), \ \ \gamma \in (0, 1), \\ x(0) &=& x_0 > 0, \ y(0) = y_0 > 0. \end{cases} \tag{3}$$

In the following, we will call γ the Hassell-Varley constant. A unified mechanistic approach was provided by Cosner et al. (1999) where the functional response in system (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, $\gamma \in [1/2, 1)$. Our main results are applicable to these realistic cases.

Mathematically, systems (1) or (2) can be viewed as limiting cases of systems (3) if one chooses $\gamma = 0$ or 1 in system (3).

2. **Preliminary analysis.** The main objective of this paper is to gain a detailed global understanding of the dynamics of system (3) . In this section, we present the basic results on the boundedness of positive solutions and the local stabilities

of nonnegative equilibria in (3). To this end, we nondimensionalize the system (3) with the following scaling

$$t \to at, \quad x \to x/K, \quad y \to \alpha y$$

then the system (3) takes the form

$$
\begin{cases}
x'(t) &=& x(1-x) - sxy/(x + y^\gamma) &\equiv& F(x,y), \\
y'(t) &=& \delta y(-d + x/(x + y^\gamma)) &\equiv& G(x,y), \\
x(0) &=& x_0 > 0, \quad y(0) = y_0 > 0,
\end{cases}
\tag{4}
$$

where

$$\alpha = (\frac{m}{K})^{\frac{1}{\gamma}}, \ s = \frac{c}{a}\frac{1}{K}(\frac{K}{m})^{\frac{1}{\gamma}}, \ \delta = \frac{f}{a}, \ d = \frac{D}{f}. \tag{5}$$

Observe that $\lim_{(x,y)\to(0,0)} F(x,y) = \lim_{(x,y)\to(0,0)} G(x,y) = 0$. We thus define that $F(0,0) = G(0,0) = 0$. Clearly, with this assumption, both F and G are continuous on the closure of $\mathbb{R}_+^2$ where $\mathbb{R}_+^2 = \{(x,y)| \ x > 0, y > 0\}$.

The variational matrix of the system (4) is given by

$$
A(x,y) = \left[
\begin{array}{cc}
1 - x - \dfrac{sy}{x + y^\gamma} + x(-1 + \dfrac{sy}{(x + y^\gamma)^2}), & -\dfrac{sx}{(x + y^\gamma)^2}(x + (1-\gamma)y^\gamma) \\[4mm]
\dfrac{\delta y^{1+\gamma}}{(x + y^\gamma)^2}, & \delta(\dfrac{x}{x + y^\gamma} - \dfrac{\gamma x y^\gamma}{(x + y^\gamma)^2} - d)
\end{array}
\right].
\tag{6}
$$

The following proposition shows that system (4) is dissipative.

Proposition 1. *Let $(x(t), y(t))$ be any solution of (4) with $(x(0), y(0)) \in \mathbb{R}_+^2$, then*

$$\limsup_{t\to\infty}(x(t) + sy(t)/\delta) \leqslant \frac{(1 + d\delta)^2}{4d\delta}.$$

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

$$V'(t) = x(t)(1 + d\delta - x(t)) - d\delta V(t) \leqslant (1 + d\delta)^2/4 - d\delta V(t).$$

Hence, we have $0 < V(t) \leqslant (1+d\delta)^2/4d\delta + (V(0) - (1+d\delta)^2/4d\delta)e^{-d\delta t}$. This gives the desired result. $\qquad\square$

Notice that if $d \geq 1$ then $(x(t), y(t)) \to (1,0)$ as $t \to \infty$ for all $(x(0), y(0)) \in \mathbb{R}_+^2$. In the following, we assume that $d \in (0,1)$.

For $d \in (0,1)$, system (4) has three equilibria. They are $E_0 = (0,0)$, $E_1 = (1,0)$ and $E_* = (x_*, y_*)$, where $x_* > 0$, $y_* > 0$ and

$$
\begin{cases}
1 - x_* - \dfrac{sy_*}{x_* + y_*^\gamma} &=& 0, \\[4mm]
\dfrac{x_*}{x_* + y_*^\gamma} &=& d.
\end{cases}
\tag{7}
$$

Since the vector field (F, G) is not C^1 at E_0, the standard local stability analysis method can not be applied to E_0.

At E_1, we have

$$A(1,0) = \left[\begin{array}{cc} -1, & -s \\ 0, & \delta(1-d) \end{array}\right]. \tag{8}$$

This shows that E_1 is a saddle point.

At E_*, we have

$$A(x_*, y_*) = \begin{bmatrix} x_*(-1 + \dfrac{sy_*}{(x_* + y_*^\gamma)^2}), & -\dfrac{sx_*}{(x_* + y_*^\gamma)^2}(x_* + (1 - \gamma)y_*^\gamma) \\ \dfrac{\delta y_*^{1+\gamma}}{(x_* + y_*^\gamma)^2}, & -\delta\dfrac{\gamma x_* y_*^\gamma}{(x_* + y_*^\gamma)^2} \end{bmatrix}. \tag{9}$$

A straightforward calculation shows that

$$\det A(x_*, y_*) = \delta\gamma\frac{x_*^2 y_*^\gamma}{(x_* + y_*^\gamma)^2} + s(1 - \gamma)\delta\frac{x_* y_*^{1+2\gamma}}{(x_* + y_*^\gamma)^4} + s\delta(1 - \gamma)\frac{x_*^2 y_*^{1+\gamma}}{(x_* + y_*^\gamma)^4} > 0$$

and

$$\text{tr}\, A(x_*, y_*) = x_*\left(\frac{sy_*}{(x_* + y_*^\gamma)^2} - 1 - \frac{\delta\gamma y_*^\gamma}{(x_* + y_*^\gamma)^2}\right).$$

Hence, the stability of E_* is determined by the sign of $\text{tr}\, A(x_*, y_*)$. This gives that E_* is locally asymptotically stable (or unstable) if $\text{tr}\, A(x_*, y_*) <$ (or $>$) 0.

Summarizing these discussion, we arrive at the following proposition.

Proposition 2. *For system* (4), *the following statements hold.*
a. E_1 is a saddle point.
b. E_* is locally asymptotically stable if $\text{tr}\, A(x_*, y_*) < 0$.
c. E_* is unstable if $\text{tr}\, A(x_*, y_*) > 0$.

3. **Uniform persistence.** The objective of this section is to present conditions ensuring the system (4) is uniformly persistent. To this end, we make the change of variables $(x, y) \to (u, z)$ in system (4), where $u = x/y^\gamma, z = y^\sigma$ and σ will be chosen later. This reduces it to the following system

$$\begin{array}{rcl} u'(t) & = & g(u) - \varphi_1(u)z^{\sigma_1} - \varphi_2(u)z^{\sigma_2} \equiv f_1(u, z), \\ z'(t) & = & \psi(u)z \equiv f_2(u, z), \\ u(0) & > & 0, z(0) > 0 \end{array} \tag{10}$$

with

$$\begin{array}{rcl} g(u) & = & u[1 + \gamma\delta d + (1 + \gamma\delta d - \gamma\delta)u]/(1 + u), \\ \varphi_1(u) & = & u^2, \\ \varphi_2(u) & = & su/(1 + u), \\ \psi(u) & = & \sigma\delta(u/(1 + u) - d) \end{array} \tag{11}$$

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

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

Hence, $\sigma_i \geq 1, i = 1, 2$ and the vector field (f_1, f_2) is C^1 smooth on the closure of $\mathbb{R}_+^2$. Observe that the numbers of nontrivial positive equilibria and periodic orbits (if any) of systems (4) and (10) are the same.

Since $0 < d < 1$, we have $\psi(u_*) = 0$ where $u_* = d/(1 - d) > 0$ and

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

Moreover, $g(u) > 0$ on $\mathbb{R}_+$ if $\gamma\delta \leqslant \frac{1}{1-d}$ and $g(u)$ has exactly one positive zero $u_0 = (1 + d\gamma\delta)/[(1-d)\gamma\delta - 1]$ if $\gamma\delta > \frac{1}{1-d}$. In last case, we have $g(u)(u - u_0) < 0$ for $u \neq u_0$.

From system (10), we see that the prey isocline, $z = h(u)$, is implicitly defined by $f_1(u, z) = 0$. Since $f_1(u, 0) = g(u), \lim_{z\to\infty} f_1(u, z) = -\infty$ and $\frac{\partial f_1}{\partial z}(u, z) < 0$ it follows from the implicit function theorem that $z = h(u)$ is a C^1 function defined on $[0, \infty)$ if $\gamma\delta \leqslant \frac{1}{1-d}$ or on $[0, u_0]$ if $\gamma\delta > \frac{1}{1-d}$. Moreover, $h(0) = (\frac{1+\gamma\delta d}{s})^{\frac{1}{\sigma_2}}$ and

$$h'(u) = -\frac{\frac{\partial f_1}{\partial u}(u, h(u))}{\frac{\partial f_1}{\partial z}(u, h(u))} = \frac{(\frac{g(u)}{\varphi_2(u)})' - (\frac{\varphi_1(u)}{\varphi_2(u)})'[h(u)]^{\sigma_1}}{\frac{\varphi_1(u)}{\varphi_2(u)}\sigma_1[h(u)]^{\sigma_1-1} + \sigma_2[h(u)]^{\sigma_2-1}}. \tag{12}$$

The qualitative behavior of $z = h(u)$ is given in the following lemma (see Fig.1 (a)-(d) and Fig.2 (a)-(d)).

Lemma 3.1.
(a) If $\gamma\delta \in (\frac{1}{1-d}, \infty)$ then $h(u) \geqslant 0 > h'(u)$ for all $u \in [0, u_0]$.
(b) If $\gamma\delta \in (0, \frac{1}{1-d}]$ and $(\frac{1+\gamma\delta d}{s})^{\sigma_1} \geqslant (1 + \gamma\delta d - \gamma\delta)^{\sigma_2}$ then $h(u) > 0 > h'(u)$ for all
$u \in (0, \infty)$.
(c) If $\gamma\delta \in (0, \frac{1}{1-d}]$ and $(\frac{1+\gamma\delta d}{s})^{\sigma_1} < (1 + \gamma\delta d - \gamma\delta)^{\sigma_2}$ then $h(u) > 0$ for all $u \in [0, \infty)$
and
$h'(u)$ has exactly one positive zero u_1. Moreover, $h'(u)(u - u_1) < 0$ for all
$u \neq u_1$.

Proof. From (12), we have $h'(u) < 0$ as long as

$$h^{\sigma_1}(u) > (\frac{g(u)}{\varphi_2(u)})'/(\frac{\varphi_1(u)}{\varphi_2(u)})' = \frac{1 + \gamma\delta d - \gamma\delta}{1 + 2u}.$$

Since $1 + \gamma\delta d - \gamma\delta < 0 < h(u)$ for $u \in [0, u_0)$, so we have

$$h^{\sigma_1}(u) > 0 > \frac{1 + \gamma\delta d - \gamma\delta}{1 + 2u} \text{ for all } u \in [0, u_0).$$

Hence, the assertion (a) follows immediately.

Now let $1 + \gamma\delta d - \gamma\delta \geqslant 0$. It is sufficient to show that h' has at most one positive zero in $(0, \infty)$. To see this, notice that if $\overline{u} \geqslant 0$ and $h'(\overline{u}) = 0$ then

$$h''(\overline{u}) = -2h^{\sigma_1}(\overline{u})/\left(\frac{\varphi_1(\overline{u})}{\varphi_2(\overline{u})}\sigma_1[h(\overline{u})]^{\sigma_1-1} + \sigma_2[h(\overline{u})]^{\sigma_2-1}\right)^2 < 0.$$

This implies that $h'(u) < (>)0$ if $u > (<)\overline{u}$ and near $\overline{u}$. Hence, $h'(u) < 0$ for $u > \overline{u}$. For otherwise, there is $\hat{u} > \overline{u}$ such that $h'(u) < 0$ on $(\overline{u}, \hat{u})$ and $h'(\hat{u}) = 0$. This implies that $0 \leqslant h''(\hat{u}) = -2h^{\sigma_1}(\hat{u})/\left(\frac{\varphi_1(\hat{u})}{\varphi_2(\hat{u})}\sigma_1[h(\hat{u})]^{\sigma_1-1} + \sigma_2[h(\hat{u})]^{\sigma_2-1}\right)^2 < 0$, a contradiction.

Since $h'(0) \leqslant 0$ if $h^{\sigma_1}(0) = (\frac{1+\gamma\delta d}{s})^{\frac{\sigma_1}{\sigma_2}} \geqslant 1 + \gamma\delta d - \gamma\delta$. Hence, assertion (b) follows.

For part (c), we have $h'(0) > 0$. Hence, $h'(u) > 0$ as u close to 0. Since h is increasing as long as h^{σ_1} is bounded by a decreasing function $\frac{1+\gamma\delta d-\gamma\delta}{1+2u}$. There must exist $u_1 > 0$ such that $h'(u_1) = 0$. Thus, $h'(u) < 0$ for $u > u_1$. This proves the assertion (c). $\qquad\square$

Remark 1. According to the Implicit Function Theorem, the function h is also dependent on s. The partial derivative of h with respect to s is given by

$$\frac{\partial h}{\partial s}(s,\,u) = -(\frac{u}{1+u}h^{\sigma_2}(s,\,u))/(\sigma_1\varphi_1(u)h^{\sigma_1-1}(s,\,u) + \sigma_2\varphi_2(u)h^{\sigma_2-1}(s,\,u)) < 0.$$

Remark 2. As a consequence of Remark 1, the positive zero u_1, is also a function of s, whenever it is defined. So, for $(\frac{1+\gamma\delta d}{s})^{\sigma_1} < (1 + \gamma\delta d - \gamma\delta)^{\sigma_2}$ or equivalently, $s > (1 + \gamma\delta d)/(1 + \gamma\delta d - \gamma\delta)^{\frac{\sigma_2}{\sigma_1}}$, we have $h^{\sigma_1}(s, u_1(s)) = \frac{1+\gamma\delta d - \gamma\delta}{1+2u_1(s)}$. Differentiating with respect to s yields

$$2(1 + \gamma\delta d - \gamma\delta)^{\frac{1}{\sigma_1}}u_1'(s) = -\sigma_1(1 + 2u_1(s))^{\frac{1}{\sigma_1}+1}\frac{\partial h}{\partial s}(s,\,u_1(s)).$$

Now from Remark 1, we obtain $u_1'(s) > 0$. Moreover, u_1 is unbounded. Because if it is not the case, then there are suitable positive constants c_1, c_2, c_3 such that $u_1'(s) \geqslant \frac{c_1}{c_2+c_3s}$, which leads to a contradiction.

Notice that $\varphi_1(u_*)[h(u_*)]^{\sigma_1} + \varphi_2(u_*)[h(u_*)]^{\sigma_2} = g(u_*) = u_* > 0$. The system (10) always has the trivial equilibrium $e_0 = (0,0)$ and the positive equilibrium $e_* = (u_*, z_*)$ where $z_* = h(u_*)$. Since $g(u_0) = 0$, the system (10) has a boundary equilibrium $e_1 = (u_0, 0)$ if and only if $\gamma\delta(1 - d) > 1$. The variational matrix of the system (10) is given by

$$J(u, z) = \begin{bmatrix} g'(u) - \varphi_1'(u)z^{\sigma_1} - \varphi_2'(u)z^{\sigma_2} & -\sigma_1\varphi_1(u)z^{\sigma_1-1} - \sigma_2\varphi_2(u)z^{\sigma_2-1} \\ \sigma\delta z/(1+u)^2 & \sigma\delta(u/(u+1) - d) \end{bmatrix}. \tag{13}$$

The stability of equilibria e_0, e_1 and e_* is determined by the eigenvalues of the matrices $J(e_0), J(e_1), J(e_*)$ respectively and is given in the following lemma.

Lemma 3.2. *For the system (10), the following statements are true.*
(a) e_0 is a saddle point with stable manifold $\{(0, z)|z > 0\}$.
(b) If $\gamma\delta \in (\frac{1}{1-d}, \infty)$ then e_1 is a saddle point with stable manifold $\{(u, 0)|u > 0\}$; and e_*
    is locally asymptotically stable.
(c) If $tr(J(e_*)) < 0$ then e_* is locally asymptotically stable.
(d) If $tr(J(e_*)) > 0$ then e_* is an unstable focus or node.

Proof. The variational matrix of the system (10) at e_0 is

$$J(e_0) = \begin{bmatrix} 1 + \gamma\delta d & 0 \\ 0 & -\sigma d\delta \end{bmatrix}.$$

Obviously, the assertion (a) hold.

For part (b), the variational matrix at e_1 is

$$J(e_1) = \begin{bmatrix} g'(u_0) & \frac{\partial f_1}{\partial z}(e_1) \\ 0 & \sigma/\gamma \end{bmatrix}.$$

Since $g'(u_0) = (1 + \gamma\delta d - \gamma\delta)u_0/(1 + u_0) < 0$, so e_1 is a saddle point.

To discuss the stability of e_*, observe that the variational matrix at e_* is

$$J(e_*) = \begin{bmatrix} \frac{\partial f_1}{\partial u}(e_*) & \frac{\partial f_1}{\partial z}(e_*) \\ \sigma\delta z_*/(1+u_*)^2 & 0 \end{bmatrix}.$$

Since $\frac{\partial f_1}{\partial z}(e_*) < 0$ so the determinant of $J(e_*)$ is positive and the stability of e_* is determined by the sign of the trace of $J(e_*)$. Thus e_* is an unstable focus or node if $tr(J(e_*)) > 0$ and e_* is locally asymptotically stable, if $tr(J(e_*)) < 0$. Moreover,

if $\gamma\delta \in (\frac{1}{1-d}, \infty)$, then from (12) and Lemma 3.1 (a), one obtains $tr(J(e_*)) = \frac{\partial f_1}{\partial u}(e_*) < 0$. This proves the assertions (b), (c) and (d). $\qquad \square$

Remark 3. Notice that, under the change of variables, the boundary equilibrium E_1 is transformed to $(\infty, 0)$ and E_0 splits into two equilibria e_0 and e_1.

Remark 4. Since $(x_*, y_*) = (u_* z_*^{\frac{\gamma}{\sigma}}, z_*^{\frac{1}{\sigma}})$, we have

$$\operatorname{tr} A(x_*, y_*) = \frac{s x_* y_*}{(x_* + y_*^\gamma)^2} - x_* - \frac{\delta\gamma x_* y_*^\gamma}{(x_* + y_*^\gamma)^2} = u_*\left(\frac{-\gamma\delta}{(1+u_*)^2} - z_*^{\sigma_1} + \frac{s}{(1+u_*)^2} z_*^{\sigma_2}\right) = \operatorname{tr} J(e_*).$$

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

From the Proposition 1, we can prove (see below) the system (10) is uniformly persistent and dissipative.

Lemma 3.3. *The system* (10) *is uniformly persistent in* $\mathbb{R}_+^2$.

Proof. Let $(u(t), z(t))$ be the solution starting at $A = (u_*, M_* + 1)$ where $M_* = [\frac{(1+d\delta)^2}{4sd}]^\sigma$ and Γ be its orbit. Then since $(x(t), y(t)) = (u(t)z^{\frac{\gamma}{\sigma}}(t), z^{\frac{1}{\sigma}}(t))$ is a solution of system (4) and Proposition 1, we have $\limsup_{t\to\infty} z(t) \leqslant M_*$. Hence, $\Gamma \subseteq \mathbb{R}_+ \times (0, M_* + 1)$. The flow analysis gives that Γ must intersect the prey isocline $\{(u, h(u)) \mid 0 < u < u_*\}$, let B be the first point that they intersect. Since e_0 is a saddle point, there are two possibilities for Γ.

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

Case 2. $\Gamma \cap \{(u_*, z) \mid z \in (0, h(u_*))\} = \emptyset$.
This implies $\lim_{t\to\infty}(u(t), z(t)) = e_*$. Let Ω be the bounded region enclosed by Γ and $\overline{e_*A}$. Since e_1 (if exists) is a saddle point, thus every trajectory will either enter Ω or tend to e_* as t goes to ∞.

Hence, from the above discussion, we show that the system (10) is permanent. $\quad \square$

Since every solution of system (4) takes the form $(u(t)z^{\frac{\gamma}{\sigma}}(t), z^{\frac{1}{\sigma}}(t))$, where $(u(t), z(t))$ is some solution of system (10). Thus, as a consequence of Lemma 3.3, we have the following theorem for system (4).

Theorem 3.4. *The system* (4) *is uniformly persistent in* $\mathbb{R}_+^2$.

Remark 5. From Proposition 2, Theorem 3.4 and the Poincaré-Bendixson Theorem, the system (4) has at least one limit cycle in $\mathbb{R}_+^2$, provided $\operatorname{tr} A(x_*, y_*) > 0$.

4. **Global stability results.** As we have mentioned at the end of section 1, the most biologically interesting cases for the system (4) are when $\gamma = 1/2$ or $2/3$. We thus will focus on the cases when $\gamma \geq 1/2$ in this and next sections.
    To study the global behavior of solutions for system (4), we need following lemma.

Lemma 4.1. *Let $\gamma \in [\frac{1}{2}, 1)$ and $\Gamma(t) = (u(t), z(t))$ be any periodic solution of system* (10) *with period $T > 0$. Then*

$$\int_0^T \mathrm{tr}(J(\Gamma(t)))dt = \mathrm{tr}(J(e_*))T - \int\int_\Omega P(u, z)dudz$$

where Ω is the bounded region enclosed by Γ. The function P is given as follow

$$P(u, z) = \frac{(u_* q(z) + 2s)z^{\sigma_1 - 1}}{\sigma\delta(u_* q(z) + s(1 - d))} + \frac{sd(1 + d)q'(z)}{u(u_* q(z) + s(1 - d))^2}$$

where $q(z) = \begin{cases} \dfrac{z^{\sigma_1} - z_*^{\sigma_1}}{z - z_*} & \text{if } z \neq z_* \\ \sigma_1 z_*^{\sigma_1 - 1} & \text{if } z = z_* \end{cases}$

Proof: First, let us consider the following function:

$$q(z, \theta) = \begin{cases} \dfrac{z^\theta - z_*^{*\theta}}{z - z_*} & \text{if } z \neq z_* \\ \theta(z_*)^{\theta - 1} & \text{if } z = z_* \end{cases}$$

where $\theta > 0$. Clearly, $q(\cdot, \theta)$ is a positive, C^1 function on $[0, \infty)$ and $q(z, 1) = 1$ for $z \geqslant 0$. Moreover, $q'(z, \theta) > (<) 0$ for $z > 0$ if $\theta > (<) 1$.

Since $\gamma \in [\frac{1}{2}, 1)$, we have $\sigma_1 = \frac{\gamma}{1-\gamma} \geqslant \sigma_2 = 1$. Hence, $q'(z) \equiv q'(z, \sigma_1) \geqslant 0$ for $z > 0$. Let $A = 1 + \gamma\delta(d - 1)$ and $B = 1 + d\gamma\delta$. From (10), we have

$$\frac{z'(t)}{z(t)} = \sigma\delta(1 - d)\frac{u(t) - u_*}{1 + u(t)},$$

and

$$\begin{aligned}
\frac{u'(t)}{u(t)} &= \frac{Au(t) + B}{1 + u(t)} - u(t)z^{\sigma_1}(t) - \frac{s}{1 + u(t)}z(t) \\
&= \frac{Au(t) + B}{1 + u(t)} - u(t)z^{\sigma_1}(t) - \frac{s}{1 + u(t)}z(t) - \left(\frac{Au_* + B}{1 + u_*} - u_*z_*^{\sigma_1} - \frac{s}{1 + u_*}z_*\right) \\
&= \frac{(B - A)(u_* - u(t))}{(1 + u_*)(1 + u(t))} - (u(t) - u_*)z^{\sigma_1}(t) - \frac{s(u_* - u(t))}{(1 + u_*)(1 + u(t))}z(t) \\
&\quad -(u_*(z^{\sigma_1}(t) - z_*^{\sigma_1}) + s(1 - d)(z(t) - z_*)) \\
&= \left(\frac{\sigma_1}{z} - \frac{1 + u}{\sigma\delta(1 - d)}z^{\sigma_1 - 1} + \frac{s}{\sigma\delta}\right)z'(t) - (z - z_*)(u_* q(z) + s(1 - d)).
\end{aligned}$$

This gives

$$u(t) - u_* = \frac{1 + u(t)}{\sigma\delta(1 - d)}\frac{z'(t)}{z(t)} \tag{14}$$

and

$$z(t) - z_* = \frac{-1}{u_* q(z) + s(1 - d)}\frac{u'(t)}{u(t)} + \frac{\sigma\delta\sigma_1(1 - d) + s(1 - d)z - (1 + u)z^{\sigma_1}}{\sigma\delta(1 - d)(u_* q(z) + s(1 - d))}\frac{z'(t)}{z(t)}. \tag{15}$$

Observe that

$$\mathrm{tr}(J(\Gamma(t))) = \frac{\varphi_2'(u)}{\varphi_2(u)}u'(t) + \varphi_2(u)\left(\left(\frac{g(u)}{\varphi_2(u)}\right)' - \left(\frac{\varphi_1(u)}{\varphi_2(u)}\right)'z^{\sigma_1}\right)_{\Gamma(t)} + \frac{z'(t)}{z(t)}$$

and

$$\int_0^T \frac{\varphi_2'(u(t))}{\varphi_2(u(t))}u'(t)dt = 0, \quad \int_0^T \frac{z'(t)}{z(t)}dt = 0.$$

So, from (11), we have

$$\int_0^T \text{tr}(J(\Gamma(t)))dt = \int_0^T \varphi_2(u)\left(\left(\frac{g(u)}{\varphi_2(u)}\right)' - \left(\frac{\varphi_1(u)}{\varphi_2(u)}\right)'z^{\sigma_1}\right)dt \quad (16)$$

$$= \int_0^T \left(\frac{Au(t)}{1+u(t)} - \frac{u(t)(1+2u(t))}{1+u(t)}z^{\sigma_1}(t)\right)dt. \quad (17)$$

Using the fact that $d = u_*/(1 + u_*)$, we have

$$\int_0^T \text{tr}(J(\Gamma(t)))dt - \text{tr}(J(e_*))T$$

$$= \int_0^T \left(\frac{Au(t)}{1+u(t)} - \frac{u(t)(1+2u(t))}{1+u(t)}z^{\sigma_1}(t)\right)dt - \int_0^T \left(\frac{Au_*}{1+u_*} - \frac{u_*(1+2u_*)}{1+u_*}z_*^{\sigma_1}\right)dt$$

$$= \int_0^T \left(\frac{A}{\sigma\delta}\frac{z'(t)}{z(t)} - \frac{(1+d+2u(t))(u(t)-u_*)}{1+u(t)}z^{\sigma_1}(t) - (1+d)u_*q(z(t))(z(t)-z_*)\right)dt.$$

Now from (10), (14) $\sim$ (17), we obtain

$$\int_0^T \text{tr}(J(\Gamma(t)))dt - \text{tr}(J(e_*))T$$

$$= -\int_0^T \frac{1+d+2u(t)}{\sigma\delta(1-d)}z^{\sigma_1-1}(t)z'(t)dt + \int_0^T (1+d)u_*\frac{q(z)}{u_*q(z)+s(1-d)}\frac{u'(t)}{u(t)}dt$$

$$\quad -\int_0^T (1+d)u_*\frac{q(z)(\sigma\delta\sigma_1(1-d)+s(1-d)z-(1+u)z^{\sigma_1})}{\sigma\delta(1-d)(u_*q(z)+s(1-d))}\frac{z'(t)}{z(t)}dt$$

$$= \int_0^T \frac{(1+d)u_*q(z)}{u_*q(z)+s(1-d)}\frac{u'(t)}{u(t)}dt$$

$$\quad -\int_0^T \left(\frac{1+d+2u}{\sigma\delta(1-d)}z^{\sigma_1} + (1+d)u_*\frac{q(z)(\sigma\delta\sigma_1(1-d)+s(1-d)z-(1+u)z^{\sigma_1})}{\sigma\delta(1-d)(u_*q(z)+s(1-d))}\right)\frac{z'(t)}{z(t)}dt$$

$$\equiv \oint_\Gamma M(u,z)du + N(u,z)dz,$$

where

$$M(u,z) = \frac{(1+d)u_*q(z)}{u(u_*q(z)+s(1-d))}$$

and

$$N(u,z) = -\left(\frac{1+d+2u}{\sigma\delta(1-d)}z^{\sigma_1} + (1+d)u_*\frac{q(z)(\sigma\delta\sigma_1(1-d)+s(1-d)z-(1+u)z^{\sigma_1})}{\sigma\delta(1-d)(u_*q(z)+s(1-d))}\right)\frac{1}{z}.$$

The Green's Theorem implies that

$$\int_0^T \operatorname{tr}(J(\Gamma(t)))dt - \operatorname{tr}(J(e_*))T = \int\int_\Omega \left(\frac{\partial N}{\partial u} - \frac{\partial M}{\partial z}\right)dudz$$

$$= -\int\int_\Omega \frac{sd(1+d)q'(z)}{u(u_*q(z)+s(1-d))^2}dudz$$

$$- \int\int_\Omega \left(\frac{2}{\sigma\delta(1-d)}z^{\sigma_1} - \frac{(1+d)u_*q(z)z^{\sigma_1}}{\sigma\delta(1-d)(u_*q(z)+s(1-d))}\right)\frac{1}{z}dudz$$

$$= -\int\int_\Omega \left(\frac{sd(1+d)q'(z)}{u(u_*q(z)+s(1-d))^2} + \frac{(u_*q(z)+2s)z^{\sigma_1-1}}{\sigma\delta(u_*q(z)+s(1-d))}\right)dudz$$

$$= -\int\int_\Omega P(u,z)dudz,$$

where Ω is the bounded region enclosed by Γ. This proves the lemma. $\qquad\square$

Lemma 4.2. *Let $\gamma \in [\frac{1}{2}, 1)$. If e_* is locally asymptotically stable, then the system* (10) *has no nontrivial periodic orbit in $\mathbb{R}_+^2$.*

Proof. Let $\Gamma(t) = (x(t), y(t))$ be any one nontrivial periodic orbit of system (10) with period $T > 0$. It is sufficient to show that

$$\int_0^T \operatorname{tr}(J(x(t), y(t)))dt < 0. \tag{18}$$

But (4.4) follows immediately form Lemma 4.1. Hence, the lemma holds. $\qquad\square$

Since the systems (4) and (10) have same numbers of periodic solutions in $\mathbb{R}_+^2$, so we have the following theorem for system (4).

Theorem 4.3. *For system* (4), *the local and global asymptotic stability of e_* coincide, provided $\gamma \in [\frac{1}{2}, 1)$.*

Notice that the function $q'(z, \theta) < 0$ if $\theta \in (0, 1)$. So, the Lemma 4.1 can not be applied to the case $\gamma \in (0, \frac{1}{2})$. In such case, we may construct a Lyapunov function for system (10), if $1 + \gamma\delta d - \gamma\delta \leqslant 0$. A global stability result for system (10) and its consequence are given as follows.

Lemma 4.4. *Let $1 + \gamma\delta d - \gamma\delta \leqslant 0$. Then the equilibrium e_* is globally asymptotically stable for system* (10) *in $\mathbb{R}_+^2$.*

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

$$V(u,z) = z^{-\frac{g(u_*)}{\varphi_2(u_*)}} \exp\left(\frac{\varphi_1(u_*)}{\varphi_2(u_*)}\frac{z^{\sigma_1}}{\sigma_1} + \frac{z^{\sigma_2}}{\sigma_2} + e^{\int_{u_*}^u \frac{\psi(\xi)}{\varphi_2(\xi)}d\xi}\right)$$

for $(u, z) \in \mathbb{R}_+^2$. The derivative of V along the solution of system (10) is

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

$$= \frac{1}{s}\psi(u)(u - u_*)(1 + \gamma\delta d - \gamma\delta - (1 + u_* + u)z^{\sigma_1}).$$

Clearly, $1 + \gamma\delta d - \gamma\delta \leqslant 0$ implies $\dot{V}(u, z) \leqslant 0$ for $(u, z) \in \mathbb{R}_+^2$. Hence, the lemma follows from Lyapunov-LaSalle's invariance principle (Hale (1980)). $\qquad\square$

Theorem 4.5. *Let $1 + \gamma\delta d - \gamma\delta \leqslant 0$. Then the equilibrium E_* is globally asymptotically stable for system* (4) *in $\mathbb{R}^2_+$.*

5. **Uniqueness of limit cycle for the case $\gamma = 1/2$..** The most interesting case for system (4) is when $\gamma = 1/2$, which corresponds to the scenario of a terrestrial predator-prey interaction where predators form groups (Cosner et al. 1999). In this case, $\sigma = \gamma = \frac{1}{2}$, $\sigma_1 = \sigma_2 = 1$ and the system (10) is equivalent to the following Gause type predator-prey system:

$$\begin{aligned} u'(t) &= g(u) - (\varphi_1(u) + \varphi_2(u))z \equiv g(u) - \varphi(u)z, \\ z'(t) &= \psi(u)z, \\ u(0) &= u_0 > 0, \; z(0) = z_0 > 0 \end{aligned} \tag{19}$$

and

$$h(u) = \frac{g(u)}{\varphi(u)} = \frac{Au + B}{u^2 + u + s}, \tag{20}$$

where $A = 1 + \gamma\delta(d-1)$, $B = 1 + \gamma\delta d$. A straightforward computation yields

$$(u^2 + u + s)^2 h'(u) = -Au^2 - 2Bu + As - B \equiv l(u). \tag{21}$$

Lemma 5.1. *Let $A \neq 0$. Then*

$$\begin{aligned} \varphi(u)h'(u) &= -\frac{1 + \gamma\delta(1-d)}{\sigma\delta(1-d)^2 A}\psi(u)h(u) + \frac{l(u_*)u}{(1+u)(s+u+u^2)} \\ &\quad + \frac{u - u_*}{1+u}\frac{C - Au - Au^2}{s+u+u^2}. \end{aligned}$$

where $C = \dfrac{(1 + \gamma\delta(1-d))B}{(1-d)A}$.

Proof. From (19), (20) and (21) we have

$$\begin{aligned} \varphi(u)h'(u) &= \frac{ul(u)}{(1+u)(s+u+u^2)}, \\ \psi(u)h(u) &= \sigma\delta(1-d)\frac{u-u_*}{1+u}\frac{Au+B}{s+u+u^2}. \end{aligned}$$

Since $ul(u) = ul(u_*) + u(l(u) - l(u_*))$ and

$$\begin{aligned} u(l(u) - l(u_*)) &= u(u_* - u)(A(u_* + u) + 2B)) \\ &= (u_* - u)(Au^2 + (Au_* + 2B)u) \\ &= (u_* - u)(Au^2 + (1 + \gamma\delta d + \frac{1}{1-d})u) \\ &= (u_* - u)(Au^2 + Au - (\frac{1}{1-d} + \gamma\delta)\frac{B}{A}) \\ &\quad + (u_* - u)(\frac{1}{1-d} + \gamma\delta)(u + \frac{B}{A}). \end{aligned}$$

The lemma follows immediately. $\qquad\square$

Lemma 5.2. *If $h'(u_*) > 0$ then system* (19) *has at most one limit cycle in $\mathbb{R}^2_+$. Moreover, if it exists, then it is a stable limit cycle.*

Proof. As a consequence of $h'(u_*) > 0$ and Lemma 3.1, we have $A > 0$ and $C > 0$. Now, it is sufficient to show $\frac{d}{du}(\frac{\varphi(u)h'(u)}{\psi(u)h(u)}) < 0$ for $u \in \mathbb{R}_+ - \{u_*\}$. From Lemma 5.1, we obtain

$$
\begin{aligned}
\frac{\varphi(u)h'(u)}{\psi(u)h(u)} &= \frac{1}{\sigma\delta(1-d)}\left(-\frac{1+\gamma\delta(1-d)}{\sigma\delta(1-d)^2 A} + \frac{u}{u-u_*}\frac{l(u_*)}{Au+B} + \frac{C-A(u+u^2)}{Au+B}\right) \\
&\equiv \frac{1}{\sigma\delta(1-d)}\left(-\frac{1+\gamma\delta(1-d)}{\sigma\delta(1-d)^2 A} + l(u_*)q_1(u) + q_2(u)\right).
\end{aligned}
$$

Since $l(u_*) > 0$,

$$
\begin{aligned}
&(u-u_*)^2(Au+B)^2 q_1'(u) \\
&= (u-u_*)(Au+B) - u(Au+B+A(u-u_*)) \\
&= -Au^2 - u_* B < 0,
\end{aligned}
$$

and

$$
\begin{aligned}
&(Au+B)^2 q_2'(u) \\
&= -A(1+2u)(Au+B) - (AC - A^2(u+u^2)) \\
&= -A^2 u^2 - 2ABu - AB - AC < 0,
\end{aligned}
$$

thus we have $\frac{d}{du}(\frac{\varphi(u)h'(u)}{\psi(u)h(u)}) < 0$ for $u \in \mathbb{R}_+ - \{u_*\}$. Now according to Theorem 2.2 in Hwang (1999), the system (19) has at most one limit cycle and if it exists then it is stable. □

A parallel result for system (4) can be obtained easily from the fact that both systems (10) and (4) has the same number of periodic solutions in $\mathbb{R}^2$. This is given in the following theorem.

Theorem 5.3. *Let $\gamma = \frac{1}{2}$. The system (4) has at most one limit cycle in $\mathbb{R}^2$, provided $tr\,A(x_*, y_*) > 0$. Moreover, if a limit cycle exists, then it is orbitally asymptotically stable.*

6. **Discussion.** To facilitate the discussion section, we summarize our findings into the following table (Table 6.1).

		Conditions	Results
1.		$d \geqslant 1, \gamma \in (0, 1)$	$E_1 = (1, 0)$ is G. A. S.
2.		$d < 1, \gamma \in (0, 1), \operatorname{tr}(A(x_*, y_*)) > 0$	At least one limit cycle.
3.		$d < 1, \gamma \in [\frac{1}{2}, 1), \operatorname{tr}(A(x_*, y_*)) \leqslant 0$	$E_* = (x_*, y_*)$ is G. A. S.
4.		$d < 1, \gamma \in (0, 1), \operatorname{tr}(A(x_*, y_*)) \leqslant 0,$ $1 + \delta d - \delta \leqslant 0$	$E_* = (x_*, y_*)$ is G. A. S.
5.		$d < 1, \gamma = \frac{1}{2}, \operatorname{tr}(A(x_*, y_*)) > 0$	There is an unique limit cycle.

TABLE 1. Qualitative Behavior of Solutions of System (4). The "G. A. S." stands for "globally asymptotically stable".

Recall that $s = \frac{c}{a}\frac{1}{K}(\frac{K}{m})^{\frac{1}{\gamma}}$, $\delta = \frac{f}{a}$, $d = \frac{D}{f}$. Since $d \geqslant 1$ is equivalent to $D \geqslant f$, and from the first assertion in Table 6.1, we conclude that, if the growth ability of predator (f) is no larger than its death rate (D), then the predators are doomed.
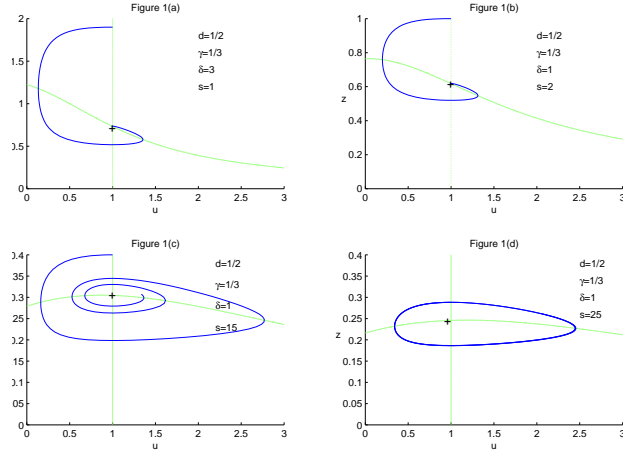
FIGURE 1. Typical isoclines and dynamics of system (3) for $d = \frac{1}{2}$ and $\gamma = \frac{1}{3}$.
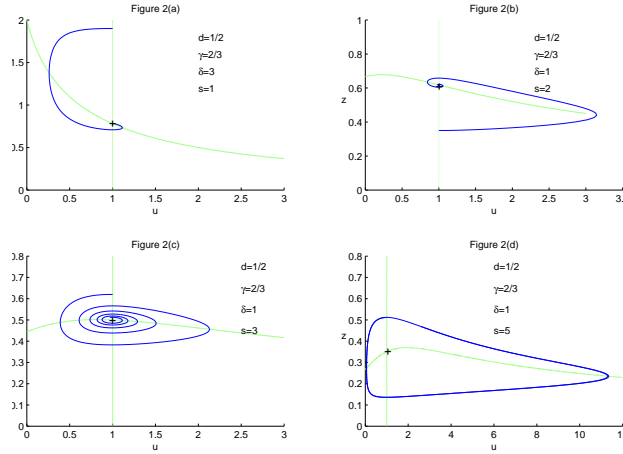

FIGURE 2. Typical isoclines and dynamics of system (3) for $d = \frac{1}{2}$ and $\gamma = \frac{2}{3}$. In Figures 1 and 2, panels (a)-(c) show that the local and global stability for the positive equilibrium of (3) coincide. When the positive equilibrium of (3) is unstable, then a unique limit cycle is observed (Figures 1(d), 2(d)).

In the following, we assume that $D < f$, i.e. $0 < d < 1$. From Theorem 3.4, the system (4) or equivalently (3), is uniformly persistent. This means neither predator nor prey can die out. Moreover, there is only one positive equilibrium and the existence of limit cycles is guaranteed by Poincaré-Bendixson Theorem when the system (3) possesses an unstable positive equilibrium. From (12), Lemmas

3.1, 3.2, and Remark 4, we have, if $u_1 < (>) \frac{d}{1-d} = \frac{D}{f-D}$ then E_* is locally asymptotically stable (unstable). Since Remark 2 shows that u_1 is an increasing, unbounded function with respect to s (or equivalently, K). So, *the stability of E_* changes from stable to unstable as K increases.* Notice that the equilibrium density of both species are increasing if K increases.

The above discussion strongly supports that phenomena exhibited by systems (1) and (3) are similar, although the smoothness of their vector fields are different. (The vector field of (3) is not smooth at $(0, 0)$.) It is quite nature to make the following **conjectures**:

1. *The local and global stability of the positive equilibrium of* (3) *coincide.*

2. *There is a unique limit cycle if the positive equilibrium of* (3) *is unstable.*

Our findings (assertions $2 \sim 5$ in Table 6.1,) partially answer these conjectures. However, significant improvements appear to be difficult.

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