Mathematical Biology

Sze-Bi Hsu · Tzy-Wei Hwang · Yang Kuang

Global analysis of the Michaelis–Menten-type ratio-dependent predator-prey system

Abstract. The recent broad interest on ratio-dependent based predator functional response calls for detailed qualitative study on ratio-dependent predator-prey differential systems. A first such attempt is documented in the recent work of Kuang and Beretta(1998), where Michaelis-Menten-type ratio-dependent model is studied systematically. Their paper, while contains many new and significant results, is far from complete in answering the many subtle mathematical questions on the global qualitative behavior of solutions of the model. Indeed, many of such important open questions are mentioned in the discussion section of their paper.

Through a simple change of variable, we transform the Michaelis-Menten-type ratio-dependent model to a better studied Gause-type predator-prey system. As a result, we can obtain a complete classification of the asymptotic behavior of the solutions of the Michaelis-Menten-type ratio-dependent model. In some cases we can determine how the outcomes depend on the initial conditions. In particular, open questions on the global stability of all equilibria in various cases and the uniqueness of limit cycles are resolved. Biological implications of our results are also presented.

1. Introduction

One of the most popular mathematical model describing a predator-prey interaction is the following well-known Lotka-Volterra type predator-prey model with Michaelis-Menten (or Holling type II) functional response (Freedman (1980), May (1974)):

$$\begin{cases} x'(t) = ax(1 - x/K) - cxy/(m + x) \\ y'(t) = y(fx/(m + x) - d) \\ x(0) > 0, \ y(0) > 0 \end{cases} \tag{1.1}$$

S.-B. Hsu: Department of Mathematics, National Tsing Hua University, Hsinchu, Taiwan, R.O.C. Research supported by National Council of Science, Republic of China

T.-W. Hwang: Department of Mathematics, Kaohsiung Normal University, 802, Kaohsiung, Taiwan, R.O.C. Research supported by National Council of Science, Republic of China

Y. Kuang: Department of Mathematics, Arizona State University, Tempe, AZ 85287-1804, USA. e-mail: `kuang@asu.edu`. Work is partially supported by NSF grant DMS-0077790 and is initiated while visiting the National Center for Theoretical Science, Tsing Hua University, Hsinchu, Taiwan R.O.C.

where x, y stand 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 saturation constant, maximal predator growth rate, predator death rate, respectively. This model exhibit the well-known "paradox of enrichment" observed by Hairston et al. (1960) and by Rosenzweig (1969) which states that according to model (1.1), enriching a predator-prey system (increasing the carrying capacity K) will cause an increase in the equilibrium density of the predator but not in that of the prey, and will destabilize the positive equilibrium (the positive steady state changes from stable to unstable as K increases). An equivalent paradox is the so called "biological control paradox" which was recently brought into discussion by Luck (1990), stating that according to (1.1), we cannot have both a low and stable prey equilibrium density. However, in reality, there are numerous examples of successful biological control where the prey are maintained at densities less than 2% of their carrying capacities (Arditi and Berryman (1991)). This clearly indicates that the paradox of biological control is not intrinsic to predator-prey interactions. Another noteworthy prediction from model (1.1) is that prey and predator species can not extinct simultaneously (mutual extinction). This, however, clearly contradicts Gause's classic observation of mutual extinction in the protozoans, *Paramecium* and its predator *Didinium* (Gause (1934), Abrams and Ginzburg (2000)).

Recently there is a growing evidences (Arditi et al. (1991), Akcakaya et al. (1995), Cosner et al. (1999)) that in some situations, especially when predator 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. This is supported by numerous field and laboratory experiments and observations (Arditi and Ginzburg (1989), Arditi et al. (1991)). Generally, a ratio-dependent predator-prey model takes the form

$$x'(t) = xf(x) - yp(x/y)$$
$$y'(t) = (cq(x/y) - d)y.$$

Here $p(x)$ is the so-called predator functional response. Often, $q(x)$ is replaced by $p(x)$, in which case c becomes the conversion rate. $p(x)$, $q(x)$ satisfy the usual properties such as being nonnegative and increasing, and equal to zero at zero.

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 analysis and simulations (Arditi and Ginzburg (1989), Berryman (1992)) show that the ratio-dependent models are capable of producing richer and more reasonable dynamics biologically. Specifically, it will not produce the paradox of biological control and the so-called paradox of enrichment. It also allows mutual extinction as a possible outcome of a given predator-prey interaction (Kuang and Beretta (1998), Jost et al. (1999)).

In this paper we study following ratio-dependent predator-prey system which was discussed in Kuang and Beretta (1998) (see also Jost et al. (1999)):

$$\begin{cases} x'(t) = ax(1 - x/K) - cxy/(my + x) \equiv F(x, y), \\ y'(t) = y(-d + fx/(my + x)) \equiv G(x, y), \\ x(0) = x_0 > 0, \quad y(0) = y_0 > 0 \end{cases} \tag{1.2}$$

where a, K, c, m, f, d are positive constants and $x(t), y(t)$ represent the population density of prey and predator at time t respectively. The prey grows with intrinsic growth rate a and carrying capacity K in the absence of predation. The predator consumes the prey with functional response of Michaelis-Menten type $cuy/(m + u), u = x/y$ and contributes to its growth with rate $fuy/(m + u)$. The constant d is the death rate of predator. Observe that $\lim_{(x,y) \to (0,0)} F(x, y) = G(x, y) = 0$. 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 $\mathbf{R}_+^2$ where $\mathbf{R}_+^2 = \{(u, y)| u > 0, y > 0\}$.

Kuang and Beretta (1998) presented some global qualitative analysis of solutions of system (1.2). The authors showed that ratio-dependent predator-prey models are rich in boundary dynamics. For example, for some initial conditions, both predator and prey can go extinction simultaneously. They also established that the system has no nontrivial periodic solutions provided the positive steady state is locally asymptotic stable. Similar results for more general Gause-type ratio-dependent predator-prey systems can be found in Kuang (1999).

For simplicity, we nondimensionalizes the system (1.2) as in Kuang and Beretta (1998) with the following scaling

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

then the system (1.2) takes the form

$$\begin{cases} x'(t) = x(1 - x) - sxy/(x + y), \\ y'(t) = \delta y(-r + x/(x + y)), \\ x(0) = x_0 > 0, \quad y(0) = y_0 > 0, \end{cases} \tag{1.3}$$

where

$$s = \frac{c}{ma}, \quad \delta = \frac{f}{a}, \quad r = \frac{d}{f}. \tag{1.4}$$

Results of Kuang and Beretta (1998) and their open questions are summarized in table 1.

In this paper we shall give an almost complete classification for the asymptotic behavior of the solutions of (1.3). The open questions proposed by Kuang and Beretta in (1998) are all answered here. When relevant, it is determined how the outcomes depends on the initial conditions. We also establish the uniqueness of limit cycles if it exists.

The rest of this paper is organized as follows. In section 2, by a simple but crucial change of variables, we transform the system (1.3) into a Gause-type predator-prey system (2.1) where a wealth of existing methods and results are applicable. We thus obtain a better understanding of the rich asymptotic behavior of the solutions of the system (1.3) through that of system (2.1). Section 3 presents direct biological implications of all our mathematical results in terms of the original parameters in system (1.2).

Table 1. Established results and open questions of Kuang and Beretta (1998) in terms of s, δ, r.

	Conditions	Results or question
1.	$r \geq 1, s > 0,$	$(1, 0)$ is locally asymptotically stable.
2.	$r \geq 1, 0 < s \leq 1,$	$(1, 0)$ is globally asymptotically stable.
3.	$s > 1 + \delta r,$	There exists $(x(t), y(t)) \rightarrow (0, 0)$. as $t \rightarrow \infty$
		Hence, the system is not persistent.
4.	$r \geq 1, 1 < s \leq 1 + \delta r,$	$(1, 0)$ is locally stable.
		OPEN QUESTION 1: Is $(1, 0)$ globally stable?
5.	$0 < r < 1, 0 < s \leq 1,$	E^* is globally stable.
6.	$0 < r < 1, s > \frac{1}{1-r},$	$(0, 0)$ is globally stable.
7.	$0 < r < 1, 1 < s < \frac{1}{1-r}$	E^* is locally stable.
	$\delta(1 - r) \geq 1$	OPEN QUESTION 2: Is E^* globally stable?
8.	$0 < r < 1, 1 < s < \frac{1}{1-r}$	(i) OPEN QUESTION 3: Is it true that if $1 < s \leq 1 + \delta r$,
	$\delta(1 - r) < 1$	then E^* is globally stable?
		(ii) If $1 + \delta r < s < \frac{1}{1-r^2} + \frac{r\delta}{1+r}$, E^* is locally.
		stable and the system is not persistent.
		(iii) $\frac{1}{1-r^2} + \frac{r\delta}{1+r} < s < \frac{1}{1-r}$ then E^* is unstable.
		and the system is not persistent.

2. Main results

We make the change of variable $(x, y) \rightarrow (u, y)$ where $u = x/y$ in system (1.3). This reduces it to the following Gause-type predator-prey system (2.1)

$$
\begin{aligned}
u'(t) &= g(u) - \varphi(u)y, \\
y'(t) &= \psi(u)y, \\
u(0) &= u_0 > 0, \ y(0) = y_0 > 0
\end{aligned}
\tag{2.1}
$$

where

$$
\begin{aligned}
g(u) &= u(1 + \delta r - s + (1 + \delta r - \delta)u)/(1 + u), \\
\varphi(u) &= u^2 \\
\psi(u) &= \delta(u/(u + 1) - r).
\end{aligned}
\tag{2.2}
$$

Since (2.1) can also be rewritten as

$$
\begin{aligned}
u'(t) &= \varphi(u)(h(u) - y), \\
y'(t) &= \psi(u)y,
\end{aligned}
\tag{2.3}
$$

we see that the prey isocline of the system (2.1) is given by

$$
y = \frac{g(u)}{\varphi(u)} = h(u) = (1 + \delta r - s + (1 + \delta r - \delta)u)/u(u + 1).
\tag{2.4}
$$

Clearly, $\lim_{u \to +\infty} h(u) = 0$ and

$$h'(u) = -[(1 + \delta r - \delta)u^2 + 2(1 + \delta r - s)u + (1 + \delta r - s)]/u^2(1 + u)^2. \quad (2.5)$$

From (2.4), (2.5) and some routine calculations, we have the following simple lemma which describes the qualitative behavior of the function $y = h(u)$ (see Fig.1(a)-(d)). The proof is omitted.

Lemma 2.1. *Let $A = 1 + \delta r - \delta$ and $B = 1 + \delta r - s$.*

(a) *If $A \geq 0$, $B \geq 0$ and $A^2 + B^2 > 0$ then $h(u) > 0 > h'(u)$ for all $u > 0$.*
(b) *If $AB < 0$ then $h(u), h'(u)$ has exactly one positive zero θ_0, θ_1 respectively and*

$$\theta_0 = -\frac{B}{A} < \theta_1 = \theta_0 + \sqrt{\theta_0^2 + \theta_0}.$$

2.1. Equilibrium analysis

System (2.1) always has the trivial equilibrium $E_0 = (0, 0)$ and the boundary equilibrium $E_1 = (\theta_0, 0)$ provided $AB < 0$. Clearly, if $r \geq 1$ then $\psi(u) < 0$ for all $u > 0$. On the other hand, if $0 < r < 1$ then $\psi(u^*) = 0$ where $u^* = r/(1-r) > 0$ and

$$\psi(u) = \delta(1 - r)(u - u^*)/(1 + u).$$

Hence the system (2.1) has a unique positive equilibrium $E^* = (u^*, y^*)$ if and only if $r \in (0, 1)$ and $y^* = h(u^*) > 0$. From (2.2), (2.3) the variational matrix of the system (2.1) is given by

$$J(u, y) = \begin{bmatrix} \varphi'(u)(h(u) - y) + \varphi(u)h'(u) & -u^2 \\ \delta y/(1 + u)^2 & \delta(u/(u + 1) - r) \end{bmatrix}. \quad (2.6)$$

The stability of equilibria E_0, E_1 and E^* is determined by the eigenvalues of the matrix $J(E_0)$, $J(E_1)$ and $J(E^*)$ respectively.

Lemma 2.2. *Let $A = 1 + \delta r - \delta$ and $B = 1 + \delta r - s$. For the system (2.1), the following statements are true.*

(i) *If $B < 0$ then E_0 is locally asymptotically stable.*
  If $B > 0$ then E_0 is a saddle point with stable manifold $\{(0, y)|y > 0\}$.
  If $A > 0, B = 0$ then E_0 remains a saddle point with stable manifold $\{(0, y)|y > 0\}$.
(ii) *If $A < 0, B > 0$ then E_1 is a saddle point when $u^* < \theta_0$ and E_1 is locally asymptotically stable when $u^* > \theta_0$. (See Fig. 1(c)).*
  Let $A > 0, B < 0$. Then E_1 is a saddle point when $r \geq 1$. For $0 < r < 1$, E_1 is a saddle point when $\theta_0 < u^*$ and E_1 is a unstable node when $\theta_0 > u^*$. (See Fig. 1(d)).

(iii) *If $A < 0$, $B > 0$ then E^* is locally asymptotically stable when $u^* < \theta_0$. (See Fig. 1(c)).*
If $A > 0$, $B < 0$ then E^* is a unstable focus or node if $\theta_0 < u^* < \theta_1$ and E^* is asymptotically stable if $u^* > \theta_1$.
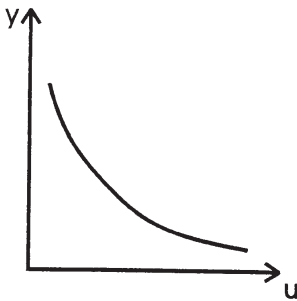*If $A \geq 0$, $B > 0$ then E^* is asymptotically stable. (See Fig. 1(a)).*

Proof. From(2.6) and (2.4), (2.5), the variational matrix of the system (2.1) at E_0 is

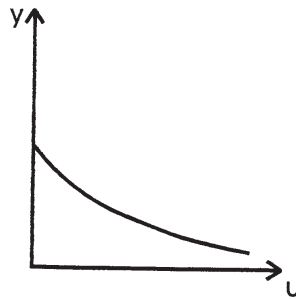$$J(E_0) = \begin{bmatrix} 1 + \delta r - s & 0 \\ 0 & -\delta r \end{bmatrix}.$$

Obviously the first two cases of (i) hold. The last case of (i) can be seen directly from the system (2.1).
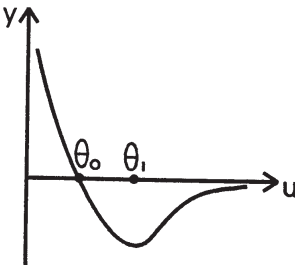
For part(ii), the variational matrix at E_1 is

$$J(E_1) = \begin{bmatrix} \varphi(\theta_0)h'(\theta_0) & -\theta_0^2 \\ 0 & \delta(\theta_0/(\theta_0 + 1) - r) \end{bmatrix}.$$
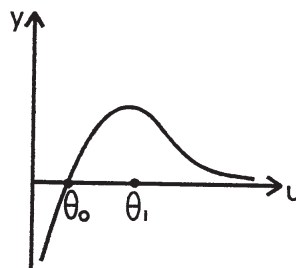

(a) $A \geqslant 0$, $B > 0$

(b) $A > 0$, $B = 0$.

(c) $A < 0$, $B > 0$.

(d) $A > 0$, $B < 0$.

Fig. 1. Scenarios of the shape of $y = h(u)$.

If $A < 0$, $B > 0$ then $h'(\theta_0) < 0$ (See Fig. 1(c)). Similarly if $A > 0$, $B < 0$ then $h'(\theta_0) > 0$ (See Fig 1(d)). Since $\delta(\theta_0/(\theta_0 + 1) - r) < 0$ if and only if $\theta_0 < u^*$, the proof of part(ii) follows.

For part(iii), from (2.6) the variational matrix at E^* is

$$J(E^*) = \begin{bmatrix} \varphi(u^*)h'(u^*) & -(u^*)^2 \\ \delta y^*/(1 + u^*)^2 & 0 \end{bmatrix}. \tag{2.7}$$

Since the determinant of $J(E^*)$ is positive and the trace of $J(E^*)$ is $\varphi(u^*)h'(u^*)$. It is easy to verify that E^* is a unstable focus or node if $h'(u^*) > 0$ and E^* is locally asymptotically stable, if $h'(u^*) < 0$. Then the proof of (iii) follows from the Fig. 1(c), 1(d). □

Remark 2.1. For the case $A > 0$, $B < 0$, if $r \geq 1$ or $\theta_0 < u^*$, then it is easy to verify that the stable manifold Γ of the saddle point E_1 has slope $h'(\theta_0) - (\delta/\theta_0^2)(\theta_0/(\theta_0 + 1) - r)$ which is greater than $h'(\theta_0)$, the slope of $u-$isocline $y = h(u)$ at θ_0. (See Fig. 4(d))

In the following (Lemma 2.3, Theorem 2.1 and Theorem 2.2), we consider the case $r \geq 1$.

Lemma 2.3. If $r \geq 1$ and $s \in (0, 1 + \delta r]$, then $\lim_{t \to \infty} u(t) = +\infty$ and $\lim_{t \to \infty} y(t) = 0$.

Proof. Since $A = 1 + \delta r - \delta > 0$, $B = 1 + \delta r - s \geq 0$ and $r \geq 1$, then from Lemma 2.1(a), the system (2.1) has only one equilibrium E_0. From Lemma 2.2, E_0 is a saddle point and its stable, unstable manifolds are $\{(0, y)| \; y > 0\}$ and $\{(u, 0)| \; u > 0\}$, respectively. (See Fig. 2(a), (b).)

Recall that $\mathbf{R}_+^2 = \{(u, y)| \; u > 0, y > 0\}$, and

$$\Omega_1 = \{(u, y) \in \mathbf{R}_+^2 | \; y \geq h(u)\};$$
$$\Omega_2 = \{(u, y) \in \mathbf{R}_+^2 | \; 0 < y < h(u)\}.$$

Since there is no steady state in Ω_1, the trajectories that start in Ω_1 will enter Ω_2 by crossing the $u-$isocline downward vertically. Since E_0 is a saddle point and there is no other equilibrium in Ω_2, we must have $y(t) \to 0$ and $u(t) \to +\infty$ as $t \to +\infty$. Thus we complete the proof of the lemma. □

In the next Theorem we improve a result of Kuang and Beretta (1998) about the global stability of the equilibrium $(1, 0)$ of the system (1.3). Note that our result provides an affirmative answer to their OPEN QUESTION 1.

Theorem 2.1. If $r > 1$ and $s \in (0, 1 + \delta r]$, then the equilibrium $(1, 0)$ is globally asymptotically stable for system (1.3) in $\mathbf{R}_+^2$.

Proof. For $0 < s \leq 1$, Kuang and Beretta (1998) showed that the equilibrium $(1, 0)$ of the system (1.3) is globally asymptotically stable by a standard phase plane analysis. Now we consider the case $1 < s \leq 1 + \delta r$. Let $(x(t), y(t))$ be the solution of system (1.3) and we divide $\mathbf{R}_+^2$ into two sets:
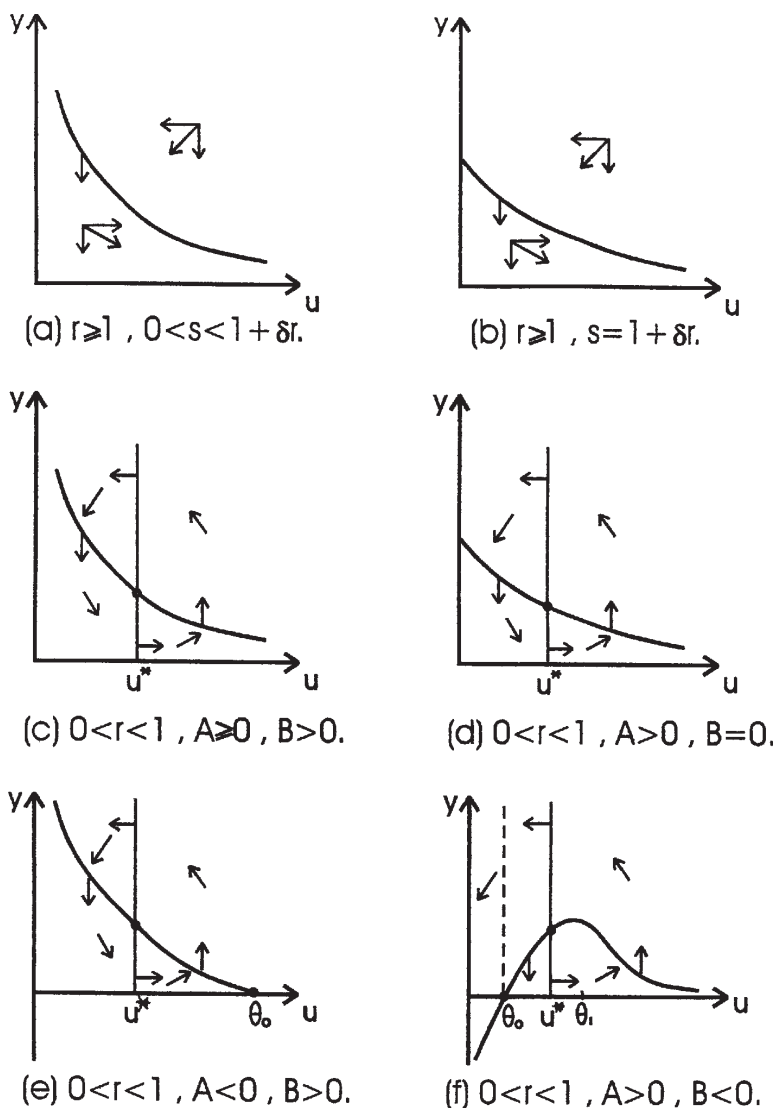
(a) $r \geqslant 1$, $0 < s < 1 + \delta r$.

(b) $r \geqslant 1$, $s = 1 + \delta r$.

(c) $0 < r < 1$, $A \geqslant 0$, $B > 0$.

(d) $0 < r < 1$, $A > 0$, $B = 0$.

(e) $0 < r < 1$, $A < 0$, $B > 0$.

(f) $0 < r < 1$, $A > 0$, $B < 0$.

Fig. 2. The direction field chart for system (2.1) under various conditions.

$$Z_1 = \{(x, y) \in \mathbf{R}_+^2 \mid y > \widehat{h}(x), x > 0\},$$
$$Z_2 = \{(x, y) \in \mathbf{R}_+^2 \mid 0 < y \leq \widehat{h}(x), x \in (0, 1)\}.$$

Here $y = \widehat{h}(x) = x(1 - x)/((s - 1) + x)$ is the prey isocline of the system (1.3). Consider the following two cases.

Case 1. $x(t) > 1$ for all $t \geq 0$. Since $r \geq 1$ and from (1.3), we have $x'(t) < 0$ and $y'(t) < 0$ for $t > 0$. Hence, the limit of $(x(t), y(t))$ exists as $t \to +\infty$. By a standard argument, we conclude that $\lim_{t \to +\infty}(x(t), y(t)) = (1, 0)$.

Case 2. $x(t^*) \leq 1$ for some $t^* \geq 0$. Since the set $\{(x, y) \in \mathbf{R}_+^2 | 0 < x < 1\}$ is positive invariant, we have $x(t) < 1$ for all $t > t^*$. Claim: There exists $T > t^*$ such that $(x(T), y(T)) \in Z_2$. If the claim does not hold, then $(x(t), y(t)) \in Z_1$ for all $t > t^*$. This implies that $x'(t) < 0$ and $y'(t) < 0$ for $t > t^*$ and hence $\lim_{t \to +\infty}(x(t), y(t)) = (0, 0)$. Thus we have(since $y > \widehat{h}(x) = x(1 - x)/((s - 1) + x))$

$$\overline{\lim}_{t \to \infty} \frac{x(t)}{y(t)} \leq \overline{\lim}_{t \to +\infty} \frac{s - 1 + x(t)}{1 - x(t)} = s - 1.$$

On the other hand, $\frac{x(t)}{y(t)} = u(t)$ and from Lemma 2.3 it follows that $\lim_{t \to +\infty} u(t) = +\infty$. This leads to a contradiction and hence we proves the claim.

Since Z_2 is positively invariant, we have $(x(t), y(t)) \in Z_2$ for $t > T$. From (1.3), we have $x'(t) > 0$ and $y'(t) < 0$ for $t > T$. Therefore, $\lim_{t \to +\infty}(x(t), y(t)) = (1, 0)$. Thus, form both cases, we conclude that the equilibrium $(1, 0)$ is globally stable in $\mathbf{R}_+^2$. □

For the case $r > 1$ and $s > 1 + \delta r$, Kuang and Beretta (1998) proved that the system (1.3) is not persistent by showing the existence of a trajectory $(x(t), y(t)) \to (0, 0)$ as $t \to \infty$. In the following we state precisely how the outcomes depend on the initial condition for the system(1.3) or (2.1).

Theorem 2.2. *Let $r \geq 1$ and $s > 1 + \delta r$. For the system (2.1), the stable manifold Γ of E_1 separates $\mathbf{R}_+^2$ into two regions Ω_1 and Ω_2 such that if $(u(0), y(0)) \in \Omega_1$ then $(u(t), y(t)) \to (0, 0)$ as $t \to \infty$ and if $(u(0), y(0)) \in \Omega_2$ then $(u(t), y(t)) \to (\infty, 0)$ as $t \to \infty$. Equivalently for the system (1.3) there exists a separatrix Γ' connecting $(0, 0)$ and two regions Ω_1', Ω_2' such that if $(x(0), y(0)) \in \Omega_1'$ then $(x(t), y(t)) \to (0, 0)$ as $t \to \infty$ and if $(x(0), y(0)) \in \Omega_1'$ then $(x(t), y(t)) \to (1, 0)$ as $t \to \infty$.*

Proof. Since $A > 0$, $B < 0$, from Figure 1(d), Remark 2.1 and phase plane analysis the stable manifold Γ of E_1 lies above the prey isocline $y = h(u)$. Obviously for $(u(0), y(0)) \in \Omega_1$, the region on the left of Γ, we have $(u(t), y(t)) \to (0, 0)$ as $t \to \infty$. For $(u(0), y(0)) \in \Omega_2$, the region on the right of Γ, it follows directly from the proof of Lemma 2.3 that $(u(t), y(t)) \to (\infty, 0)$ as $t \to \infty$. The statements for the system (1.3) follows naturally. □

From now on we discuss the case $0 < r < 1$. First we consider the case $\delta \geq 1/(1 - r)$.

Remark 2.2. It is easy to verify that

(i) $\delta \geq 1/(1 - r)$ if and only if $1/(1 - r) \leq 1 + \delta r$.
(ii) If $B > 0$ and $A < 0$ then $u^* = r/(1 - r) < \theta_0 = B/(-A)$ if and only if $s < 1/(1 - r)$.
(iii) If $B < 0$ and $A > 0$ then $u^* < \theta_0$ if and only if $1/(1 - r) < s$.

Our next theorem provides YES as the answer to the OPEN QUESTION 2 of Kuang and Beretta (1998).

Theorem 2.3. *If $r \in (0, 1)$, $\delta \in [1/(1 - r), \infty)$ and $s \in (0, 1/(1 - r))$ then the positive equilibrium E^* exists and is globally asymptotically stable in $\mathbf{R}_+^2$ for the system (2.1).*

Proof. From Remark 2.2, $r \in (0, 1)$ and $s < 1/(1 - r) \leq \delta$, we have $A = 1 + \delta r - \delta \leq 0$ and $B = 1 + \delta r - s \geq 1/(1 - r) - s > 0$. Now we consider the following two cases.

Case 1. $A = 0$. Lemma 2.1(a) implies that $h(u) > 0 > h'(u)$ for $u > 0$. (See Fig. 2(c).) Hence, $h(u^*) > 0 > h'(u^*)$. This shows that the system (2.1) has a unique positive equilibrium E^* and it is locally asymptotically stable.

Case 2. $A < 0$. Lemma 2.1(b) gives that $h(u)$ and $h'(u)$ has exactly one positive zero θ_0, θ_1 respectively and $\theta_0 < \theta_1$. (See Fig. 2(e).) Since $B > 0$, we have $h(u) > 0 > h'(u)$ for $u \in (0, \theta_0)$. So, $h(u^*) > 0$ if and only if $u^* < \theta_0$ or equivalently $s \in (0, 1/(1 - r))$ by Remark 2.2 . Hence, the system (2.1) has a positive equilibrium E^* and from Lemma 2.2 it is locally asymptotically stable.

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

$$V(u, y) = \int_{u^*}^u \frac{\psi(\xi)}{\varphi(\xi)} d\xi + \int_{y^*}^y \frac{\eta - y^*}{\eta} d\eta$$

for $(u, y) \in \mathbf{R}_+^2$. Notice that $(u - u^*)(h(u) - h(u^*)) \leq 0$, which implies that $\psi(u)(h(u) - h(u^*)) \leq 0$. The derivative of V along the solution of system (2.1) is

$$\begin{aligned}
\dot{V}(u, y) &= (g(u) - \varphi(u)y)\psi(u)/\varphi(u) + \psi(u)y - h(u^*)\psi(u) \\
&= \psi(u)(h(u) - h(u^*)) \leq 0
\end{aligned} \tag{2.8}$$

for $(u, y) \in \mathbf{R}_+^2$. Hence, Theorem 2.3 follows from (2.8) and Lyapunov-LaSalle's invariance principle (Hale (1980)). □

Theorem 2.4. *Let $r \in (0, 1)$, $\delta \in [1/(1 - r), \infty)$.*

 (i) *If $1/(1 - r) \leq s \leq 1 + \delta r$ then the equilibrium $E_1 = (\theta_0, 0)$ of the system (2.1) is globally asymptotically stable.*
 (ii) *If $s > 1 + \delta r$ then the equilibrium $E_0 = (0, 0)$ of the system (2.1) is globally asymptotically stable.*

Proof. From the assumption $s > 1/(1 - r)$ and Remark 2.2 , we have $u^* > \theta_0$. If $1/(1-r) \leq s \leq 1+\delta r$ then $A < 0$ and $B > 0$. The prey isocline $y = h(u)$ satisfies $h'(u) < 0$ for $0 < u < \theta_1, h(u) < 0$ for $u > \theta_0$ and $h(u) > 0$ for $0 < u < \theta_0$. From the phase plane analysis it is easy to verify that $E_1 = (\theta_0, 0)$ is globally asymptotically stable and (i) is proved.

If $s > 1+\delta r$ then $A < 0$ and $B < 0$. Obviously $h(u) < 0$ for all $u > 0, u'(t) < 0$ for all $t > 0$ and $y'(t) < 0$ if and only if $u < u^*$. From phase plane analysis, the equilibrium $E_0 = (0, 0)$ is globally asymptotically stable. □

Remark 2.3. If we return to the original system (1.3), both (i) and (ii) of Theorem 2.4 say that the solution $(x(t), y(t)) \rightarrow (0, 0)$ as $t \rightarrow \infty$. The only difference between

(i) and (ii) is that $x(t)/y(t) \to \theta_0$ as $t \to \infty$ in (i) while $x(t)/y(t) \to 0$ as $t \to \infty$ in (ii).

Next we consider the case $0 < \delta < 1/(1-r)$. From Remark 2.2 , we have $1 + \delta r < 1/(1-r)$. There are three subcases, namely, $0 < s \le 1 + \delta r, 1 + \delta r < s \le 1/(1-r)$ and $s > 1/(1-r)$ to be discussed.

First we consider the case $r \in (0, 1), \delta \in (0, 1/(1-r))$ and $s \in (0, 1 + \delta r]$. Then we have $A = 1 + \delta r - \delta > 0$ and $B = 1 + \delta r - s \ge 0$, and Lemma 2.1(a) implies $h(u) > 0 > h'(u)$ for $u > 0$. Hence the system (2.1) has a unique positive equilibrium E^* and it is locally asymptotically stable. (See Figs.2(c),(d).) Applying the same Lyapunov function in the proof of Theorem 2.3, we have the following theorem which gives positive answer to the OPEN QUESTION 3 of Kuang and Beretta (1998).

Theorem 2.5. *If $r \in (0, 1), \delta \in (0, 1/(1-r))$ and $s \in (0, 1 + \delta r]$ then E^* is globally asymptotically stable in $\mathbf{R}_+^2$ for the system (2.1).*

Now we consider the case $r \in (0, 1), \delta \in (0, 1/(1-r))$ and $s \ge 1/(1-r)$. Then $A > 0$ and $B < 0$ and from Remark 2.2, we have $u^* < \theta_0$. From Lemma 2.2, $E_1 = (\theta_0, 0)$ is an unstable node and $(0, 0)$ is locally asymptotically stable. From the phase plane analysis, it is easy to show that $(0, 0)$ is globally asymptotically stable (See Fig. 1(d)). Hence we have:

Theorem 2.6. *If $r \in (0, 1), \delta \in (0, 1/(1-r))$ and $s \ge 1/(1-r)$ the $E_0 = (0, 0)$ is globally asymptotically stable in $\mathbf{R}_+^2$ for the system (2.1).*

The last case

$$r \in (0, 1), \delta \in (0, 1/(1-r)), 1 + \delta r < s < 1/(1-r) \qquad (2.9)$$

is easily the most interesting and important case in this paper.

For the rest of this section, we assume that (2.9) holds. Since $A = 1 + \delta r - \delta > 0$, $B = 1 + \delta r - s < 0$, from Remark 2.2 (iii) the system (2.1) has three equilibria $E_0 = (0, 0)$, $E_1 = (\theta_0, 0)$ and $E^* = (u^*, h(u^*))$. Moreover from Lemma 2.2, E_0 is locally asymptotically stable, E_1 is a saddle point and E^* is unstable(stable) if $\theta_0 < u^* < \theta_1 (u^* > \theta_1)$. In the following Theorem 2.7 we assert that the system (2.1) has at most one positive limit cycle.

Theorem 2.7. *Let (2.9) hold. Then the system (2.1) has at most one limit cycle in $\mathbf{R}_+^2$. Moreover, if it exists, then it is a stable limit cycle.*

Proof. Let $\Omega^* = (0, \theta_0] \times \mathbf{R}_+$. Then for $(u(0), y(0)) \in \Omega^*$ we have $u'(t) < 0$ and $y'(t) < 0$ for $t \ge 0$ and hence $(u(t), y(t)) \to E_0$ as $t \to \infty$. Thus it suffices to show that system (2.1) has at most one limit cycle in $\mathbf{R}_+^2 \backslash \Omega^*$. According to Hwang (1999), it suffices to show that

$$q(u) = \frac{\varphi(u)h'(u) - \varphi(u^*)h'(u^*)}{\psi(u)} \qquad (2.10)$$

is C^1 and $q'(u) < 0$ for $u > 0$. From (2.4) and a straight forward computation, it follows that

$$q(u) = \frac{\delta - s}{\delta} \frac{((1+r)u + r)}{1 + u} \quad \text{for } u > 0. \tag{2.11}$$

Since $\delta < 1 + \delta r < s$, we have

$$q'(u) = \frac{\delta - s}{\delta} \frac{1}{(1 + u)^2} < 0 \quad \text{for } u > 0. \tag{2.12}$$

Hence the system (2.1) has at most one limit cycle in $\mathbf{R}_+^2 - \Omega^*$ and it is stable when exists.   □

As a result of the above theorem, we see that if E^* is locally asymptotically stable, then there is no positive periodic solution surrounding it. This is precisely the main statement of Theorem 3.1 in Kuang and Beretta (1998).

In the following Lemma 2.4 we classify the behavior of the stable manifold Γ of the equilibrium E_1.

Lemma 2.4. *Let (2.9) hold and Γ be the stable manifold of E_1. Then*

  (i) *If Γ intersects the prey isocline $y = h(u)$, then Γ connects E_1 and E^*.*
 (ii) *If Γ does not intersects the prey isocline $y = h(u)$ then $\Gamma = \{(u(t), y(t))\}_{t=-\infty}^{+\infty}$ satisfies $\lim_{t \to -\infty} u(t) = \infty$ and $\lim_{t \to -\infty} y(t) = 0$. Moreover either $\Gamma' = \gamma$ or Γ' lies above γ where $\Gamma' = \{(x, y) : x = yu, (u, y) \in \Gamma\}$ and γ is the unstable manifold of the equilibrium $(1, 0)$ for the system (1.3), connecting $(1, 0)$ to $(0, 0)$ or (x^*, y^*) in xy-plane.*

Proof. From Remark 2.1, the stable manifold Γ of E_1 lies above the prey isocline $y = h(u)$ when $u > \theta_0$ and u is near θ_0. From the phase plane analysis, Γ is above the prey isocline $y = h(u)$ until Γ meets the predator isocline $u = u^*$ at $t = t^*$. If Γ intersects the prey isocline $y = h(u)$ at point P_2, then Γ will meet $u = u^*$ at P_3, P_5 and meet $y = h(u)$ at P_4 (See Fig. 3). Consider the region $\widetilde{\Omega}$ bounded by the arc $P_1 P_2 P_3 P_4 P_5$ and segment $\overline{P_5 P_1}$. $\widetilde{\Omega}$ is negatively invariant. The α-limit set $\alpha(P_5)$ is contained in $\widetilde{\Omega}$. Claim that $\alpha(P_5) = \{E^*\}$. If not, then $\alpha(P_5)$ is a periodic orbit. However from Theorem 2.7, $\alpha(P_5)$ is a unique stable limit cycle for the system (2.1). This is a contradiction since $\alpha(P_5)$ is unstable from outside. Thus we prove the claim and Γ connects E_1 and E^*.

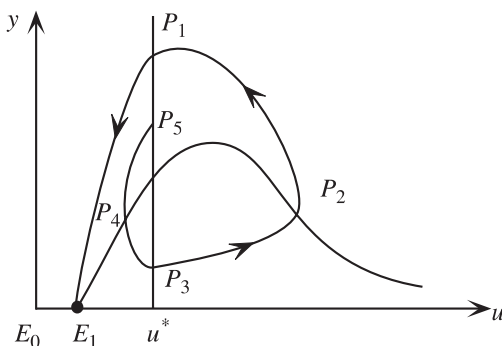If Γ does not intersect the prey isocline $y = h(u)$ then Γ is above $y = h(u)$. Let $\tau = -t$, then

$$\begin{aligned} u'(\tau) &= -(u(\tau))^2 [h(u(\tau)) - y(\tau)] \\ y'(\tau) &= -\delta y(\tau)(u(\tau)/(u(\tau) + 1) - r). \end{aligned} \tag{2.13}$$

Then $u'(\tau) > 0$ and $y'(\tau) < 0$ for $\tau > t^*$. Obviously $\lim_{\tau \to \infty} u(\tau) = \infty$. Hence there is a $t_1 > t^*$, such that $u(t_1) = 2u^*$. Let

$$a = 2u^*/(2u^* + 1) - r.$$

Then $a > 0$. For $t > t_1$, we have

$$y'(\tau) = -\delta y(\tau)(u(\tau)/(u(\tau) + 1) - r) < -a\delta y(\tau).$$

Fig. 3. Illustration for the proof of Lemma 2.4.

This shows that $\lim_{\tau\to\infty} y(\tau) = 0$.

Since Γ is above $y = h(u)$, we have

$$y(\tau) > \frac{Au(\tau) + B}{u(\tau)\,(1 + u(\tau))} = h(u(\tau)).$$

From $\lim_{\tau\to\infty} u(\tau) = \infty$ and $0 < \delta < 1/(1-r)$, it follows that $\lim_{\tau\to\infty} \inf x(\tau) \geq A, 0 < A < 1$. Γ' connects $(0, 0)$ because Γ connects $(\theta_0, 0)$. If $\Gamma' \neq \gamma$ then $\lim_{\tau\to\infty} x(\tau) = \infty$ and obviously γ lies below Γ' and γ connects $(0, 0)$ to $(1, 0)$ or (x^*, y^*) in xy−plane. $\qquad\square$

Our next theorem deals with the case when E^* is stable.

Theorem 2.8. *Let (2.9) hold and $u^* > \theta_1$. Then the following are true.*

(i) *The stable manifold Γ of E_1 lies above the prey isocline $y = h(u)$ and separates $\mathbf{R}_+^2$ into two regions Ω_1 (lying above Γ) and Ω_2 (lying below Γ).*

(ii) *If $(u(0), y(0)) \in \Omega_1$, then $\lim_{t\to\infty}(u(t), y(t)) = (0, 0)$. If $(u(0), y(0)) \in \Omega_2$, then we have $\lim_{t\to\infty}(u(t), y(t)) = E^*$.*

Proof. If Γ intersects the prey isocline $y = h(u)$ then from Lemma 2.4 (i), Γ connects E_1 and E^*. However E^* is locally asymptotically stable for $u^* > \theta_1$. This leads to a contradiction. Hence Γ lies above $y = h(u)$. Obviously for $(u(0), y(0)) \in \Omega_1$ $\lim_{t\to\infty}(u(t), y(t)) = (0, 0)$. To prove that $(u(0), y(0)) \in \Omega_2$ implies $\lim_{t\to\infty}(u(t), y(t)) = E^*$, we shall use Theorem 2.7. Since E^* is locally asymptotically stable, we see that there is no nontrivial positive periodic solution surrounding it(from Theorem 2.7). Since all solutions are either forward or backward bounded, a simple application of the Poincaré-Bendixson theorem yields our conclusion. $\qquad\square$

Our last theorem in this section deals with the case when E^* is unstable.

Theorem 2.9. *Let (2.9) hold and $\theta_0 < u^* < \theta_1$. Then the following are true.*

(i) *The stable manifold Γ of E_1 intersects the prey isocline $y = h(u)$. In this case, the equilibria E^* and E_1 will be connected by Γ at two ends. Each point except those on Γ is attracted to the equilibrium $E_0 = (0, 0)$. (See Fig. 4(a))*

(ii) *The stable manifold Γ lies above $y = h(u)$ separating $\mathbf{R}_+^2$ into two regions Ω_1(above Γ) and Ω_2(below Γ). If $(u(0), y(0)) \in \Omega_1$ then $\lim_{t \to \infty}(u(t), y(t)) = (0, 0)$. If $(u(0), y(0)) \in \Omega_2$ or equivalently $(x(0), y(0)) \in \Omega_2'$(where $\Omega_2' = \{(x, y) : x = yu, (u, y) \in \Omega_2\}$), then there are two possible cases:*

   (a) *The ω-limit set $\omega(x(0), y(0)) = \gamma \bigcup \{(x, y) : y = 0, 0 \le x \le 1\}$. (See Fig. 4(c))*

   (b) *$(x(t), y(t))$ approaches a unique limit cycle as $t \to \infty$. (See Fig. 4(e))*

Proof. If Γ intersects the prey isocline $y = h(u)$ then from Lemma 2.4 (i), E^* and E_1 will be connected by Γ as two ends. For any $(u(0), y(0)) \in \mathbf{R}_+^2 \backslash \Gamma$, it is easy to show by phase plane analysis that $(u(t), y(t)) \in \Omega^* = (0, \theta_0] \times \mathbf{R}_+$ for t sufficiently large. Thus $\lim_{t \to \infty}(u(t), y(t)) = E_0$.

If Γ does not intersect the prey isocline $y = h(u)$, then Γ lies above $y = h(u)$. Obviously if $(u(0), y(0)) \in \Omega_1$ then $\lim_{t \to \infty}(u(t), y(t)) = E_0$. From Lemma 2.4 (ii) $\Gamma' = \gamma$ or Γ' lies above γ. Since $\hat{E}^* = (x^*, y^*)$ is a unstable focus or node, the unstable manifold γ obviously connects to $(0, 0)$. In this case, we must have $\Gamma' = \gamma$. Otherwise, for $(x(0), y(0))$ in Ω_2' lying between Γ' and γ, $\lim_{t \to \infty}(x(t), y(t)) = (0, 0)$. This indicates that the solutions of system (2.1) with initial data $(x(0)/y(0), y(0))$ will tend to E_1. (can not tend to the origin since it is below the stable manifold Γ.) This implies that the stable manifold Γ has more than one trajectories. However, since system (2.1) is continuously differentiable in the neighborhood of E_1, we must have a unique trajectory in Γ.(Theorem 3.6.1 in Hale (1980)) This is a contradiction.

For $(x(0), y(0))$ lying in the region bounded by γ and $\{(x, y) : y = 0, 0 \le x \le 1\}$, there are two possible cases. If the w-limit set $\omega(x(0), y(0))$ contains an equilibrium, then from Butler-McGehee Lemma (Smith and Waltman (1995), p12), $\omega(x(0), y(0)) = \gamma \bigcup \{(x, y) : y = 0, 0 \le x \le 1\}$, i.e. (ii)(a) holds. If $\omega(x(0), y(0))$ contains no equilibrium, then from Poincaré-Bendixson Theorem, Theorem 2.7 and that fact that $\hat{E}^*$ is unstable, the trajectory $(x(t), y(t))$ approaches a unique limit cycle.   □

While the case (ii)(a) seems to be unlikely, it can not be ruled out by standard phase plane analysis or from our extensive numerical simulations.

3. Discussion

In this paper we provide a complete classification of the asymptotic behavior of the solutions of ratio-dependent predator-prey model (1.2). *As a result, we solved all the three open questions listed in Kuang and Beretta (1998)* (Theorems 2.1, 2.3, 2.5 provide positive answer to OPEN QUESTIONS 1, 2, 3, respectively). **The only issue left open is how to determine the relative location of the stable manifold Γ of equilibrium E_1 of system (2.1).**

Comparing with the classical prey-dependent predator-prey model (1.1), the ratio-dependent models (1.2) are capable of producing richer and more reasonable dynamics and the paradox of biological control is no longer valid. In the classical model (1.1), the following results are well known: (Kuang and Freedman (1988))

(i) If $(K - m)/2 \le x^*$ then $\lim_{t\to\infty}(x(t), y(t)) = E^* = (x^*, y^*)$ where $x^* = m/((f/d) - 1) > 0$, $y^* > 0$.

(ii) If $(K - m)/2 > x^*$ then the solution $(x(t), y(t))$ approaches a unique limit cycle as $t \to \infty$.

We observe that in the model (1.1), the carrying capacity K plays the key role in determining the asymptotic behavior of solutions of (1.1). However, for the ratio-dependent model (1.2), the asymptotic behavior of the solutions of (1.2) is independent of the carrying capacity K. On the other hand, the capturing rate c is independent of the behavior of the solution of model (1.1) while c plays an important role in the model (1.2). We will elaborate this below.

In the following, we shall discuss the many biological implications of our results (Theorem 2.1–2.9). To facilitate this, recall that $s = c/ma$, $\delta = f/a$, $r = d/f$.

First we consider the case $r \ge 1$, i.e. the predator death rate d is larger or equal to its maximal growth rate f, then from Theorem 2.1 and Theorem 2.2 the predator will go to extinction. Since $s > 1 + \delta r$ if only if $c/m > (a+d)$. Theorem 2.1 says if c/m, the ratio of capturing rate c to the half saturation constant m, is small then the prey survives and goes to its carrying capacity K. However if c/m is large, for fixed predator initial population $y(0)$, if the ratio $x(0)/y(0)$ is small then both prey and predator go to extinction while if $x(0)/y(0)$ is large then prey survives to its carrying capacity.

Next, we consider the case $0 < r < 1$, i.e. the predator death rate d is less than its maximal growth rate f. Since $\delta \ge 1/(1 - r)$ if and only if $f \ge d + a$ and $0 < s < 1/(1 - r)$ if and only if $0 < c/m < a/(1 - d/f)$, Theorem 2.3 says if $f \ge d + a$, i.e., the maximal growth rate f is large or the prey intrinsic growth rate a is small, then the prey and predator coexist in the form of equilibrium provided c/m is small. Under the same conditions of Theorem 2.3, Theorem 2.4 says that if c/m is large, then both predator and prey go to extinction.

If the prey intrinsic growth rate $a > f - d$, then predator and prey coexist in the form of equilibrium if c/m is small. Since $s > 1/(1 - r)$ if and only if $c/m > a/(1 - (d/f))$, Theorem 2.6 states that if $a > f - d$, then both predator and prey go to extinction provided c/m is large. When $a + d < c/m < a/(1 - (d/f))$, Theorem 2.7 says that if the ratio at equilibrium $(u^* = x^*/y^*)$ is large, i.e., $u^* \ge \theta_1$, and if $x(0)/y(0)$ is small then both predator and prey go to extinction while if $x(0)/y(0)$ is large then predator and prey coexist in the form of equilibrium.

Under the same condition of Theorem 2.7, i.e. $a + d < c/m < a/(1 - (d/f))$, Theorem 2.8 says if $\theta_0 < u^* < \theta_1$, there are three possible cases. (i): There is an orbit Γ connecting $E_1 = (\theta_1, 0)$ and $E^* = (u^*, y^*)$ for the system (2.1) such that for any $(u(0), y(0)) \notin \Gamma$ $\lim_{t\to\infty}(u(t), y(t)) = (0, 0)$ (See Fig. 4(b)). Equivalently for system (1.2), there is an orbit Γ' connecting $(0, 0)$ and (x^*, y^*) such that for all $(x(0), y(0)) \notin \Gamma'$, $\lim_{t\to\infty}(x(t), y(t)) = (0, 0)$. In this case, except $(x(0), y(0)) = (x^*, y^*)$ both predator and prey go to extinction (See Fig. 4(a)). (ii): The stable manifold Γ of $E_1 = (\theta_1, 0)$ does not intersect the prey isocline $y = h(u)$. For $(u(0), y(0))$ above Γ, $\lim_{t\to\infty}(u(t), y(t)) = (0, 0)$ while for $(u(0), y(0)) \ne E^*$ below Γ, the ω-limit set of $(u(0), y(0))$ equals to $\Gamma \bigcup \{(u, y): y = 0, u \ge \theta_1\}$, i.e., the solution $(u(t), y(t))$ exhibit aperiodic oscillation. (See

Fig. 4(d)). Equivalently for system (1.2), the unstable manifold γ of the equilibrium $(1, 0)$ is connected to the origin $(0, 0)$. For $(x(0), y(0))$ above γ, both predator and prey go to extinction, while for $(x(0), y(0))$ below γ, $(x(0), y(0)) \neq (x^*, y^*)$, the ω-limit set of $(x(0), y(0))$ equals to $\gamma \bigcup \{(x, y) : 0 \leq x \leq K, y = 0\}$ i.e., the predator and prey population oscillate aperiodically (See Fig. 4(c)). (iii): This case is similar to case (ii). The only difference is that for $(u(0), y(0)) \neq E^*$ below Γ (or $(x(0), y(0)) \neq (x^*, y^*)$ below γ for system (1.2)) the solution $(u(t), y(t))$ approaches a unique limit cycle. Thus the predator and prey population exhibit periodic oscillation (See Fig. 4(e) and Fig. 4(f)).

In Abrams and Ginzburg (2000), the authors claimed that there is the possibility that mutual(deterministic) extinction of both prey and predator may result from functional responses that are not ratio-dependent, but there is a time lag in the predator's numeric response to food intake. While delay plays a natural role in the predator-prey dynamics (Harrison(1995), Jost and Arditi (2000), Jost and Ellner
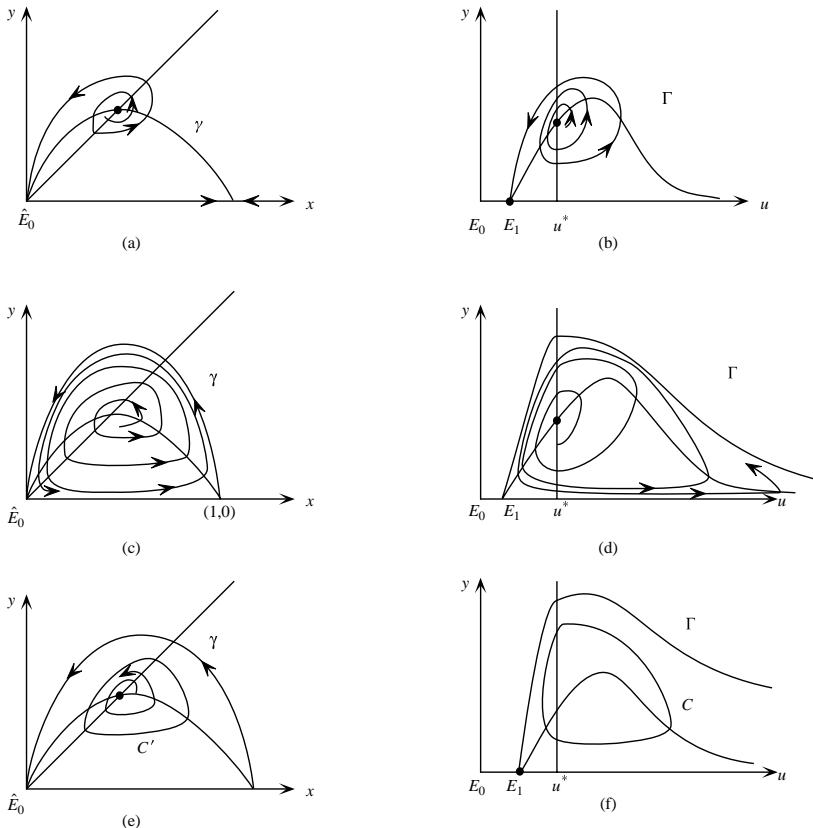
Fig. 4. (a) and (b) illustrate the case when origin is the global attractor. (c) and (d) illustrate the case when a heteroclinic cycle is the global attractor. (e) and (f) illustrate the case when a limit cycle is the global attractor.

(2000)), we would like to point out that delay alone does not cause mutual extinction. In fact, on the contrary, the delayed numeric response can often moderate the mutual extinction dynamics, due to the fact that in a declining population, the delayed numeric response which in positive correlation to past more robust population density can bring in larger recruitment to the predator population than that can be brought in by the current smaller population. Near the origin, where both species face the possibility of extinction, the predation in the prey-dependent form can be approximated by a linear form of the product of prey and predator densities, which is no match to the strong recruitment of prey from specific growth. In other words, time delay alone will not cause, nor prevent the mutual extinction of both species in both prey-dependent and ratio-dependent cases (as well as for the general predator-dependent cases)(Kuang(1993), Beretta and Kuang (1998)).

Deterministic extinction of both species is an extreme outcome of the predator-prey interaction, but seems to become ever more frequent and worrisome. The public believes this resulted from the fragmentation of habitats and the ever shrinking sizes of these patches which may diminish or deprive of prey refugees (Fischer (2000)). The consensus view is that ratio dependent formulation breaks down when the patch size is large and both the prey and predator densities are low (Arditi and Ginzburg (1989), Cosner et al. (1999), Abrams and Ginzburg (2000)), since in such case, predators will spend most effort in searching rather than interfering each other. Hence, the functional response is likely to be much more sensible to prey density than predator density. However, if the habitat is small and free of refugees for prey, then ratio dependence formulation may remain valid even when densities are low, since predators can remain effectively interfering each other. In such case, ratio-dependence suggests that mutual extinction is possible. This provides an explanation for Gause's classic observation of mutual extinction in the protozoans, *Paramecium* and its predator *Didinium* (Abrams and Ginzburg (2000)). In short, deterministic mutual extinction is an extreme outcome calls for extreme measures. Ratio dependence, while a special case of the general predator dependence ones, such as the Beddington-DeAngelis or Hassel-Varley type (Cosner et al. (1999)), is currently the only one that provides a simple and plausible explanation of such extinction dynamics.

References

Abrams, P.A., Ginzburg, L.R.: The nature of predation: prey dependent, ratio-dependent or neither? Trends in Ecology and Evolution, **15**, 337–341 (2000)

Akcakaya, H.R., Arditi, R., Ginzburg, L.R.: Ratio-dependent prediction: an abstraction that works, Ecology, **76**, 995–1004 (1995)

Arditi, R., Berryman, A.A.: The biological paradox, Trends in Ecology and Evolution, **6**, 32 (1991)

Arditi, R., Ginzburg, L.R.: Coupling in predator-prey dynamics: ratio-dependence, J. Theor. Biol., **139**, 311–326 (1989)

Arditi, R., Ginzburg, L.R., Akcakaya, H.R.: Variation in plankton densities among lakes: a case for ratio-dependent models, American Natrualist, **138**, 1287–1296 (1991)

Berryman, A.A.: The origins and evolution of predator-prey theory, Ecology, **73**, 1530–1535 (1992)

Berryman, A.A., Gutierrez, A.P., Arditi, R.: Credible, realistic and useful predator-prey models, Ecology, **76**, 1980–1985 (1995)

Cosner, C., DeAngelis, D.L., Ault, J.S., Olson, D.B.: Effects of spatial grouping on the functional response of predators, Theor. Pop. Biol., **56**, 65–75 (1999)

Fischer, M.: Species loss after habitat fragmentation, Trends in Ecology and Evolution, **15**, 396 (2000)

Freedman, H.I.: Deterministic Mathematical Models in Population Ecology, Marcel Dekker, New York (1980)

Gause, G.F.: The struggle for existence, Williams & Wilkins, Baltimore, Maryland, USA (1934)

Hairston, N.G., Smith, F.E., Slobodkin, L.B.: Community structure, population control and competition, American Naturalist, **94**, 421–425 (1960)

Hale, J.: Ordinary Differential Equations, Krieger Publ. Co., Malabar (1980)

Harrison, G.W.: Comparing predator-prey models to Luckinbill's experiment with Didinium and Paramecium, Ecology, **76**, 357–374 (1995)

Hsu, S.-B., Hwang, T.-W.: Global stability for a class of predator-prey systems, SIAM J. Appl. Math., **55**, 763–783 (1995)

Hwang, T.-W.: Uniqueness of limit cycle for Gause-type predator-prey systems, J. Math. Anal. Appl., **238**, 179–195 (1999)

Jost, C., Arditi, R.: Identifying predator-prey process from time-series, Theor. Pop. Biol., **57**, 325–337 (2000)

Jost, C., Ellner, S.P.: Testing for predator dependence in predator-prey dynamics: a non-parametric approach, Proc. Roy. Soc. Lond. B., **267**, 1611–1620 (2000)

Jost, C., Arino, O., Arditi, R.: About deterministic extinction in ratio-dependent predator-prey models, Bull. Math. Biol., **61**, 19–32 (1999)

Kuang, Y.: Delay Differential Equations with Applications in Population Dynamics. Mathematics in Science and Engineering, 191. Academic Press, Inc., Boston, MA, 1993 (1993)

Kuang, Y.: Rich dynamics of Gause-type ratio-dependent predator-prey system, The Fields Institute Communications, **21**, 325–337 (1999)

Kuang, Y., Beretta, E.: Global qualitative analysis of a ratio-dependent predator-prey system, J. Math. Biol., **36**, 389–406 (1998)

Kuang, Y., Freedman, H.I.: Uniqueness of limit cycles in Gause-type predator-prey ststems, Math. Biosci., **88**, 67–84 (1988)

Luck, R.F.: Evaluation of natural enemies for biological control: a behavior approach, Trends in Ecology and Evolution, **5**, 196–199 (1990)

May, R.M.: Stability and Complexity in Model Ecosystems, Princeton Univ. Press (1974)

Rosenzweig, M.L.: Paradox of enrichment: destabilization of exploitation systems in ecological time, Science, **171**, 385–387 (1969)

Smith, H., Waltman, P.: The Theory of the Chemostat, Cambridge University Press (1995)