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RICH DYNAMICS OF GAUSE-TYPE
RATIO-DEPENDENT PREDATOR-PREY SYSTEM

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ABSTRACT

Ratio-dependent predator-prey models are increasingly favored by field ecologists as an alternative or more suitable ones for predator-prey interactions where predation involves searching process. However, such models are not well studied mathematically in the past. In our recently work, we have shown that such models exhibit much richer dynamics than the traditional ones. This is especially true in boundary dynamics. For example, the ratio-dependent models can exhibit dynamics such as for some parameters and initial conditions, both species can become extinct. In this paper, we consider the global behaviors of solutions of the rather general Gause-type ratio-dependent predator-prey system. In addition to confirm that Gause-type ratio dependent predator-prey models are rich in boundary dynamics, we shall also present very sharp sufficient conditions to assure that if the positive steady state of the ratio-dependent predator-prey system is locally asymptotically stable, then the system has no nontrivial positive periodic solutions. We also give sufficient conditions for each of the possible three steady states to be globally asymptotically stable. We note that for ratio-dependent systems, paradox of enrichment can not occur. In general, local asymptotic stability of the positive steady state does not even guarantee the so-called persistence of the system, and therefore does not imply global asymptotic stability.

Keywords. Global stability, Gause-type predator-prey system, ratio-dependent, persistence, Dulac criterion

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1. INTRODUCTION

A milestone progress in the study of predator-prey interactions was the discovery of the now well known “paradox of enrichment” by Hairston et al. [1960] and by Rosenzweig [1969], which states that according to the Lotka-Volterra type predator-prey theory (with Michaelis-Menten-Holling type functional response) enriching a predator-prey system will cause an increase in the equilibrium density of the predator but not in that of the prey, and will destabilize the community equilibrium. Another similar paradox is the so-called “biological control paradox”, which was recently brought into discussion by Luck [1990], stating that according to the classic predator-prey theory, you can not have both a low and stable prey equilibrium density. Both these two paradoxes can be easily illustrated by a standard local stability analysis for the following well studied Lotka-Volterra type predator-prey model with Michaelis-Menten (or Michaelis-Menten-Holling) type functional response (Freedman [1980], May [1974], Maynard Smith [1974])

$$\begin{cases} dx/dt = x' = ax(1 - x/K) - cxy/(m + x) \\ dy/dt = y' = y(-d + fx/(m + x)) \\ x(0) > 0, y(0) > 0 \end{cases} \quad (1.1)$$

where x, y stands for prey and predator density, respectively. a, K, c, m, f, d are positive constants that stand for prey intrinsic growth rate, carrying capacity, capturing rate, half capturing saturation constant, conversion rate, predator death rate, respectively. While many of the mathematicians working in mathematical biology may regard these as important contributions that mathematics had for ecology, they are very controversial among ecologists up to this day. Indeed, some ecologist may simply view it as a problem (Arditi and Ginzburg [1989], Arditì and Berryman [1991], Arditì and Saiah [1992], Berryman [1992], Getz [1984], Hanski [1991]). Indeed, the above predictions are simply not in line with many field observations (Arditi and Ginzburg [1989], Arditì et al. [1991], Ginzburg and Akcakaya [1992]).

The controversial part is, of course, not the mathematical analyses of the model, rather, it is the model itself. Recently, there is a growing explicit biological and physiological evidences (Arditi and Saiah [1992], Arditì et al. [1991], Gutierrez [1992]) that in many situations, especially when predators have to search for food (and therefore have to share or compete for food), a more suitable general predator-prey theory should be based on the so-called **ratio-dependent** theory, which can be roughly stated as that the per capita predator growth rate should be a function of the ratio of prey to predator abundance, and so should

be the so-called predator functional responses (see below). This is strongly supported by numerous field and laboratory experiments and observations (Arditi and Ginzburg [1989], Arditi et al. [1991], Hanski [1991]). Generally, a ratio-dependent predator-prey model takes the form

$$\begin{cases} x' = xg(x/K) - yp(x/y) \equiv F(x, y) \\ y' = cyp(x/y) - dy \equiv G(x, y) \\ x(0) > 0, y(0) > 0 \end{cases} \quad (1.2)$$

while the traditional (or **prey-dependent**) model takes the form

$$\begin{cases} x' = xg(x/K) - yp(x) \\ y' = cyp(x) - dy \\ x(0) > 0, y(0) > 0 \end{cases} \quad (1.3)$$

Here $g(x/K)$ is the so-called per capita growth rate, $p(x/y)$ is the so-called predator functional response and c is the conversion rate. $g(x), p(x)$ satisfy the usual properties that make system (1.3) a predator-prey one. Specifically, we shall assume in the rest of this paper that $g(x), p(x)$ are continuously differentiable and

(A1) $g(0) > 0$, there is a $K > 0$ such that $g(x/K)(x - K) < 0$ for $x > 0, x \neq K$. Also, $g'(x) < 0$ for $K \geq x \geq 0$;

(A2) $p(0) = 0, p'(x) > 0$ for $x \geq 0, \lim_{x \rightarrow \infty} p(x) = p^* < \infty$, and $\lim_{(x,y) \rightarrow (0,0)} yp(x/y) = 0$.

In the following, the constant K is referred as the carrying capacity.

Very recently and independently, Thieme [1997] and Cosner et al. [1997] were able to justify through some very basic (but different) principles that indeed, ratio dependent models are more reasonable choices for many predator-prey interactions.

Geometrically, the differences of prey-dependent and ratio-dependent models are obvious, the former has a vertical predator isocline, while the latter has a slanted one. There are even more differences in their prey isoclines. Local stability analyses and simulations (Arditi and Ginzburg [1989], Berryman [1992]) show that the ratio-dependent models are capable of producing richer and more reasonable dynamics. It is easy to show that the paradox of biological control is no longer valid for ratio-dependent systems. It can also be shown (in the next section) that the ratio-dependent type models do not produce the so-called paradox of enrichment.

Our recent work (Kuang and Beretta [1997]) focused on the ratio-dependent type predator-prey model with Michaelis-Menten type functional response, which takes the form of

$$\begin{cases} x' = ax(1 - x/K) - cxy/(my + x) \\ y' = y(-d + fx/(my + x)) \\ x(0) > 0, y(0) > 0 \end{cases} \quad (1.4)$$

Clearly, the above system is a special case of system (1.2). The objective of that paper was to perform a global qualitative study on system (1.4). The present paper has the same objective for system (1.2). In particular, we shall systematically study the boundary dynamics and give sharp sufficient conditions for the positive steady state to be globally asymptotically stable. This is mainly accomplished by find conditions for the system to have no nontrivial positive periodic solutions. Our method involves a nontrivial application of the so-called divergency criterion for the stability of periodic solutions in planar systems (see Hale [1980], Lemma 3.1 on p224) and some critical transformations. This is the same method that was successfully used on system (1.4) (Kuang and Beretta [1997]). We will also present some other related qualitative results for system (1.2). All our results here are either more general or sharper than similar ones for system (1.4) (Kuang and Beretta [1997]).

This paper is organized as follows: in the next section, we present results on the boundedness of solutions (or dissipativity of the systems), local stability analysis, and nonexistence of paradox of enrichment. Some permanence results and global stability results of $(K, 0)$ and $(0, 0)$ are given in section 3. Section 4 contains the main result, namely, sufficient conditions for the nonexistence of nontrivial positive periodic solutions. It also contains some results on the global stability of the positive steady state. The paper ends with a brief discussion section.

2. PRELIMINARIES, NONEXISTENCE OF PARADOX OF ENRICHMENT

In this section, we shall present some preliminary results, including the boundedness of solutions, local stability analysis, and show that for the Gause-type ratio-dependent predator-prey model (1.2), the so-called paradox of enrichment can not happen. We shall point out here that although $(0, 0)$ is defined for system (1.2), it usually (see (1.4)) can not be linearized at. So, local stability of $(0, 0)$ can not be studied in the usual way. Indeed, this singularity at the origin, while causes much difficulty in our analysis of the system, contributes significantly to the richness of dynamics of the model.

Clearly, in the interior of the positive cone, solution exist and is unique. The only possible trouble is when $y = 0$. However, the predator equation gives us $ly < y' < Ly$ for some constants l, L . This indicates that no solution can bifurcate from the x - axis in finite time. Hence, solution of system (1.2) is unique even if for $x(0) \geq 0, y(0) \geq 0$.

System (1.2) always has equilibria $(0, 0), (K, 0)$ and has a unique positive equilibrium $E^* = (x^*, y^*)$ if and only if the following two conditions are true:

(B1) There is a $z^* > 0$ such that $p(z^*) = d/c$, which is equivalent to $cp^* > d$.

(B2) There is a unique $x^* \in (0, K)$ such that $g(x^*/K) = d/[cp^{-1}(d/c)]$.

Here $p^{-1}(s)$ stands for the inverse function of $s = p(x)$. When both conditions are satisfied, we have an unique positive steady state $E^* = (x^*, x^*/z^*)$.

The Jacobian matrix $J_K = J(K, 0)$ of system (1.2) at $(K, 0)$ takes the form of

$$\begin{pmatrix} g'(1) & -p^* \\ 0 & cp^* - d \end{pmatrix}.$$

Clearly, whenever the positive steady state E^* exists, $(K, 0)$ is unstable.

The Jacobian matrix $J^* = J(x^*, y^*)$ of system (1.2) at E^* takes the form of (recall $z^* = x^*/y^*$)

$$\begin{pmatrix} (x^*/K)g'(x^*/K) + p(z^*)/z^* - p'(z^*) & -p(z^*) + z^*p'(z^*) \\ cp'(z^*) & -cz^*p'(z^*) \end{pmatrix}.$$

It is easy to see that the determinant of J^* is

$$\det J^* = -(x^*/K)g'(x^*/K)cz^*p'(z^*) > 0.$$

Its trace is

$$\delta^* \equiv (x^*/K)g'(x^*/K) + p(z^*)/z^* - p'(z^*) - cz^*p'(z^*).$$

Clearly, E^* is locally asymptotically stable if the trace is less than zero. If we let $r = d/c$, than we have $p(z^*) = r$ or $z^* = p^{-1}(r)$. If we let g^{-1} stand for the inverse function of g on $[0, g(0)]$, than $x^*/K = g^{-1}(r/p^{-1}(r)) \equiv k$. Clearly, both z^*, k are independent of K . By straightforward computation, we can have

$$\delta^* = kg'(k) + p(z^*)/z^* - p'(z^*) - cz^*p'(z^*),$$

Which is also independent of K . This shows that the stability of E^* is independent of K . Hence we have shown

Theorem 2.1. *Increasing the carrying capacity K in system (1.2) will not change the stability of E^* . Hence, paradox of enrichment can not happen to system (1.2).*

The prey isocline inside the positive cone is described by

$$xg(x/K) = yp(x/y).$$

By differentiate it implicitly and solve for y' , we obtain

$$(p(z) - zp'(z))y' = (x/K)g'(x/K) + p(z)/z - p'(z).$$

Since $zp'(z) > 0$ for $z > 0$, we have the following simple geometric criterion for the stability of positive equilibrium E^* . In applications, this can be very convenient to use, since all we need to know is the prey isocline shape (slope) near the equilibrium, not the precise analytic expression (which is impossible to obtain).

Corollary 2.1. *In system (1.2), assume that $p(z) > zp'(z)$ for $z > 0$. Let $y = f(x)$ be the prey isocline inside the positive cone. If $f'(x^*) \leq 0$, then E^* is locally asymptotically stable.*

Standard and simple arguments show that solutions of system (1.2) always exist and stay positive. Indeed, it is obvious that for system (1.2), we have

$$\limsup_{t \rightarrow \infty} x(t) \leq K, \quad (2.1)$$

and

$$y(t) < y(0)e^{(cp^* - d)t}.$$

We consider now the boundedness of $y(t)$ for system (1.2). Clearly, if $d \geq cp^*$, then $\lim_{t \rightarrow \infty} y(t) = 0$. So we assume below that $cp^* > d$. In the following, we denote by y_M the unique value of y such that $cp(K/y) = d$. We shall show that

Theorem 2.2. *For system (1.2), if $cp^* > d$,*

$$\limsup_{t \rightarrow \infty} y(t) \leq y_M \quad (2.2)$$

Proof. Observe that there exists a $T > 0$ such that, for $t > T$, $x(t) < K$ (otherwise, from the prey equation and the fact that $-dy \leq y' \leq (cp^* - d)y$, we have $\lim_{t \rightarrow \infty} x(t) = K$, $\lim_{t \rightarrow \infty} y(t) = 0$; while from the predator equation we see that $\lim_{t \rightarrow \infty} y(t) = +\infty$, a contradiction). From the predator equation, we see that, for $t > T$, we have

$$y'(t) \leq y(cp(K/y) - d).$$

A standard comparison argument shows that

$$\limsup_{t \rightarrow \infty} y(t) \leq y_M.$$

□

Therefore we have shown that system (1.2) is dissipative.

3. PERMANENCE, RICH BOUNDARY DYNAMICS

In this section, we shall present some results on permanence, and boundary dynamics (the global stability of boundary equilibria $(K, 0)$ and $(0, 0)$) for system (1.2). We also would like to point out that some of the results in this section are modified from similar ones in Beretta and Kuang (1997).

For convenience, we let

$$p_1 \equiv \sup\{p(x)/x : x > 0\}.$$

It is easy to see that, for system (1.4), if $g(0) > p_1$, then

$$x' = x[g(x/K) - p(x/y)/(x/y)] \geq x(g(x/K) - p_1). \quad (3.1)$$

If we let \underline{x} be the root of $g(x/K) - p_1 = 0$, then we see that the above inequality implies (again, by standard comparison argument) that $\liminf_{t \rightarrow +\infty} x(t) \geq \underline{x}$. Hence, for large t , $x(t) > \underline{x}/2$, and

$$y' \geq y[-d + cp(\underline{x}/(2y))].$$

Let \underline{y} be the root of $-d + cp(\underline{x}/(2y)) = 0$. Then, we obtain

$$\liminf_{t \rightarrow +\infty} y(t) \geq \underline{y}.$$

The above arguments and Theorem 2.2 imply that:

Theorem 3.1. *If $cp^* > d$ and $g(0) > p_1$, then system (1.2) is permanent.*

Recall that system (1.3) is permanent if and only if it has a positive steady state. The above theorem is not nearly as sharp (see (B1), (B2)). The same can be said for most results in the rest of this section.

Assume below that

$$p'(0) > g(0) + d$$

in system (1.4). Then there is an $\alpha > 0$, such that for all $s \in (0, \alpha]$,

$$p(s)/s \geq g(0) + d.$$

Let $\delta = x(0)/y(0) < \alpha$. We claim that for all $t > 0$, $x(t)/y(t) < \alpha$ and $\lim_{t \rightarrow +\infty} x(t) = 0$. Otherwise, there is a first time t_1 , $x(t_1)/y(t_1) = \alpha$ and for $t \in [0, t_1)$, $x(t)/y(t) < \alpha$. Then for $t \in [0, t_1]$, we have

$$x'(t) = x[g(x/K) - (y/x)p(x/y)] \leq x[g(0) - p(x/y)/(x/y)] \leq -dx(t)$$

which implies that $x(t) \leq x(0)e^{-dt}$. However, for all $t \geq 0$,

$$y'(t) \geq -dy(t)$$

which implies that $y(t) \geq y(0)e^{-dt}$. This shows that for $t \in [0, t_1]$,

$$x(t)/y(t) \leq x(0)/y(0) = \delta < \alpha,$$

a contradiction to the existence of t_1 , proving the claim. This in turn implies that $x(t) \leq x(0)e^{-dt}$ for all $t \geq 0$. That is, $\lim_{t \rightarrow +\infty} x(t) = 0$. Hence we have established the following result (recall that system (1.2) is said to be *not persistent* if $\min(\liminf_{t \rightarrow +\infty} x(t), \liminf_{t \rightarrow +\infty} y(t)) = 0$ for some of its positive solutions):

Theorem 3.2. *If $p'(0) > g(0) + d$, then system (1.2) is not persistent.*

In fact, we also have

Theorem 3.3. *If $p'(0) > g(0) + d$, then there exist positive solutions $(x(t), y(t))$ of system (1.2) such that $\lim_{t \rightarrow +\infty} (x(t), y(t)) = (0, 0)$.*

Proof. If $cp^* \leq d$, then this is obvious from the previous argument that leads to Theorem 3.2. Assume now that $cp^* > d$. Again, the argument leading to Theorem 3.2 shows that $\lim_{t \rightarrow +\infty} x(t) = 0$ and for $t \geq 0$, $x(t)/y(t) \leq \delta$, provided that $\delta = x(0)/y(0) < \alpha$, where α is as described in the proof of Theorem 3.2. Let $(x(t), y(t))$ be the solution of (1.2), with $x(0)/y(0) < \alpha$. Since $y(t)$ is bounded, we have

$$0 \leq s_1 \equiv \limsup_{t \rightarrow +\infty} y(t) < +\infty, \quad 0 \leq s_2 \equiv \liminf_{t \rightarrow +\infty} y(t) < +\infty.$$

If $s_2 > 0$, then we see that for large t , $y'(t) < -dy(t)/2$, which leads to $\lim_{t \rightarrow +\infty} y(t) = 0$. This is a contradiction. So we must have $s_2 = 0$. Assume below that $s_1 > 0$. Let k_1 be the root of $cp(x/(s_1/2)) - d = 0$. Since $\lim_{t \rightarrow +\infty} x(t) = 0$, we see that

(i) there is a t_1 , such that for $t > t_1$, we have $x(t) < k_1$.

From the assumption $s_1 > 0$, we see that there is a $t_2 > t_1$ such that $y(t_2) > s_1/2$, and $y'(t_2) > 0$. However, we note that $y'(t_2) > 0$ leads to

$$cp(x(t_2)/(s_1/2)) > cp(x(t_2)/y(t_2)) > d,$$

Which implies that $x(t_2) > k_1$. This is a contradiction to (i). Hence we must have $s_2 = 0$. This completes the proof. \square

Note that under the assumption $p'(0) > g(0) + d$, system (1.2) may have positive steady state. This shows that system (1.2) can have both positive steady state and positive solutions that tend to the origin. **In particular, we can see that if cp^* is just slightly greater than d and $p'(0) > g(0) + d$, then E^* is locally asymptotically stable but not globally asymptotically stable.**

Theorem 3.3 generalizes theorem 2.6 in Beretta and Kuang [1997]. Clearly, Theorem 3.3 implies that if $p'(0) > g(0) + d$, then the boundary equilibrium $(K, 0)$ of system (1.2) is not globally asymptotically stable.

Note that under the condition $p'(0) > g(0) + d$, system (1.2) can have no positive steady state and at the same time, $(K, 0)$ is locally stable (just add the assumption $cp^* \leq d$). In such case, some solutions tend to $(K, 0)$ and some tend to $(0, 0)$. Hence the above theorem shows that system (1.2) can exhibit behavior similar to bistability. However, we can also show that

Theorem 3.4. *If $p_1 < g(0)$ and $cp^* \leq d$, then $(K, 0)$ is globally asymptotically stable for system (1.2).*

Proof. It is easy to see that $\lim_{t \rightarrow +\infty} y(t) = 0$, and $\liminf_{t \rightarrow +\infty} x(t) \geq \underline{x} > 0$, where $g(\underline{x}/K) = p_1$. Then, for any $\varepsilon \in (0, a)$, there exists $T = T(\varepsilon)$, such that for $t > T$,

$$x(t)(g(x(t)/K) - \varepsilon) \leq x'(t) \leq x(t)g(x(t)/K).$$

This clearly shows that

$$\lim_{t \rightarrow +\infty} x(t) = K.$$

This proves the theorem. \square

Our last theorem of this section shows that under some conditions, the origin can be globally attractive!

Theorem 3.5. *Assume that $p(z)/z$ is nonincreasing for $z > 0$ and $p_1 > g(0)$. Let z_1 be the root of $p(z)/z - g(0) = 0$. If $z_1 \geq p^{-1}(d/c)$, then $(0, 0)$ is globally asymptotically stable for system (1.2).*

Proof. This theorem can be proved by a simple flow analysis. The prey isocline in the positive quadrant is the curve described by $g(x/K) = p(z)/z$, $z = y/x$. Since $p(z)/z$ is nonincreasing, we see that the least value that z can possibly attain is when $x = 0$, which is the value z_1 . Note also that the predator isocline is simply the line $x/y = p^{-1}(d/c)$. Since $z_1 \geq p^{-1}(d/c)$, we see that the whole predator isocline lies above the prey isocline. So, we can divide the positive cone into three regions, *I*, *II*, *III*.

$$III = \{(x, y) : x \geq 0, y \geq 0, F(x, y) \geq 0, G(x, y) > 0\};$$

$$II = \{(x, y) : x \geq 0, y \geq 0, F(x, y) < 0, G(x, y) \geq 0\};$$

$$I = \{(x, y) : x \geq 0, y \geq 0, F(x, y) < 0, G(x, y) < 0\}.$$

Clearly, solutions that start in region *III* will enter region *II* by crossing the prey isocline vertically (upwards) in finite time, since there is no steady state in *III*. And then, for the same reason, the solutions will enter region *I* in finite time by crossing the predator isocline horizontally (left wards). Once in region *I*, it is easy to see that solutions are trapped (cannot cross the predator isocline from left to right) and we

must have $(x(t), y(t)) \rightarrow (0, 0)$ as $t \rightarrow +\infty$. This proves the theorem. \square

4. GLOBAL STABILITY OF POSITIVE EQUILIBRIUM AND MORE ON PERMANENCE

In this section we shall obtain some sufficient conditions for the positive equilibrium of system (1.2) to be globally attractive. In addition, we will present another permanence result. Obviously, we shall assume that the positive steady state E^* exists in the rest of this section. This is equivalent to assuming (B1)-(B2). In particular, this implies that throughout this section, we assume that $cp^* > d$. If we let $z = x/y$, and

$$f(x, z) \equiv g(x/K) - p(z)/z.$$

Then we can rewrite system (1.2) as

$$\begin{cases} x' = xf(x, z) \equiv F_1(x, z) \\ z' = z[f(x, z) - cp(z) + d] \equiv F_2(x, z). \end{cases} \quad (4.1)$$

System (4.1) has $(0, 0)$, (x^*, z^*) , and possibly $(0, z_*)$ and/or $(x_*, 0)$ as its equilibria, where z_* is any positive root of

$$f(0, z) - cp(z) + d = 0$$

and x_* is the any positive root of

$$g(x/K) - p'(0) = 0.$$

The Jacobian matrix $J(0, 0)$ of system (4.1) at $(0, 0)$ takes the form of

$$J(0, 0) = \begin{pmatrix} g(0) - p'(0) & 0 \\ 0 & g(0) - p'(0) + d \end{pmatrix}.$$

Clearly, $(0, 0)$ is a repeller if $g(0) > p'(0)$. The Jacobian matrix $J(0, z_*)$ of system (4.1) at $(0, z_*)$ takes the form of

$$J(0, z_*) = \begin{pmatrix} g(0) - p(z_*)/z_* & 0 \\ (z_*/K)g'(0) & -cz_*p'(z_*) - p'(z_*) + p(z_*)/z_* \end{pmatrix}.$$

If $g(0) > p(z_*)/z_*$, then $(0, z_*)$ is unstable. Clearly, if $g(0) > p_1$, then both $(0, 0)$, $(0, z_*)$ are unstable. The Jacobian matrix $J(x_*, 0)$ of system (4.1) at $(x_*, 0)$ takes the form of

$$J(x_*, 0) = \begin{pmatrix} x_*g'(x_*/K) & -x_*p''(0)/2 \\ 0 & d \end{pmatrix}.$$

Clearly, when exists, $(x_*, 0)$ is always a saddle, stable along x direction.

Using a method involving a nontrivial application of the so-called divergency criterion for the stability of periodic solutions in planar systems (see Hale [1980], Lemma 3.1 on p224) and some critical transformations, Kuang and Beretta [1997] succeeded in showing that whenever E^* is locally stable, there exists no nontrivial positive periodic solutions in system (1.4). This approach, however, seems formidable to be applied to the more general setting of system (1.2). Nevertheless, applying Dulac criterion, we can obtain some simple yet practical conditions for the positive equilibrium E^* to be globally asymptotically stable.

Let $b_1(x, z) \equiv 1/(xz)$ and

$$D_1 \equiv \frac{\partial(b_1 F_1)}{\partial x} + \frac{\partial(b_1 F_2)}{\partial z}.$$

Then we have

$$D_1 = g'(x/K)/(zK) + [p(z) - p'(z)z - cp'(z)z^2]/(xz^2).$$

Recall that $g'(x/K) \leq 0$ for $x \in [0, K]$. It is easy to see that any nontrivial positive periodic solutions must surround E^* and be contained in the strip $\{(x, z) : x \in [0, K], z > 0\}$. By Dulac criterion, we arrive at:

Theorem 4.1. *If the predator response function $p(z)$ satisfies*

$$\Delta \equiv p(z) - p'(z)z - cp'(z)z^2 \leq 0, \quad (4.2)$$

then system (1.2) has no nontrivial positive periodic solutions. If, in addition, that $g(0) > p_1$, then E^ is globally asymptotically stable.*

Proof. From Dulac criterion, we see that system (1.2) has no nontrivial positive periodic solutions. $\Delta \leq 0$ implies that E^* is locally asymptotically stable. While $cp^* > d$ (since E^* exists) and $g(0) > p_1$ assures that the system is permanent (Theorem 3.1). These together yield the conclusion. \square

An alternative proof of Theorem 4.1 can bypass Theorem 3.1 by simply making use of the facts that when $g(0) > p_1$, both $(0, 0)$ and $(0, z_*)$ (if any) are unstable plus that $(K, 0)$ is a saddle in the original system (1.2).

As a simple example for Theorem 4.1. Consider the case that

$$p(z) = \frac{bz}{a+z}.$$

Then, condition (4.2) is reduced to $ca \geq 1$. Notice that we assume only that $g(x/K)$ is decreasing.

Let $b_2(x, z) \equiv 1/(xp(z))$ and

$$D_2 \equiv \frac{\partial(b_2F_1)}{\partial x} + \frac{\partial(b_2F_2)}{\partial z}.$$

Then we have

$$D_2 = g'(x/K)/(p(z)K) + [(z/p(z))'g(x/K) - c + d(z/p(z))']/x.$$

Hence, $D_2 \leq 0$, if $(z/p(z))'(g(x/K) + d) \leq c$. This is equivalent to

$$cp(z)^2 \geq (g(x/K) + d)(p(z) - zp'(z)). \quad (4.3)$$

Again, by Dulac criterion, we obtain:

Theorem 4.2. *If the predator response function $p(z)$ satisfies $p(z) \geq zp'(z)$, and*

$$cp(z)^2 \geq (g(0) + d)(p(z) - zp'(z)), \quad (4.4)$$

then system (1.2) has no nontrivial positive periodic solutions. If, in addition, that E^ is locally asymptotically stable and $g(0) > p_1$, then E^* is globally asymptotically stable.*

Proof. Clearly condition (4.4) implies (4.3). The rest of the proof is the same as that for Theorem 4.1. \square

As applications of Theorem 4.2, we again consider

$$p(z) = \frac{bz}{a+z}.$$

We can easily show that condition (4.4) is reduced to

$$cb \geq g(0) + d, \quad (4.5)$$

instead of $ca \geq 1$ from the previous theorem.

We can obtain the following somewhat general and practically useful result (independent of Theorems 4.1 and 4.2) by a simple flow analysis.

Theorem 4.3. *Let x_*, x_u be two constants such that $0 \leq x_* < K < x_u$. Suppose that $z_1(x)$ is the prey isocline defined on $[x_*, K)$ and $z_2(x)$ is the z isocline defined on $[0, x_u)$ in the interior of the first quadrant of $x - z$ plane. Assume that $z_2(x) > z^* > z_1(x)$ for $x < x^*$ and $z_2(x) < z^* < z_1(x)$ for $x > x^*$. Assume also that $p(z)/z$ is strictly decreasing, $p_1 < g(0) + d$. For any $x_1 \in (x^*, K)$, let $x_2 \in [0, x^*)$ be such that $z_1(x_2) = z_2(x_1)$. If for all $x_1 \in (x^*, K)$*

$$z_1(x_1) > z_2(x_2), \quad (4.6)$$

then system (1.2) has no nontrivial positive periodic solutions and E^ is globally asymptotically stable.*

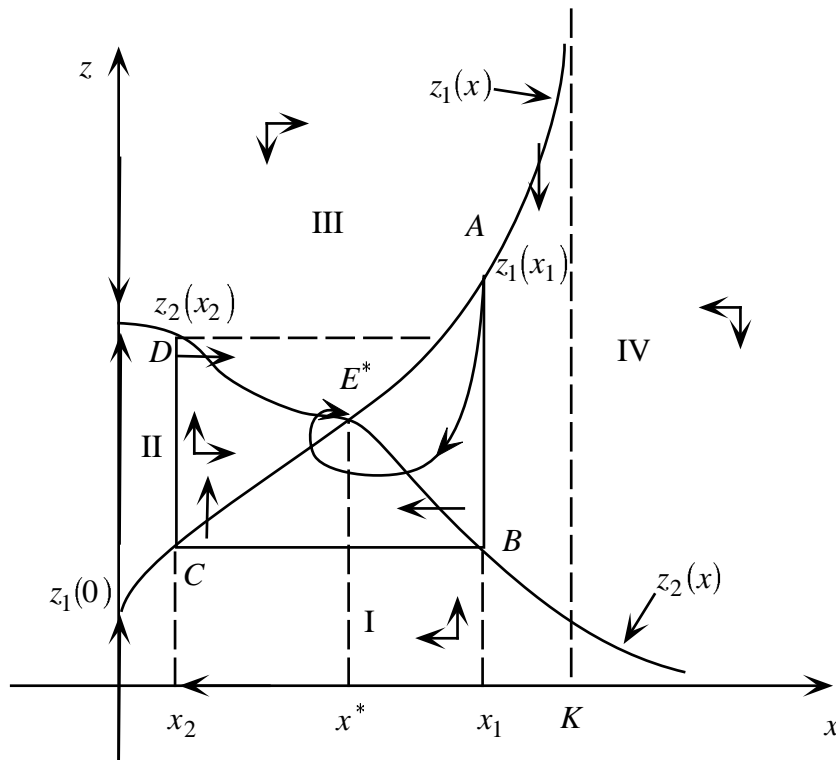


FIGURE 1. A flow diagram of system (4.1).

Proof. Since $p(z)/z$ is strictly decreasing, we see that $z_1(x)$ is strictly increasing. So the value of x_2 in the theorem is uniquely defined.

We divide the interior of the positive cone into four regions (see Figure 1) I, II, III, IV .

$$I = \{(x, z) : x > 0, z > 0, F_1(x, z) < 0, F_2(x, z) > 0\};$$

$$II = \{(x, z) : x > 0, z > 0, F_1(x, z) > 0, F_2(x, z) > 0\};$$

$$III = \{(x, z) : x > 0, z > 0, F_1(x, z) > 0, F_2(x, z) < 0\};$$

$$IV = \{(x, z) : x > 0, z > 0, F_1(x, z) < 0, F_2(x, z) < 0\}.$$

Let $A = (x_1, z_1(x_1)), B = (x_1, z_2(x_1)), C = (x_2, z_1(x_2)), D = (x_2, z_2(x_2))$. If we follow the solution starting at $A = (x_1, z_1(x_1))$, we see that it is trapped inside the polygon $ABCD$. The solution either tends to E^* before return to the upper portion of the x isocline $z_1(x > x^*)$, or will reach it in finite time at, say $(x_3, z_1(x_3))$. We define a function $h(x)$ on (x^*, K) as follows. Let $h(x_1) = x_3$ if x_3 exists, otherwise we set $h(x_1) = x^*$. Clearly $h(x)$ is well defined and strictly monotone decreasing. If we continue to follow the flow and repeat this simple argument,

we see that the solution must have E^* as the limit or there is a monotone decreasing sequence $\{x_{2n+1}\}_{n=1}^{n=+\infty}$. If $\lim_{n \rightarrow \infty} x_{2n+1} = x_0 \neq x^*$, then we must have $h(x_0) = x_0$, a contradiction to assumption (4.6). Similar argument can be applied to all other positive solutions. This proves the theorem. \square

As a consequence of the local stability analysis at the beginning of this section and the thought contained in the proof of the previous theorem, we can obtain the following permanence result, which is quite different from Theorem 3.1.

Theorem 4.4. *If E^*, z_* exist, $p'(0) < g(0) + d$ and $g(0) > p(z_*)/z_*$. Then system (1.2) is permanent.*

Proof. Clearly, x is eventually bounded above by $K + 1$. Again, we divide the interior of the positive cone into four separate regions as in the proof of the previous theorem. Since z_* exists and $p'(0) < g(0) + d$, we see that for any positive solution $(x(t), z(t))$, we have

$$\limsup_{t \rightarrow \infty} z(t) \leq z_M,$$

where $z_M \equiv \sup\{z_2(x) : x \geq 0\}$.

Assume first that $g(0) < p_1$. Notice that as a result of $g(0) < p_1$, we have $x_* = 0$ and $z_1(0) > 0$. Also, $(0, 0)$ is a saddle due to $g(0) < p_1 < g(0) + d$. For the same reason, we see that at a given point (x, z) , if $0 < z < z_2(x)$, then $z' = z[f(x, z) - cp(z) + d] > 0$, while if $z > z_2(x)$, then $z' = z[f(x, z) - cp(z) + d] < 0$. This indicates that $-cz_*p'(z_*) - p'(z_*) + p(z_*)/z_* \leq 0$ where $z_* = z_2(0)$. More specifically, we can see that z_* is locally attractive for the scalar equation

$$z' = z[g(0) - p(z)/z - cp(z) + d.]$$

Observe that $g(0) = p(z_1(0))/z_1(0)$. Since $z_2(0) > z_1(0)$, and $p(z)/z$ is strictly decreasing, we see that $g(0) - p(z_2(0))/z_2(0) > 0$. Thus, we have shown that $(0, z_2(0))$ is also a saddle. If $g(0) \geq p_1$, then $x_* \geq 0$ and $(x_*, 0)$ is an equilibrium. We can show that if $z_* > 0$, then $(0, 0)$ is an unstable node and $(0, z_*)$ remains a saddle. While if $z_* = 0$, then $(0, 0) = (0, z_*)$ is a saddle. As a consequence, in all the above possible cases, we see that no positive solution can tend to either $(0, 0)$, or $(0, z_*)$, or $(x_*, 0)$. This together with the fact that x, z are eventually bounded above by $K + 1, z_M + 1$ respectively, implies (by standard permanence theory) that system (4.1) is permanent. This is equivalent to say that the original system (1.2) is also permanent. \square

5. DISCUSSION

In this paper, we have conducted a preliminary qualitative study on the global dynamics of Gause-type ratio-dependent predator-prey models. We have shown that compare to the traditional predator-prey system (1.3), the ratio-dependent predator-prey system (1.2) has much richer boundary dynamics. For ratio-dependent predator-prey models, there can be no paradox of enrichment or paradox of biological control. Even when there is a positive steady state, both prey and predator can become extinct. Such extinction (the collapse of the system) occurs in two cases. In one case, both species become extinct regardless of the initial data. In the other case, both species will die out only if initial prey/predator ratio is too low (otherwise, only the predator goes extinct, while prey tends to carrying capacity). The first case is often the result of the intrinsic high efficiency of the predator species (e.g., too efficient in catching and/or converting the prey biomass). The second case is most subtle and interesting in application. It indicates that over harvesting (or catching) certain prey species, or stocking too much predator species at a given time may lead to the collapse of the whole system (the extinction of both species). These are all clearly reasonable outcomes that are frequently observed (Getz [1984]) in the nature. However, traditional predator-prey systems fail to exhibit these. Simulation work that illustrates these and other dynamics for system (1.4) can be found in Kuang and Beretta [1997].

While the above facts do not provide enough evidences to discredit the traditional predator-prey models, it suggests the traditional predator-prey models have a number of limitations. Our conviction is that the ratio-dependent predator-prey models are more appropriate for predator-prey interactions where predation involve serious searching processes (like animals hunting for animals), while the traditional ones may be more suitable to those involve no or random searching process (like chemostat situation, plant-herbivore interaction, etc.).

There are still many interesting and challenging mathematical questions need to be studied for system (1.2) (in fact, even for system (1.4)). For example, most of our results in section 3 and 4 have much room for improvement. However, significant improvements appear to be difficult at this moment. Some obviously important questions that left untouched here are the existence and uniqueness of limit cycle of system (1.2) when E^* becomes unstable. These should be some of the worthy objectives of future work. Nevertheless, with standard phase plane analysis, one can easily show that whenever E^* is unstable, system (1.2) always has a cycle (limit cycle or heterclinic cycle connecting

$(0, 0)$ to $(K, 0)$). If in addition that the system is permanent (sufficient conditions are given in Theorem 3.1 and 4.4), then the system has a nontrivial positive limit cycle. At this moment, we are still unable to show system (1.4) has unique positive limit cycle, when E^* exists and is unstable. This is, however, known to be true for system (1.1) (see Kuang and Freedman [1988] and the reference cited).

Finally, we would like to point out that there is almost nothing has been done to the qualitative analyses of food chains or multi-species or patchy interaction models based on ratio-dependent approach. It is easy to conceive that such models should possess much richer and reasonable dynamics (such as the collapse of the whole ecosystem in a closed environment) than the traditional counterparts can provide. And most surely, they pose more interesting and challenging questions both mathematically and biologically.

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