HARMLESS DELAYS IN A DISCRETE RATIO-DEPENDENT PERIODIC PREDATOR-PREY SYSTEM

YONG-HONG FAN AND WAN-TONG LI

Verifiable criteria are established for the existence of positive periodic solutions and permanence of a delayed discrete periodic predator-prey model with Holling-type II functional response $N_1(k+1) = N_1(k)\exp\{b_1(k) - a_1(k)N_1(k - [\tau_1]) - \alpha_1(k)N_2(k)/(N_1(k) + m(k)N_2(k))\}$ and $N_2(k+1) = N_2(k)\exp\{-b_2(k) + \alpha_2(k)N_1(k - [\tau_2])/(N_1(k - [\tau_2]) + m(k)N_2(k - [\tau_2]))\}$. Our results show that the delays in the system are harmless for the existence of positive periodic solutions and permanence of the system. In particular our investigation confirms that if the death rate of the predator is rather small as well as the intrinsic growth rate of the prey is relatively large, then the species could coexist in the long run.

1. Introduction

In mathematical biology, the dynamics of the growth of a population can be described if the functional behavior of the rate of growth is known. It is this functional behavior which is usually measured in the laboratory or in the field. Among the relationships between the species living in the same outer environment, the predator-prey theory plays an important and fundamental role. The dynamic relationship between predators and their preys has long been and will continue to be one of the dominant themes in both ecology and mathematical ecology due to its universal existence and importance (Berryman [4]). These problems may appear to be simple mathematically at first sight, they are in fact very challenging and complicated. There are many different kinds of predator-prey models in the literature; for more details we can refer to [4, 7]. In general, a predator-prey system takes the form

$$x' = rx\left(1 - \frac{x}{K}\right) - \varphi(x)y,$$
$$y' = y(\mu\varphi(x) - D), \tag{1.1}$$

where $\varphi(x)$ is the functional response function, which reflects the capture ability of the predator to prey. For more biological meaning, the reader may consult [7, 19]. Massive work has been done on this issue. We refer to the monographs [8, 16, 21, 24] for general delayed biological systems and to [18, 22, 23, 25, 26, 28, 29] for investigations on predator-prey systems.

Until very recently, both ecologists and mathematicians chose to base their studies on this traditional prey-dependent functional response predator-prey system which is called prey-dependent model [12]. But there is a growing explicit biological and physiological evidence [3, 11, 14, 17] 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 ratio-dependent functional response. This is strongly supported by numerous field and laboratory experiments and observations [2, 9]. A general form of a ratio-dependent model is

$$
\begin{aligned}
x' &= rx\left(1 - \frac{x}{K}\right) - \varphi\left(\frac{x}{y}\right)y, \\
y' &= y\left(\mu\varphi\left(\frac{x}{y}\right) - D\right).
\end{aligned}
$$

(1.2)

Here the predator-prey interactions are described by $\varphi(x/y)$ instead of $\varphi(x)$ in (1.1). This can be interpreted as when the numbers of predators change slowly (relative to the change of their prey), there is often competition among the predators, and the per capita rate of predation depends on the numbers of both prey and predator, most likely and simply on their ratio. For the system (1.2) with periodic coefficients, in [5] we explored the existence of periodic solutions with delays. In addition, most research works concentrate on the so-called Michaelis-Menten-type ratio-dependent predator-prey model:

$$
\begin{aligned}
x' &= rx\left(1 - \frac{x}{K}\right) - \frac{\alpha x y}{my + x}, \\
y' &= y\left(-d + \frac{fx}{my + x}\right);
\end{aligned}
$$

(1.3)

see [3, 11, 14, 17, 27] and references therein. The functional response function $\varphi(u) = cu/(m + u)$, $u = x/y$, in the above model was used by Holling [10] as Holling-type II functional response, it usually describes the uptake of substrate by the microorganisms in microbial dynamics or chemical kinetics [7].

On the other hand, though most predator-prey theories are based on continuous models governed by differential equations, the discrete time models are more appropriate than the continuous ones when the size of the population is rarely small or the population has nonoverlapping generations [1, 21]. And in ecosystems, an important theme that interested mathematicians as well as biologists is whether the species in these systems would survive in the long run. That is, whether the ecosystems are permanent. As far as we know,

few investigations have been carried out for the permanence on delayed discrete ecological systems since the dynamics of these systems are usually more complicated than the continuous ones. Just as pointed out in [8], even if the coefficients are constants, the asymptotic behavior of the discrete system is rather complex and "chaotic" than the continuous one. For example, consider the logistic equation

$$x'(t) = rx(t)\left[1 - \frac{x(t)}{K}\right], \quad t \geq 0, \tag{1.4}$$

where r and K are both positive constants, and its corresponding discrete equation

$$x(n+1) = x(n)\exp\left\{r\left[1 - \frac{x(n)}{K}\right]\right\}, \quad n = 0, 1, 2, \dots. \tag{1.5}$$

It is known from the works of May [20] that for certain parameter values of r, the asymptotic behavior of the solutions of (1.5) is complex and "chaotic." While the solutions of (1.4) are normal.

Now we introduce some notations and definitions for the sake of convenience. Denote $\mathbb{Z}$, $\mathbb{R}$, and $\mathbb{R}^+$ as the sets of all integers, real numbers, and nonnegative real numbers, respectively. Let C denote the set of all bounded sequence $f : \mathbb{Z} \to \mathbb{R}$, C_+ the set of all $f \in C$ such that $f > 0$, and $C_\omega = \{f \in C_+ \mid f(k+\omega) = f(k), k \in \mathbb{Z}\}$, $I_\omega = \{0, 1, \dots, \omega - 1\}$. We also define

$$f^M = \sup_{k \in I_\omega} f(k), \qquad f^L = \inf_{k \in I_\omega} f(k), \qquad \overline{f} = \frac{1}{\omega}\sum_{k=0}^{\omega-1} f(k) \tag{1.6}$$

for any ω-periodic sequence $\{f(k)\}$, where $k \in \mathbb{Z}$.

In view of periodicity of the actual environment, we begin with the periodic continuous ratio-dependent predator-prey system with Holling-type II functional response:

$$\frac{dN_1(t)}{dt} = N_1(t)\left[b_1(t) - a_1(t)N_1(t - \tau_1)\right] - \frac{\alpha_1(t)N_1(t)N_2(t)}{N_1(t) + m(t)N_2(t)},$$

$$\frac{dN_2(t)}{dt} = N_2(t)\left[-b_2(t) + \frac{\alpha_2(t)N_1(t - \tau_2)}{N_1(t - \tau_2) + m(t)N_2(t - \tau_2)}\right], \tag{1.7}$$

where $N_1(t)$ and $N_2(t)$ represent the densities of the prey population and predator population at time t, respectively; $\tau_1 \geq 0$ and $\tau_2 \geq 0$ are real constants; $b_i : \mathbb{R} \to \mathbb{R}$ and $m, a_1, \alpha_i : \mathbb{R} \to \mathbb{R}^+$ $(i = 1, 2)$ are continuous periodic functions with period $\omega > 0$ and $\int_0^\omega b_i(t)dt > 0$ $(i = 1, 2)$; $b_1(t)$ stands for prey intrinsic growth rate, $b_2(t)$ stands for the death rate of the predator, $\alpha_1(t)$ and $\alpha_2(t)$ stand for the conversion rates, $m(t)$ stands for half capturing saturation; the function $N_1(t)[b_1(t) - a_1(t)N_1(t - \tau_1)]$ represents the specific growth rate of the prey in the absence of predator; and $N_1(t)/(N_1(t) + m(t)N_2(t))$ denotes the ratio-dependent response function, which reflects the capture ability of the predator. Similar

to the arguments of [6], we can obtain a discrete time analogue of (1.7):

$$N_1(k+1) = N_1(k)\exp\left\{b_1(k) - a_1(k)N_1(k - [\tau_1]) - \frac{\alpha_1(k)N_2(k)}{N_1(k) + m(k)N_2(k)}\right\},$$

$$N_2(k+1) = N_2(k)\exp\left\{-b_2(k) + \frac{\alpha_2(k)N_1(k - [\tau_2])}{N_1(k - [\tau_2]) + m(k)N_2(k - [\tau_2])}\right\},$$

(1.8)

where $[t]$ denotes the integer part of $t > 0$.

The exponential form of (1.8) assures that, for any initial condition $N(0) > 0$, $N(k)$ remains positive. In the remainder of this paper, for biological reasons, we only consider solutions $N(k)$ with

$$N_i(-k) \geq 0, \quad k = 1, 2, \ldots, \max\{[\tau_1], [\tau_2]\}; \qquad N_i(0) > 0, \quad i = 1, 2. \qquad (1.9)$$

If $[\tau_1] = [\tau_2] = 0$, then system (1.8) reduces to

$$N_1(k+1) = N_1(k)\exp\left\{b_1(k) - a_1(k)N_1(k) - \frac{\alpha_1(k)N_2(k)}{N_1(k) + m(k)N_2(k)}\right\},$$

$$N_2(k+1) = N_2(k)\exp\left\{-b_2(k) + \frac{\alpha_2(k)N_1(k)}{N_1(k) + m(k)N_2(k)}\right\}.$$

(1.10)

Recently, Fan and Wang [6] considered the existence of positive periodic solution for system (1.10) and obtained the following.

THEOREM 1.1. *Assume that the following conditions hold:*
  (H1) $\overline{b}_1 > \overline{(\alpha_1/m)}$,
  (H2) $\overline{\alpha}_2 > \overline{b}_2$.

Then (1.10) has at least one positive ω-periodic solution.

Huo and Li [13] further considered the permanent of system (1.10) and established the following result.

THEOREM 1.2. *Assume that*

$$b_1^L > \frac{\alpha_1^M}{m^L}, \qquad \alpha_2^L > b_2^M. \qquad (1.11)$$

Then system (1.10) is permanent.

In this paper, our aim is to consider the effect of delays for the existence of positive periodic solutions and permanence of system (1.8). Our results show that delays in (1.8) are harmless for the existence of positive periodic solutions and permanence of (1.8). That is to say, we establish the following results.

THEOREM 1.3. *Assume that (H1) and (H2) hold. Then (1.8) has at least one positive ω-periodic solution.*

Since its proof is similar to that of [6], we omit it here.

THEOREM 1.4. *Assume that (H1) and (H2) hold. Then system (1.8) is permanent.*

Clearly, Theorem 1.3 extends Theorem 1.1; Theorem 1.4 extends and improves Theorem 1.2 by weaker conditions (H1) and (H2) instead of (1.11). In particular our investigation confirms that if the death rate of the predator is rather small as well as the intrinsic growth rate of the prey is relatively large, then the species could coexist in the long run.

2. Proof of Theorem 1.4

In this section, we prove Theorem 1.4. Before proving our main result, we list the definition of permanence and prove a lemma.

Definition 2.1. System (1.8) is said to be *permanent* if there exists two positive constants λ_1 and λ_2 such that

$$\lambda_1 \leq \liminf_{k \to \infty} N_i(k) \leq \limsup_{k \to \infty} N_i(k) \leq \lambda_2, \quad i = 1, 2, \tag{2.1}$$

for any solution $(N_1(k), N_2(k))$ of (1.8).

The following lemma will be useful to establish the main result.

LEMMA 2.2. *The problem*

$$x(k+1) = x(k) \exp\{a(k) - b(k)x(k)\},$$
$$x(0) = x_0 > 0, \tag{2.2}$$

has at least one periodic solution U if $b \in C_\omega$, $a \in C$, and a is an ω-periodic sequence with $\bar{a} > 0$; moreover, the following properties hold:
  (a) *U is positive ω-periodic;*
  (b) *U has the following estimations for its boundary:*

$$\frac{\bar{a}}{b} \exp\{-(\overline{|a|} + \bar{a})\omega\} \leq U(k) \leq \frac{\bar{a}}{b} \exp\{(\overline{|a|} + \bar{a})\omega\}, \tag{2.3}$$

  especially,

$$\frac{\bar{a}}{b} \exp\{-\bar{a}\omega\} \leq U(k) \leq \frac{\bar{a}}{b} \exp\{\bar{a}\omega\}, \tag{2.4}$$

  if $a \in C_\omega$.

Proof. First, we prove (a). Notice that in (1.8), let $\alpha_1(k) \equiv 0$, $\tau_1 = 0$, then (1.8) can be reduced to

$$N_1(k+1) = N_1(k) \exp\{b_1(k) - a_1(k)N_1(k)\},$$

$$N_2(k+1) = N_2(k) \exp\left\{-b_2(k) + \frac{\alpha_2(k)N_1(k - [\tau_2])}{N_1(k - [\tau_2]) + m(k)N_2(k - [\tau_2])}\right\}, \tag{2.5}$$

and the condition (H1) of Theorem 1.1 reduces to $\overline{b}_1 > 0$. By Theorem 1.3, (2.5) has at least one positive ω-periodic solution provided that $\overline{b}_1 > 0$ and $\overline{\alpha}_2 > \overline{b}_2$. This implies that

$$N_1(k+1) = N_1(k) \exp \{b_1(k) - a_1(k)N_1(k)\} \tag{2.6}$$

has at least one positive ω-periodic solution under the assumptions $\overline{b}_1 > 0$. That is to say,

$$x(k+1) = x(k) \exp \{a(k) - b(k)x(k)\},$$
$$x(0) = x_0 > 0, \tag{2.7}$$

has at least one positive ω-periodic solution provided that $\overline{a} > 0$. The proof of (a) is complete.

The first part of (b) can be proved by the same method as that in [6], we only need to prove the second part of (b). In view of (a), set $U(k) = \exp\{z(k)\}$, then

$$z(k+1) - z(k) = a(k) - b(k) \exp \{z(k)\}; \tag{2.8}$$

thus

$$0 = \sum_{k=0}^{\omega-1} (z(k+1) - z(k)) = \overline{a}\omega - \sum_{k=0}^{\omega-1} b(k) \exp \{z(k)\}, \tag{2.9}$$

this implies

$$(z(k))^L \leq \ln \left(\frac{\overline{a}}{\overline{b}} \right) \leq (z(k))^M. \tag{2.10}$$

Denote $z(\xi) = (z(k))^L$, where $\xi \in I_\omega$. By (2.8), $z(k+1) - z(k) \leq a(k)$, then for any $k \in I_\omega$ and $k \geq \xi$, we have

$$\sum_{i=\xi}^{k} (z(i+1) - z(i)) \leq \sum_{i=\xi}^{k} a(i), \tag{2.11}$$

since $a \in C_\omega$,

$$\sum_{i=\xi}^{k} (z(i+1) - z(i)) \leq \sum_{i=\xi}^{k} a(i) \leq \overline{a}\omega, \tag{2.12}$$

this shows that

$$z(k+1) \leq z(\xi) + \overline{a}\omega, \quad \text{for } k \in I_\omega,\ k \geq \xi. \tag{2.13}$$

On the other hand,

$$z(k+1) - z(k) = a(k) - b(k) \exp \{z(k)\} \geq -b(k) \exp \{z(k)\}; \tag{2.14}$$

hence

$$\sum_{i=k}^{\xi-1} (z(i+1) - z(i)) \geq -\sum_{i=k}^{\xi-1} b(i) \exp\{z(i)\} \tag{2.15}$$

$$\geq -\sum_{i=0}^{\omega-1} b(i) \exp\{z(i)\} = -\bar{a}\omega, \quad \text{for } k \in I_\omega,\ k \leq \xi - 1;$$

therefore

$$z(k) \leq z(\xi) + \bar{a}\omega, \quad \text{for } k \in I_\omega,\ k \leq \xi - 1. \tag{2.16}$$

By (2.13) and (2.16), we can obtain $z(k) \leq z(\xi) + \bar{a}\omega$, for $k \in I_\omega$; thus

$$U(k) = \exp\{z(k)\} \leq \frac{\bar{a}}{b} \exp\{\bar{a}\omega\}, \tag{2.17}$$

by a similar analysis as above, we can obtain

$$U(k) \geq \frac{\bar{a}}{b} \exp\{-\bar{a}\omega\}. \tag{2.18}$$

This completes the proof of the second part of (b). $\qquad\square$

To prove Theorem 1.4, we need the following several propositions. For the rest of this paper, we consider the solution of (1.8) with initial conditions (1.9). For the definition of semicycle and related concepts, we refer to [15].

PROPOSITION 2.3. *There exists a positive constant K_1 such that $\limsup_{k \to +\infty} N_1(k) \leq K_1$.*

Proof. Given any positive solution $(N_1(k), N_2(k))$ of (1.8), from the first equation of (1.8), we have

$$N_1(k+1) \leq N_1(k) \exp\{b_1(k) - a_1(k)N_1(k - [\tau_1])\}. \tag{2.19}$$

Let $N_1(k) = \exp\{u_1(k)\}$, then

$$u_1(k+1) - u_1(k) \leq b_1(k) - a_1(k) \exp\{u_1(k - [\tau_1])\}; \tag{2.20}$$

thus

$$\sum_{i=k-[\tau_1]}^{k-1} (u_1(i+1) - u_1(i)) \leq \sum_{i=k-[\tau_1]}^{k-1} b_1(i), \tag{2.21}$$

which is equivalent to

$$u_1(k) - \sum_{i=k-[\tau_1]}^{k-1} b_1(i) \leq u_1(k - [\tau_1]); \tag{2.22}$$

hence

$$N_1(k - [\tau_1]) = \exp\{u_1(k - [\tau_1])\} \geq \exp\left\{u_1(k) - \sum_{i=k-[\tau_1]}^{k-1} b_1(i)\right\}$$

$$= N_1(k)\exp\left\{-\sum_{i=k-[\tau_1]}^{k-1} b_1(i)\right\}. \tag{2.23}$$

Therefore

$$N_1(k+1) \leq N_1(k)\exp\left\{b_1(k) - a_1(k)N_1(k)\exp\left\{-\sum_{i=k-[\tau_1]}^{k-1} b_1(i)\right\}\right\}. \tag{2.24}$$

Consider the following auxiliary equation:

$$z(k+1) = z(k)\exp\left\{b_1(k) - a_1(k)z(k)\exp\left\{-\sum_{i=k-[\tau_1]}^{k-1} b_1(i)\right\}\right\}. \tag{2.25}$$

By Lemma 2.2, (2.25) has at least one positive ω-periodic solution, denote it as $z^*(k)$, we have

$$z^*(k) \leq \frac{\overline{b_1}}{(a_1(k)\exp\{-\sum_{i=k-[\tau_1]}^{k-1} b_1(i)\})}\exp\{\overline{b_1} + |\overline{b_1}|\} := H_1. \tag{2.26}$$

Let

$$z^*(k) = \exp\{u_2(k)\}, \tag{2.27}$$

then

$$u_1(k+1) - u_1(k) \leq b_1(k) - a_1(k)\exp\{u_1(k)\}\exp\left\{-\sum_{i=k-[\tau_1]}^{k-1} b_1(i)\right\},$$

$$u_2(k+1) - u_2(k) = b_1(k) - a_1(k)\exp\{u_2(k)\}\exp\left\{-\sum_{i=k-[\tau_1]}^{k-1} b_1(i)\right\}. \tag{2.28}$$

Making the transformation $u(k) = u_1(k) - u_2(k)$, we can obtain

$$u(k+1) - u(k) \leq -a_1(k)[\exp\{u(k)\} - 1]\exp\{u_2(k)\}\exp\left\{-\sum_{i=k-[\tau_1]}^{k-1} b_1(i)\right\}. \tag{2.29}$$

Now we divide the proof into two cases according to the oscillating property of $u(k)$. First we assume that $u(k)$ does not oscillate about zero, then $u(k)$ will be either eventually positive or eventually negative. If the latter holds, that is, $u_1(k) < u_2(k)$, we have

$$N_1(k) < z^*(k) \leq (z^*(k))^M. \tag{2.30}$$

Whereas if the former holds, then by (2.29), we know $u(k+1) < u(k)$, which means that $u(k)$ is eventually decreasing, also in terms of its positivity, we know that $\lim_{k\to\infty} u(k)$ exists. Then (2.29) yields $\lim_{k\to\infty} u(k) = 0$, which leads to

$$\limsup_{k\to\infty} N_1(k) \le (z^*(k))^M. \tag{2.31}$$

Now we assume that $u(k)$ oscillates about zero, by (2.29), we know that $u(k) > 0$ implies $u(k+1) \le u(k)$. Thus, if we let $\{u(k_l)\}$ be a subsequence of $\{u(k)\}$, where $u(k_l)$ is the first element of the positive semicycle of $\{u(k)\}$, then $\limsup_{k\to\infty} u(k) = \limsup_{l\to\infty} u(k_l)$. Combining

$$u(k_l) \le u(k_l-1) - a_1(k_l-1)\left[\exp\{u(k_l-1)\}-1\right]\exp\{u_2(k_l-1)\}\exp\left\{-\sum_{i=k_l-1-[\tau_1]}^{k_l-2} b_1(i)\right\} \tag{2.32}$$

with $u(k_l-1) < 0$, we know

$$u(k_lv) \le a_1(k_l-1)\left[\exp\{u(k_l-1)\}-1\right]\exp\{u_2(k_l-1)\}\exp\left\{-\sum_{i=k_l-1-[\tau_1]}^{k_l-2} b_1(i)\right\}$$

$$\le a_1(k_l-1)\exp\{u_2(k_l-1)\}\exp\left\{-\sum_{i=k_l-1-[\tau_1]}^{k_l-2} b_1(i)\right\}$$

$$\le \left(a_1(k_l-1)\exp\{u_2(k_l-1)\}\exp\left\{-\sum_{i=k_l-1-[\tau_1]}^{k_l-2} b_1(i)\right\}\right)^M. \tag{2.33}$$

Therefore

$$\limsup_{l\to\infty} u(k_l) \le \left(a_1(k_l-1)\exp\{u_2(k_l-1)\}\exp\left\{-\sum_{i=k_l-1-[\tau_1]}^{k_l-2} b_1(i)\right\}\right)^M. \tag{2.34}$$

By the medium of (2.27), we have $\limsup_{k\to\infty} N_1(k) \le K_1$, where

$$K_1 = H_1 \exp\left\{\left(a_1(k)H_1\exp\left\{-\sum_{i=k-[\tau_1]}^{k-1} b_1(i)\right\}\right)^M\right\}. \tag{2.35}$$

$\square$

PROPOSITION 2.4. *Under the condition (H1), there exists a positive constant k_1 such that $\liminf_{k\to\infty} N_1(k) \ge k_1$.*

Proof. Given any positive solution $(N_1(k), N_2(k))$ of (1.8), from the first equation of (1.8), we have

$$N_1(k+1) \ge N_1(k)\exp\left\{b_1(k) - \frac{\alpha_1(k)}{m(k)} - a_1(k)N_1(k-[\tau_1])\right\}. \tag{2.36}$$

Set $N_1(k) = \exp\{u_1(k)\}$, then

$$u_1(k+1) - u_1(k) \geq b_1(k) - \frac{\alpha_1(k)}{m(k)} - a_1(k) \exp\{u_1(k - [\tau_1])\}, \tag{2.37}$$

which yields

$$\sum_{i=k-[\tau_1]}^{k-1} (u_1(i+1) - u_1(i)) \geq \sum_{i=k-[\tau_1]}^{k-1} \left(b_1(i) - \frac{\alpha_1(i)}{m(i)} - a_1(i)K_1 \right), \tag{2.38}$$

that is,

$$u_1(k - [\tau_1]) \leq u_1(k) - \sum_{i=k-[\tau_1]}^{k-1} \left(b_1(i) - \frac{\alpha_1(i)}{m(i)} - a_1(i)K_1 \right); \tag{2.39}$$

thus

$$N_1(k - [\tau_1]) = \exp\{u_1(k - [\tau_1])\}$$

$$\leq \exp\left\{ u_1(k) - \sum_{i=k-[\tau_1]}^{k-1} \left(b_1(i) - \frac{\alpha_1(i)}{m(i)} - a_1(i)K_1 \right) \right\}$$

$$= N_1(k) \exp\left\{ - \sum_{i=k-[\tau_1]}^{k-1} \left(b_1(i) - \frac{\alpha_1(i)}{m(i)} - a_1(i)K_1 \right) \right\}. \tag{2.40}$$

Therefore

$$N_1(k+1) \geq N_1(k) \exp\left\{ b_1(k) - \frac{\alpha_1(k)}{m(k)} \right.$$

$$\left. - a_1(k)N_1(k) \exp\left\{ - \sum_{i=k-[\tau_1]}^{k-1} \left(b_1(i) - \frac{\alpha_1(i)}{m(i)} - a_1(i)K_1 \right) \right\} \right\}. \tag{2.41}$$

Consider the following auxiliary equation:

$$z(k+1) = z(k) \exp\left\{ b_1(k) - \frac{\alpha_1(k)}{m(k)} - a_1(k)z(k) \exp\left\{ - \sum_{i=k-[\tau_1]}^{k-1} \left(b_1(i) - \frac{\alpha_1(i)}{m(i)} - a_1(i)K_1 \right) \right\} \right\}. \tag{2.42}$$

By Lemma 2.2 and (H1), (2.42) has at least one positive ω-periodic solution, denoted as $z_1^*(k)$, then

$$z_1^*(k) \geq \frac{\overline{b_1} - \overline{(\alpha_1/m)}}{\left(a_1(k) \exp\left\{ - \sum_{i=k-[\tau_1]}^{k-1} (b_1(i) - \alpha_1(i)/m(i) - a_1(i)K_1) \right\} \right)}$$

$$\times \exp\left\{ -\overline{b_1} + \overline{\left(\frac{\alpha_1}{m} \right)} - \left| b_1(k) - \frac{\alpha_1(k)}{m(k)} \right| \right\} := H_2. \tag{2.43}$$

Now make the change of variables:

$$z_1^*(k) = \exp\{u_2(k)\}, \tag{2.44}$$

then

$$u_1(k+1) - u_1(k) \geq b_1(k) - \frac{\alpha_1(k)}{m(k)}$$

$$- a_1(k)\exp\{u_1(k)\}\exp\left\{-\sum_{i=k-[\tau_1]}^{k-1}\left(b_1(i) - \frac{\alpha_1(i)}{m(k)} - a_1(i)K_1\right)\right\},$$

$$u_2(k+1) - u_2(k) = b_1(k) - \frac{\alpha_1(k)}{m(k)}$$

$$- a_1(k)\exp\{u_2(k)\}\exp\left\{-\sum_{i=k-[\tau_1]}^{k-1}\left(b_1(i) - \frac{\alpha_1(i)}{m(i)} - a_1(i)K_1\right)\right\}. \tag{2.45}$$

Denote $u(k) = u_1(k) - u_2(k)$, we have

$$u(k+1) - u(k) \geq -a_1(k)[\exp\{u(k)\} - 1]\exp\{u_2(k)\}$$

$$\times \exp\left\{-\sum_{i=k-[\tau_1]}^{k-1}\left(b_1(i) - \frac{\alpha_1(i)}{m(i)} - a_1(i)K_1\right)\right\}. \tag{2.46}$$

If $u(k)$ does not oscillate, then by a similar analysis as that in Proposition 2.3, we have

$$\liminf_{k\to\infty} N_1(k) \geq (z_1^*(k))^L. \tag{2.47}$$

Whereas if $u(k)$ oscillates about zero, by (2.46), we know that if $u(k) < 0$, then $u(k+1) \geq u(k)$. Thus, if we denote $\{u(k_l)\}$ as a subsequence of $\{u(k)\}$, where $u(k_l)$ is the first element of the negative semicycle of $\{u(k)\}$, then $\liminf_{k\to\infty} u(k) = \liminf_{l\to\infty} u(k_l)$. On the other hand, from

$$u(k_l) \geq u(k_l - 1) - a_1(k_l - 1)[\exp\{u(k_l - 1)\} - 1]\exp\{u_2(k_l - 1)\}$$

$$\times \exp\left\{-\sum_{i=k_l-1-[\tau_1]}^{k_l-2}\left(b_1(i) - \frac{\alpha_1(i)}{m(i)} - a_1(i)K_1\right)\right\}, \tag{2.48}$$

and $u(k_l - 1) > 0$, we know

$$
u(k_l) \geq a_1(k_l - 1)\left[1 - \exp\{u(k_l - 1)\}\right]\exp\{u_2(k_l - 1)\}
$$

$$
\times \exp\left\{-\sum_{i=k_l-1-[\tau_1]}^{k_l-2}\left(b_1(i) - \frac{\alpha_1(i)}{m(i)} - a_1(i)K_1\right)\right\}
$$

$$
\geq -a_1(k_l - 1)\exp\{u_1(k_l - 1)\}
$$

$$
\times \exp\left\{-\sum_{i=k_l-1-[\tau_1]}^{k_l-2}\left(b_1(i) - \frac{\alpha_1(i)}{m(i)} - a_1(i)K_1\right)\right\}
$$

$$
\geq \left(-K_1 a_1(k_l - 1)\exp\left\{-\sum_{i=k_l-1-[\tau_1]}^{k_l-2}\left(b_1(i) - \frac{\alpha_1(i)}{m(i)} - a_1(i)K_1\right)\right\}\right)^L.
$$

$$(2.49)$$

Therefore

$$
\liminf_{l\to\infty} u(k_l) \geq \left(-K_1 a_1(k_l - 1)\exp\left\{-\sum_{i=k_l-1-[\tau_1]}^{k_l-2}\left(b_1(i) - \frac{\alpha_1(i)}{m(i)} - a_1(i)K_1\right)\right\}\right)^L.
$$

$$(2.50)$$

By the medium of (2.44), we have

$$
\liminf_{k\to\infty} N_1(k)
$$

$$
\geq (z_1^*(k))^L \exp\left\{\left(-K_1 a_1(k)\exp\left\{-\sum_{i=k-[\tau_1]}^{k-1}\left(b_1(i) - \frac{\alpha_1(i)}{m(i)} - a_1(i)K_1\right)\right\}\right)^L\right\};
$$

$$(2.51)$$

hence $\liminf_{k\to\infty} N_1(k) \geq k_1$, where

$$
k_1 = H_2 \exp\left\{\left(-K_1 a_1(k)\exp\left\{-\sum_{i=k-[\tau_1]}^{k-1}\left(b_1(i) - \frac{\alpha_1(i)}{m(i)} - a_1(i)K_1\right)\right\}\right)^L\right\}. \qquad (2.52)
$$

□

PROPOSITION 2.5. *If (H2) holds, then there exists a positive constant K_2 such that*

$$
\limsup_{k\to\infty} N_2(k) \leq K_2. \qquad (2.53)
$$

Proof. Given any positive solution $(N_1(k), N_2(k))$ of (1.8), from the second equation of (1.8), we have

$$N_2(k+1) = N_2(k)\exp\left\{-b_2(k) + \frac{\alpha_2(k)N_1(k-[\tau_2])}{N_1(k-[\tau_2]) + m(k)N_2(k-[\tau_2])}\right\}$$

$$\leq N_2(k)\exp\left\{-b_2(k) + \frac{\alpha_2(k)K_1}{K_1 + m(k)N_2(k-[\tau_2])}\right\} \tag{2.54}$$

$$= N_2(k)\exp\left\{\alpha_2(k) - b_2(k) - \alpha_2(k)\left[\frac{m(k)N_2(k-[\tau_2])}{K_1 + m(k)N_2(k-[\tau_2])}\right]\right\}.$$

Set $N_2(k) = \exp\{u_1(k)\}$, then

$$u_1(k+1) - u_1(k) \leq \alpha_2(k) - b_2(k); \tag{2.55}$$

thus

$$\sum_{i=k-[\tau_2]}^{k-1}(u_1(i+1) - u_1(i)) \leq \sum_{i=k-[\tau_2]}^{k-1}(\alpha_2(i) - b_2(i)), \tag{2.56}$$

which is equivalent to

$$u_1(k) - \sum_{i=k-[\tau_2]}^{k-1}(\alpha_2(i) - b_2(i)) \leq u_1(k-[\tau_2]); \tag{2.57}$$

hence

$$N_2(k-[\tau_2]) = \exp\{u_1(k-[\tau_2])\} \geq \exp\left\{u_1(k) - \sum_{i=k-[\tau_2]}^{k-1}(\alpha_2(i) - b_2(i))\right\}$$

$$= N_2(k)\exp\left\{-\sum_{i=k-[\tau_2]}^{k-1}(\alpha_2(i) - b_2(i))\right\}. \tag{2.58}$$

Therefore

$$N_2(k+1) \leq N_2(k)\exp\left\{\alpha_2(k) - b_2(k)\right.$$

$$\left. - \alpha_2(k)\left[\frac{m(k)N_2(k)\exp\{-\sum_{i=k-[\tau_2]}^{k-1}(\alpha_2(i) - b_2(i))\}}{K_1 + m(k)N_2(k)\exp\{-\sum_{i=k-[\tau_2]}^{k-1}(\alpha_2(i) - b_2(i))\}}\right]\right\}. \tag{2.59}$$

Here we use the monotonicity of the function $u/(a+u)$.

Consider the following auxiliary equation:

$$z(k+1) = z(k) \exp \left\{ \alpha_2(k) - b_2(k) \right.$$

$$\left. - \alpha_2(k) \left[\frac{m(k)z(k)\exp\left\{-\sum_{i=k-[\tau_2]}^{k-1}(\alpha_2(i) - b_2(i))\right\}}{K_1 + m(k)z(k)\exp\left\{-\sum_{i=k-[\tau_2]}^{k-1}(\alpha_2(i) - b_2(i))\right\}} \right] \right\}.$$
(2.60)

By the same method as that in [6], (2.60) has at least one positive ω-periodic solution, denote it as $z_2^*(k)$, then through some simple calculations, we have

$$z_2^*(k) \leq \frac{(\bar{\alpha}_2 - \bar{b}_2)K_1}{\bar{b}_2 \left(m(k)\exp\left\{-\sum_{i=k-[\tau_2]}^{k-1}(\alpha_2(i) - b_2(i))\right\}\right)^L}$$
(2.61)

$$\times \exp\left\{\bar{\alpha}_2 - \bar{b}_2 + \overline{|\alpha_2(k) - b_2(k)|}\right\} := H_3.$$

Let

$$z_2^*(k) = \exp\left\{u_2(k)\right\},$$
(2.62)

then

$$u_1(k+1) - u_1(k) \leq \alpha_2(k) - b_2(k)$$

$$- \alpha_2(k)\left[\frac{m(k)\exp\left\{u_1(k)\right\}\exp\left\{-\sum_{i=k-[\tau_2]}^{k-1}(\alpha_2(i) - b_2(i))\right\}}{K_1 + m(k)\exp\left\{u_1(k)\right\}\exp\left\{-\sum_{i=k-[\tau_2]}^{k-1}(\alpha_2(i) - b_2(i))\right\}}\right],$$

$$u_2(k+1) - u_2(k) = \alpha_2(k) - b_2(k)$$

$$- \alpha_2(k)\left[\frac{m(k)\exp\left\{u_2(k)\right\}\exp\left\{-\sum_{i=k-[\tau_2]}^{k-1}(\alpha_2(i) - b_2(i))\right\}}{K_1 + m(k)\exp\left\{u_2(k)\right\}\exp\left\{-\sum_{i=k-[\tau_2]}^{k-1}(\alpha_2(i) - b_2(i))\right\}}\right].$$
(2.63)

Denote $u(k) = u_1(k) - u_2(k)$, we have

$$u(k+1) - u(k)$$

$$\leq -\alpha_2(k)\left[\frac{m(k)K_1\exp\left\{u_2(k)\right\}\exp\left\{-\sum_{i=k-[\tau_2]}^{k-1}(\alpha_2(i) - b_2(i))\right\}}{K_1 + m(k)\exp\left\{u_2(k)\right\}\exp\left\{-\sum_{i=k-[\tau_2]}^{k-1}(\alpha_2(i) - b_2(i))\right\}}\right]$$

$$\times\left[\frac{\exp\left\{u(k)\right\} - 1}{K_1 + m(k)\exp\left\{u_2(k)\right\}\exp\left\{u(k)\right\}\exp\left\{-\sum_{i=k-[\tau_2]}^{k-1}(\alpha_2(i) - b_2(i))\right\}}\right].$$
(2.64)

First we assume that $u(k)$ does not oscillate about zero, then $u(k)$ will be either eventually positive or eventually negative. If the latter holds, that is, $u_1(k) < u_2(k)$, we have

$$N_2(k) < z_2^*(k) \le (z_2^*(k))^M. \tag{2.65}$$

Whereas if the former holds, then by (2.64), we have $u(k+1) < u(k)$, which means that $u(k)$ is eventually decreasing, also in terms of its positivity, we obtain that $\lim_{k\to\infty} u(k)$ exists. Then (2.64) leads to $\lim_{k\to\infty} u(k) = 0$, this implies

$$\limsup_{k\to\infty} N_2(k) \le (z_2^*(k))^M. \tag{2.66}$$

Now we assume that $u(k)$ oscillates about zero; in view of (2.64), we know that $u(k) > 0$ implies $u(k+1) \le u(k)$. Thus, if we let $\{u(k_l)\}$ be a subsequence of $\{u(k)\}$, where $u(k_l)$ is the first element of the positive semicycle of $\{u(k)\}$, then $\limsup_{k\to\infty} u(k) = \limsup_{l\to\infty} u(k_l)$. Also, from

$u(k_l) \le u(k_l - 1)$

$$-\alpha_2(k_l-1)\left[\frac{m(k_l-1)K_1 \exp\{u_2(k_l-1)\} \exp\{-\sum_{i=k_l-1-[\tau_2]}^{k_l-2}(\alpha_2(i)-b_2(i))\}}{K_1+m(k_l-1)\exp\{u_2(k_l-1)\}\exp\{-\sum_{i=k_l-1-[\tau_2]}^{k_l-2}(\alpha_2(i)-b_2(i))\}}\right]$$

$$\times\left[\frac{\exp\{u(k_l-1)\}-1}{K_1+m(k_l-1)\exp\{u_2(k_l-1)\}\exp\{u(k_l-1)\}\exp\{-\sum_{i=k_l-1-[\tau_2]}^{k_l-2}(\alpha_2(i)-b_2(i))\}}\right], \tag{2.67}$$

and $u(k_l - 1) < 0$, we know

$u(k_l) \le \alpha_2(k_l - 1)$

$$\times\left[\frac{m(k_l-1)K_1\exp\{u_2(k_l-1)\}\exp\{-\sum_{i=k_l-1-[\tau_2]}^{k_l-2}(\alpha_2(i)-b_2(i))\}}{K_1+m(k_l-1)\exp\{u_2(k_l-1)\}\exp\{-\sum_{i=k_l-1-[\tau_2]}^{k_l-2}(\alpha_2(i)-b_2(i))\}}\right]$$

$$\times\left[\frac{1-\exp\{u(k_l-1)\}}{K_1+m(k_l-1)\exp\{u_2(k_l-1)\}\exp\{u(k_l-1)\}\exp\{-\sum_{i=k_l-1-[\tau_2]}^{k_l-2}(\alpha_2(i)-b_2(i))\}}\right]. \tag{2.68}$$

Consider the function

$$g(x) = \frac{1-x}{p+qx}, \quad p > 0,\ q > 0,\ 0 \le x \le 1. \tag{2.69}$$

It is easy to show that $g(x)$ has the property $g(x) \le g(0)$. Therefore (2.68) yields

$$u(k_l) \le \frac{\alpha_2(k_l-1)m(k_l-1)\exp\{u_2(k_l-1)\}\exp\{-\sum_{i=k_l-1-[\tau_2]}^{k_l-2}(\alpha_2(i)-b_2(i))\}}{K_1+m(k_l-1)\{u_2(k_l-1)\}\exp\{-\sum_{i=k_l-1-[\tau_2]}^{k_l-2}(\alpha_2(i)-b_2(i))\}}, \tag{2.70}$$

that is,

$$\limsup_{l \to \infty} u(k_l)$$

$$\leq \left(\frac{\alpha_2(k_l - 1)m(k_l - 1)\exp\{u_2(k_l - 1)\}\exp\{-\sum_{i=k_l-1-[\tau_2]}^{k_l-2}(\alpha_2(i) - b_2(i))\}}{K_1 + m(k_l - 1)\exp\{u_2(k_l - 1)\}\exp\{-\sum_{i=k_l-1-[\tau_2]}^{k_l-2}(\alpha_2(i) - b_2(i))\}} \right)^M$$

$$\leq (\alpha_2(k_l - 1))^M. \tag{2.71}$$

By the medium of (2.27), we have $\limsup_{k \to \infty} N_2(k) \leq K_2$, where

$$K_2 = H_3 \exp\left\{ (\alpha_2(k))^M \right\}. \tag{2.72}$$

$\square$

PROPOSITION 2.6. *Under the conditions (H1) and (H2), there exists a positive constant k_2 such that $\liminf_{k \to +\infty} N_2(k) \geq k_2$.*

Proof. Given any positive solution $(N_1(k), N_2(k))$ of (1.8), from the second equation of (1.8), we have

$$N_2(k + 1)$$

$$= N_2(k)\exp\left\{ -b_2(k) + \frac{\alpha_2(k)N_1(k - [\tau_2])}{N_1(k - [\tau_2]) + m(k)N_2(k - [\tau_2])} \right\}$$

$$= N_2(k)\exp\left\{ \alpha_2(k) - b_2(k) + \alpha_2(k)\left[\frac{N_1(k - [\tau_2])}{N_1(k - [\tau_2]) + m(k)N_2(k - [\tau_2])} - 1 \right] \right\}$$

$$= N_2(k)\exp\left\{ \alpha_2(k) - b_2(k) - \alpha_2(k)\left[\frac{m(k)N_2(k - [\tau_2])}{N_1(k - [\tau_2]) + m(k)N_2(k - [\tau_2])} \right] \right\}, \tag{2.73}$$

then

$$N_2(k + 1) \geq N_2(k)\exp\left\{ \alpha_2(k) - b_2(k) - \frac{\alpha_2(k)m(k)N_2(k - [\tau_2])}{k_1} \right\}. \tag{2.74}$$

In view of

$$N_2(k + 1) = N_2(k)\exp\left\{ -b_2(k) + \frac{\alpha_2(k)N_1(k - [\tau_2])}{N_1(k - [\tau_2]) + m(k)N_2(k - [\tau_2])} \right\}$$

$$\geq N_2(k)\exp\{ -b_2(k) \}, \tag{2.75}$$

if we let $N_2(k) = \exp\{u_1(k)\}$, then we can obtain $u_1(k+1) - u_1(k) \geq -b_2(k)$. Thus

$$\sum_{i=k-[\tau_2]}^{k-1} (u_1(i+1) - u_1(i)) \geq \sum_{i=k-[\tau_2]}^{k-1} (-b_2(i)), \tag{2.76}$$

that is,

$$u_1(k - [\tau_2]) \leq u_1(k) + \sum_{i=k-[\tau_2]}^{k-1} b_2(i); \tag{2.77}$$

hence

$$N_2(k - [\tau_2]) = \exp\{u_1(k - [\tau_2])\} \leq \exp\left\{u_1(k) + \sum_{i=k-[\tau_2]}^{k-1} b_2(i)\right\}$$

$$= N_2(k)\exp\left\{\sum_{i=k-[\tau_2]}^{k-1} b_2(i)\right\}. \tag{2.78}$$

Therefore from (2.74), we have

$$N_2(k+1) \geq N_2(k)\exp\left\{\alpha_2(k) - b_2(k) - \frac{\alpha_2(k)m(k)}{k_1}N_2(k)\exp\left\{\sum_{i=k-[\tau_2]}^{k-1} b_2(i)\right\}\right\}. \tag{2.79}$$

Consider the auxiliary equation

$$z(k+1) = z(k)\exp\left\{\alpha_2(k) - b_2(k) - \frac{\alpha_2(k)m(k)}{k_1}z(k)\exp\left\{\sum_{i=k-[\tau_2]}^{k-1} b_2(i)\right\}\right\}. \tag{2.80}$$

By Lemma 2.2 and (H2), (2.80) has at least one positive ω-periodic solution, denoted as $z_3^*(k)$, then

$$z_3^*(k) \geq \frac{(\overline{\alpha}_2 - \overline{b}_2)k_1}{(\alpha_2(k)m(k)\exp\{\sum_{i=k-[\tau_2]}^{k-1} b_2(i)\})}$$

$$\times \exp\left\{-\overline{\alpha}_2 + \overline{b}_2 - \overline{|\alpha_2(k) - b_2(k)|}\right\} := H_4. \tag{2.81}$$

If we set

$$z_3^*(k) = \exp\{u_2(k)\}, \tag{2.82}$$

then

$$u_1(k+1) - u_1(k) \geq \alpha_2(k) - b_2(k) - \frac{\alpha_2(k)m(k)}{k_1} \exp\{u_1(k)\} \exp\left\{ \sum_{i=k-[\tau_2]}^{k-1} b_2(i) \right\},$$

$$u_2(k+1) - u_2(k) = \alpha_2(k) - b_2(k) - \frac{\alpha_2(k)m(k)}{k_1} \exp\{u_2(k)\} \exp\left\{ \sum_{i=k-[\tau_2]}^{k-1} b_2(i) \right\}.$$

$$(2.83)$$

And let $u(k) = u_1(k) - u_2(k)$, we have

$$u(k+1) - u(k)$$

$$\geq -\frac{\alpha_2(k)m(k)}{k_1} \left[\exp\{u(k)\} - 1 \right] \exp\{u_2(k)\} \exp\left\{ \sum_{i=k-[\tau_2]}^{k-1} b_2(i) \right\}.$$

$$(2.84)$$

If $u(k)$ does not oscillate, then by a similar analysis as that in Proposition 2.3, we have

$$\liminf_{k\to\infty} N_2(k) \geq \left(z_3^*(k) \right)^L. \tag{2.85}$$

Whereas if $u(k)$ oscillates about zero, by (2.84), we know that $u(k) < 0$ implies $u(k+1) \geq u(k)$. Thus, if we denote $\{u(k_l)\}$ as a subsequence of $\{u(k)\}$, where $u(k_l)$ is the first element of the negative semicycle of $\{u(k)\}$, then $\liminf_{k\to\infty} u(k) = \liminf_{l\to\infty} u(k_l)$. On the other hand, the combination of

$$u(k_l) \geq u(k_l - 1) - \frac{\alpha_2(k_l - 1)m(k_l - 1)}{k_1}$$

$$\times \left[\exp\{u(k_l - 1)\} - 1 \right] \exp\{u_2(k_l - 1)\} \exp\left\{ \sum_{i=k_l-1-[\tau_2]}^{k_l-2} b_2(i) \right\}$$

$$(2.86)$$

and $u(k_l - 1) > 0$ gives

$$u(k_l) \geq \frac{\alpha_2(k_l - 1)m(k_l - 1)}{k_1} \left[1 - \exp\{u(k_l - 1)\} \right] \exp\{u_2(k_l - 1)\}$$

$$\times \exp\left\{ \sum_{i=k_l-1-[\tau_2]}^{k_l-2} b_2(i) \right\}$$

$$\geq -\frac{\alpha_2(k_l - 1)m(k_l - 1)}{k_1} \exp\{u_1(k_l - 1)\} \exp\left\{ \sum_{i=k_l-1-[\tau_2]}^{k_l-2} b_2(i) \right\}$$

$$\geq \left(-\frac{\alpha_2(k_l - 1)m(k_l - 1)}{k_1} K_2 \exp\left\{ \sum_{i=k_l-1-[\tau_2]}^{k_l-2} b_2(i) \right\} \right)^L.$$

$$(2.87)$$

Therefore

$$
\liminf_{l \to \infty} u(k_l)
$$
$$
\geq \left(-\frac{\alpha_2(k_l-1)m(k_l-1)}{k_1} K_2 \exp\left\{ \sum_{i=k_l-1-[\tau_2]}^{k_l-2} b_2(i) \right\} \right)^L. \tag{2.88}
$$

By the medium of (2.82), we have

$$
\liminf_{k \to \infty} N_1(k)
$$
$$
\geq (z_3^*(k))^L \exp\left\{ \left(-\frac{\alpha_2(k)m(k)}{k_1} K_2 \exp\left\{ \sum_{i=k-[\tau_2]}^{k-1} b_2(i) \right\} \right)^L \right\}. \tag{2.89}
$$

Hence $\liminf_{k \to \infty} N_1(k) \geq k_2$, where

$$
k_2 = H_4 \exp\left\{ \left(-\frac{\alpha_2(k)m(k)}{k_1} K_2 \exp\left\{ \sum_{i=k-[\tau_2]}^{k-1} b_2(i) \right\} \right)^L \right\}. \tag{2.90}
$$

$\square$

Proof of Theorem 1.4. From Propositions 2.3–2.6, we can easily know that system (1.8) is permanent. The proof is complete. $\square$

We remark that, in the above discussions, we have obtained that under the conditions (H1) and (H2), system (1.8) has at least one periodic solutions and it is also permanent. Naturally we may conjecture whether the existence of positive periodic solutions of system (1.8) implies its permanence or the permanence of system (1.8) implies the existence of positive periodic solutions. This is a more challenging and interesting problem for future study.

Acknowledgments

References

[1] R. P. Agarwal, *Difference Equations and Inequalities: Theory, Methods, and Applications*, Monographs and Textbooks in Pure and Applied Mathematics, vol. 228, Marcel Dekker, New York, 2000.

[2] R. Arditi, N. Perrin, and H. Saiah, *Functional response and heterogeneities: an experiment test with cladocerans*, Oikos **60** (1991), 69–75.

[3] E. Beretta and Y. Kuang, *Global analyses in some delayed ratio-dependent predator-prey systems*, Nonlinear Analysis. Theory, Methods & Applications **32** (1998), no. 3, 381–408.

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

[5] Y.-H. Fan, W.-T. Li, and L.-L. Wang, *Periodic solutions of delayed ratio-dependent predator-prey models with monotonic or nonmonotonic functional responses*, Nonlinear Analysis. Real World Applications **5** (2004), no. 2, 247–263.

[6] M. Fan and K. Wang, *Periodic solutions of a discrete time nonautonomous ratio-dependent predator-prey system*, Mathematical and Computer Modelling **35** (2002), no. 9-10, 951–961.

[7] H. I. Freedman, *Deterministic Mathematical Models in Population Ecology*, Monographs and Textbooks in Pure and Applied Mathematics, vol. 57, Marcel Dekker, New York, 1980.

[8] K. Gopalsamy, *Stability and Oscillations in Delay Differential Equations of Population Dynamics*, Mathematics and Its Applications, vol. 74, Kluwer Academic, Dordrecht, 1992.

[9] I. Hanski, *The functional response of predators: worries about scale*, Trends in Ecology & Evolution **6** (1991), no. 5, 141–142.

[10] C. S. Holling, *The functional response of predator to prey density and its role in mimicry and population regulation*, Memoirs of Entomological Society of Canada **45** (1965), 1–60.

[11] S.-B. Hsu, T.-W. Hwang, and Y. Kuang, *Global analysis of the Michaelis-Menten-type ratio-dependent predator-prey system*, Journal of Mathematical Biology **42** (2001), no. 6, 489–506.

[12] _____, *Rich dynamics of a ratio-dependent one-prey two-predators model*, Journal of Mathematical Biology **43** (2001), no. 5, 377–396.

[13] H.-F. Huo and W.-T. Li, *Permanence and global stability of positive solutions of a nonautonomous discrete ratio-dependent predator-prey model*, Discrete Dynamics in Nature and Society **2005** (2005), no. 2, 135–144.

[14] C. Jost, O. Arino, and R. Arditi, *About deterministic extinction in ratio-dependent predator-prey models*, Bulletin of Mathematical Biology **61** (1999), no. 1, 19–32.

[15] V. L. Kocić and G. Ladas, *Global Behavior of Nonlinear Difference Equations of Higher Order with Applications*, Mathematics and Its Applications, vol. 256, Kluwer Academic, Dordrecht, 1993.

[16] Y. Kuang, *Delay Differential Equations with Applications in Population Dynamics*, Mathematics in Science and Engineering, vol. 191, Academic Press, Massachusetts, 1993.

[17] Y. Kuang and E. Beretta, *Global qualitative analysis of a ratio-dependent predator-prey system*, Journal of Mathematical Biology **36** (1998), no. 4, 389–406.

[18] W.-T. Li, Y.-H. Fan, and S. Ruan, *Periodic solutions in a delayed predator-prey model with nonmonotonic functional response*, submitted.

[19] R. M. May, *Complexity and Stability in Model Ecosystems*, Princeton University Press, New Jersey, 1973.

[20] _____, *Biological populations obeying difference equations: stable points, stable cycles, and chaos*, Journal of Theoretical Biology **51** (1975), no. 2, 511–524.

[21] J. D. Murry, *Mathematical Biology*, Springer, New York, 1989.

[22] M. L. Rosenzweig, *Paradox of enrichment: destabilization of exploitation ecosystem in ecological time*, Science **171** (1971), 385–387.

[23] S. Ruan and D. Xiao, *Global analysis in a predator-prey system with nonmonotonic functional response*, SIAM Journal on Applied Mathematics **61** (2001), no. 4, 1445–1472.

[24] Y. Takeuchi, *Global Dynamical Properties of Lotka-Volterra Systems*, World Scientific, New Jersey, 1996.

[25] L.-L. Wang and W.-T. Li, *Existence and global stability of positive periodic solutions of a predator-prey system with delays*, Applied Mathematics and Computation **146** (2003), no. 1, 167–185.

[26] _____, *Periodic solutions and permanence for a delayed nonautonomous ratio-dependent predator-prey model with Holling type functional response*, Journal of Computational and Applied Mathematics **162** (2004), no. 2, 341–357.

[27] D. Xiao and S. Ruan, *Global dynamics of a ratio-dependent predator-prey system*, Journal of Mathematical Biology **43** (2001), no. 3, 268–290.

[28] D. Xiao and Z. Zhang, *On the uniqueness and nonexistence of limit cycles for predator-prey systems*, Nonlinearity **16** (2003), no. 3, 1185–1201.

[29] H. Zhu, S. A. Campbell, and G. S. K. Wolkowicz, *Bifurcation analysis of a predator-prey system with nonmonotonic functional response*, SIAM Journal on Applied Mathematics **63** (2002), no. 2, 636–682.

Yong-Hong Fan: School of Mathematics and Information, Ludong University, Yantai, Shandong 264025, China
E-mail address: fanyh02@st.lzu.edu.cn

Wan-Tong Li: School of Mathematics and Statistics, Lanzhou University, Lanzhou, Gansu 730000, China
E-mail address: wtli@lzu.edu.cn