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Permanence for a delayed discrete ratio-dependent predator–prey system with Holling type functional response [☆]

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Abstract

Sufficient conditions are established for the permanence in a delayed discrete predator–prey model with Holling type III functional response:

$$\begin{cases} N_1(k+1) = N_1(k) \exp\left\{b_1(k) - a_1(k)N_1(k - [\tau_1]) - \frac{\alpha_1(k)N_1(k)N_2(k)}{N_1^2(k) + m^2N_2^2(k)}\right\}, \\ N_2(k+1) = N_2(k) \exp\left\{-b_2(k) + \frac{\alpha_2(k)N_1^2(k - [\tau_2])}{N_1^2(k - [\tau_2]) + m^2N_2^2(k - [\tau_2])}\right\}. \end{cases}$$

Our investigation confirms that when the death rate of the predator is rather small as well as the intrinsic growth rate of the prey is relatively large, the species could coexist in the long run.

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Keywords: Discrete predator–prey model; Functional response; Permanence

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1. Introduction

Many mathematical models have been established to describe the relationships between the species and the outer environment or among the different species in biomathematics. The dynamics of the growth of a population can be described if the functional behavior of the rate of growth is known. Of course, 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 prey 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 [5]). 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 [5] and [9]. In general, a predator–prey system takes the form

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

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 [9] and [19]. Massive work has been done on this issue. We refer to the monographs [10,16,21,24] for general delayed biological systems and to [18,22,23,25–27,30,31] for investigation 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 named as prey-dependent model [14]. But there is a growing explicit biological and physiological evidence [4,13,15,17] 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 [3,11]. A general form of a ratio-dependent model is

$$\begin{cases} x' = rx\left(1 - \frac{x}{K}\right) - \varphi\left(\frac{x}{y}\right)y, \\ y' = y\left(\mu\varphi\left(\frac{x}{y}\right) - D\right). \end{cases} \quad (1.2)$$

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 [8] 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

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

see [4,13,15,17,29] and references therein. In view of periodicity of the actual environment, Fan and Wang [6] established verifiable criteria for the global existence of positive periodic solutions of a more general delayed ratio-dependent predator–prey model with periodic coefficients of the form

$$\begin{cases} x'(t) = x(t) \left[a(t) - b(t) \int_{-\infty}^t k(t-s)x(s) ds \right] - \frac{c(t)x(t)y(t)}{my(t)+x(t)}, \\ y'(t) = y(t) \left[\frac{f(t)x(t-\tau(t))}{my(t-\tau)+x(t-\tau)} - d(t) \right]. \end{cases}$$

The functional response function $\varphi(u) = cu/(m + u)$, $u = x/y$ in above models was used by Holling as Holling type II function, they usually describe the uptake of substrate by the microorganisms in microbial dynamics or chemical kinetics [9].

But when we describe the relationship between more higher animals, a more suitable response function

$$\varphi(x) = \frac{\mu x^2}{1 + \rho x^2},$$

should be taken into the predator–prey interactions, which is proposed by Holling [12] based on the fundament of experiment. This response function is usually called the Holling type III response function [9]. In two previous articles [25,26], Wang and Li established verifiable criteria for the global existence of positive periodic solutions and the stability for the following delayed predator–prey model with Holling type III response function

$$\begin{cases} N_1'(t) = N_1(t) \left[b_1(t) - a_1(t)N_1(t - \tau_1(t)) - \frac{\alpha_1(t)N_1(t)}{1+mN_1^2(t)}N_2(t - \sigma(t)) \right], \\ N_2'(t) = N_2(t) \left[-b_2(t) - a_2(t)N_2(t) + \frac{\alpha_2(t)N_1^2(t-\tau_2(t))}{1+mN_1^2(t-\tau_2(t))} \right], \end{cases}$$

where $N_1(t), N_2(t)$ are the densities of the prey population and predator population at time t , $b_i : \mathbb{R} \rightarrow \mathbb{R}$, $a_i, \tau_i, \sigma, \alpha_i : \mathbb{R} \rightarrow [0, +\infty)$ ($i = 1, 2$) are continuous functions of period T and $\int_0^T b_i(t) dt > 0$, $\alpha_i(t) \neq 0$, m is a nonnegative constant. And in [27], Wang and Li also investigated the global existence of positive periodic solutions and the permanent property of the ratio-dependent predator–prey system with Holling type III functional response which takes the form

$$\begin{cases} x'(t) = x(t) \left[a(t) - b(t) \int_{-\infty}^t k(t-s)x(s) ds \right] - \frac{c(t)x^2(t)y(t)}{m^2y^2(t)+x^2(t)}, \\ y'(t) = y(t) \left[\frac{e(t)x^2(t-\tau)}{m^2y^2(t-\tau)+x^2(t-\tau)} - d(t) \right], \end{cases} \tag{1.3}$$

where the functional response function $\varphi(u) = cu^2/(1 + m^2u^2)$, $u = x/y$; $a(t), b(t), c(t), e(t)$, and $d(t)$ are all positive periodic continuous functions; and $m > 0, \tau \geq 0$ are real constants. They found that the criteria for the permanence is exactly the same as that for the existence of the positive periodic solutions of (1.3).

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 non-overlapping generations [2,21]. For the discrete Michaelis–Menten type ratio-dependent predator–prey model, Fan and Wang [7] established the existence of positive periodic solutions. And for the discrete delayed ratio-dependent predator–prey model with Holling type

III response function, Wang and Li [28] established the existence of positive periodic solution. But in ecosystems, a more 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. In the present paper we will make our try on this problem.

Just as pointed out in [10, pp. 78–79], even if the coefficients are constants, the asymptotical behavior of the discrete system is rather complex and “chaotic” than the continuous one. For example, consider the logistic equation

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

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

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

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

Based on the above considerations, we will focus on the discrete time analogue of the ratio-dependent predator–prey system with Holling type III functional response. The present paper is organized as follows: we first make some preparations for our main work in the next section. Sufficient conditions for the permanence of the system in consideration are proposed and proved in the third section. And a brief discussion is carried out in the final section.

2. Preliminary

Throughout this paper, we always denote $\mathbb{Z}, \mathbb{Z}^+, \mathbb{R}, \mathbb{R}^+$, and \mathbb{R}^2 as the sets of all integers, nonnegative integers, real numbers, nonnegative real numbers, and two-dimensional Euclidean vector space, respectively.

We begin with the corresponding continuous ratio-dependent predator–prey system with Holling type III functional response

$$\begin{cases} \frac{dN_1(t)}{dt} = N_1(t)[b_1(t) - a_1(t)N_1(t - \tau_1)] - \frac{\alpha_1(t)N_1^2(t)N_2(t)}{N_1^2(t) + m^2N_2^2(t)}, \\ \frac{dN_2(t)}{dt} = N_2(t)\left[-b_2(t) + \frac{\alpha_2(t)N_1^2(t - \tau_2)}{N_1^2(t - \tau_2) + m^2N_2^2(t - \tau_2)}\right], \end{cases} \quad (2.1)$$

where $N_1(t)$ and $N_2(t)$ represent the densities of the prey population and predator population at time t , respectively; $m > 0$, $\tau_1 \geq 0$, $\tau_2 \geq 0$ are real constants; $b_i : \mathbb{R} \rightarrow \mathbb{R}$ and $a_i, \alpha_i : \mathbb{R} \rightarrow \mathbb{R}^+$ ($i = 1, 2$) 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 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 $N_1^2(t)/[N_1^2(t) + m^2N_2^2(t)]$ denotes the ratio-dependent response function, which reflects the capture ability of the predator.

Let us assume that the average grow rates in (2.1) change at regular intervals of time, then we can incorporate this aspect in (2.1) and obtain the following modified system:

$$\begin{cases} \frac{1}{N_1(t)} \frac{dN_1(t)}{dt} = b_1([t]) - a_1([t])N_1([t] - [\tau_1]) - \frac{\alpha_1([t])N_1([t])N_2([t])}{N_1^2([t]) + m^2N_2^2([t])}, \\ \frac{1}{N_2(t)} \frac{dN_2(t)}{dt} = -b_2([t]) + \frac{\alpha_2([t])N_1^2([t] - [\tau_2])}{N_1^2([t] - [\tau_2]) + m^2N_2^2([t] - [\tau_2])}, \quad t \neq 0, 1, 2, \dots, \end{cases} \tag{2.2}$$

where $[t]$ denotes the integer part of t , $t \in (0, +\infty)$. By a solution of (2.2), we mean a function $N = (N_1, N_2)^T$, which is defined for $t \in (0, +\infty)$, and possesses the following properties:

- (1) N is continuous on $[0, +\infty)$;
- (2) the derivative $\frac{dN_1(t)}{dt}$, $\frac{dN_2(t)}{dt}$ exist at each point $t \in [0, +\infty)$ with the possible exception of the points $t \in \{0, 1, 2, \dots\}$, where left-sided derivatives exist;
- (3) the equations in (2.2) are satisfied on each interval $[k, k + 1)$ with $k = 0, 1, 2, \dots$

On any interval of the form $[k, k + 1)$, $k = 0, 1, 2, \dots$, we can integrate (2.2) and obtain for $k \leq t < k + 1$, $k = 0, 1, 2, \dots$,

$$\begin{cases} N_1(t) = N_1(k) \exp\left\{ \left[b_1(k) - a_1(k)N_1(k - [\tau_1]) - \frac{\alpha_1(k)N_1(k)N_2(k)}{N_1^2(k) + m^2N_2^2(k)} \right] (t - k) \right\}, \\ N_2(t) = N_2(k) \exp\left\{ \left[-b_2(k) + \frac{\alpha_2(k)N_1^2(k - [\tau_2])}{N_1^2(k - [\tau_2]) + m^2N_2^2(k - [\tau_2])} \right] (t - k) \right\}. \end{cases} \tag{2.3}$$

Let $t \rightarrow k + 1$, we obtain from (2.3) that

$$\begin{cases} N_1(k + 1) = N_1(k) \exp\left\{ b_1(k) - a_1(k)N_1(k - [\tau_1]) - \frac{\alpha_1(k)N_1(k)N_2(k)}{N_1^2(k) + m^2N_2^2(k)} \right\}, \\ N_2(k + 1) = N_2(k) \exp\left\{ -b_2(k) + \frac{\alpha_2(k)N_1^2(k - [\tau_2])}{N_1^2(k - [\tau_2]) + m^2N_2^2(k - [\tau_2])} \right\}, \end{cases} \tag{2.4}$$

which is a discrete time analogue of system (2.1), where $N_1(t)$, $N_2(t)$ are the densities of the prey population and predator population at time t .

The exponential form of Eq. (2.4) 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 solution $N(k)$ with

$$N_i(-k) \geq 0, \quad k = 1, 2, \dots, \max\{[\tau_1], [\tau_2]\}; \quad N_i(0) > 0, \quad i = 1, 2. \tag{2.5}$$

For convenience, we denote

$$\bar{f} = \frac{1}{\omega} \sum_{i=0}^{\omega-1} f(i),$$

for any ω -periodic sequence $\{f(k)\}$.

In [28], Wang and Li considered the existence of positive periodic solution for Eq. (2.4) and obtained that

Lemma 2.1. Assume that the following conditions hold:

- (H1) $2m\bar{b}_1 > \bar{\alpha}_1$, and
 (H2) $\bar{\alpha}_2 > \bar{b}_2$.

Then (2.4) has at least one positive ω -periodic solution.

In order to present our main results, we need the following definition and theorem taken from [1].

Definition 2.1. Let $A \in (0, \infty]$ and let $g : [0, A) \rightarrow [0, A)$ be a continuous function. Suppose $g(0) = 0$, $g(x) > 0$ for $0 < x < A$, and assume that g has a unique fixed point $\bar{x} \in (0, A)$. Suppose also that $g(x) > x$ for $0 < x < \bar{x}$ and $g(x) < x$ for $\bar{x} < x < A$. Then the difference equation

$$x_{n+1} = g(x_n), \quad n = 0, 1, \dots, \quad (2.6)$$

is called a *population model*.

Theorem 2.1. Let $A \in (0, \infty]$ and assume that Eq. (2.6) is a population model. If $g(x) \leq \bar{x}$ for $x < \bar{x}$, then \bar{x} is a global attractor of all solutions of Eq. (2.6) with $x_0 \in (0, A)$.

And the following lemma is from [32].

Lemma 2.2. Suppose that $f : \mathbb{Z}^+ \times [0, \infty) \rightarrow [0, \infty)$ and $g : \mathbb{Z}^+ \times [0, \infty) \rightarrow [0, \infty)$ with $f(n, x) \leq g(n, x)$ ($f(n, x) \geq g(n, x)$) for $n \in \mathbb{Z}^+$ and $x \in [0, \infty)$. Assume that $g(n, x)$ is nondecreasing with respect to argument x . If $\{x(n)\}$ and $\{u(n)\}$ are solutions of

$$x(n+1) = f(n, x(n)) \quad \text{and} \quad u(n+1) = g(n, u(n)),$$

respectively, and $x(0) \leq u(0)$ ($x(0) \geq u(0)$), then

$$x(n) \leq u(n) \quad (x(n) \geq u(n)) \quad \text{for all } n \geq 0.$$

3. Main results

In this section, we consider the permanence of system (2.4). First, we introduce some definitions and notations, and state some results which will be useful to establish our main results. Let C denote the set of all bounded sequence $f : \mathbb{Z} \rightarrow \mathbb{R}$, C_+ is the set of all $f \in C$ such that $f > 0$. Given $f \in C_\omega := \{f \in C_+ \mid f(k + \omega) = f(k)\}$, we denote

$$f^M = \sup_{k \in [0, \omega]} f(k), \quad f^L = \inf_{k \in [0, \omega]} f(k).$$

Definition 3.1. System (2.4) is said to be *permanent* if there exist two positive constants λ_1, λ_2 such that

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

for any solution $(N_1(k), N_2(k))$ of (2.4).

The following lemma will be useful to establish our main results.

Lemma 3.1. *The problem*

$$\begin{cases} x(k + 1) = x(k) \exp \{a(k) - b(k)x(k)\}, \\ x(0) = x_0 > 0, \end{cases} \tag{3.1}$$

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 is constant if a/b is constant, in this case, $U = a/b$;
- (c) if $b(k) \equiv b$ is a constant and $(a(k))^M < 1$, then $bu(k) \leq 1$ for k sufficiently large, where $u(k)$ is any solution of Eq. (3.1).

Proof. Notice that in Eq. (2.4), let $\alpha_1(k) \equiv 0$, $\tau_1 = 0$, then (2.4) can be reduced to

$$\begin{cases} N_1(k + 1) = N_1(k) \exp\{b_1(k) - a_1(k)N_1(k)\}, \\ N_2(k + 1) = N_2(k) \exp\{-b_2(k) + \frac{\alpha_2(k)N_1^2(k - [\tau_2])}{N_1^2(k - [\tau_2]) + m^2N_2^2(k - [\tau_2])}\}, \end{cases} \tag{3.2}$$

and the condition (H1) of Lemma 2.1 reduces to $\bar{b}_1 > 0$. By Lemma 2.1, Eq. (3.2) has at least one positive ω -periodic solution provided that $\bar{b}_1 > 0$ and $\bar{\alpha}_2 > \bar{b}_2$. And this implies that

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

has at least one positive ω -periodic solution under the assumptions of Lemma 3.1. The proof of (a) is complete.

The proof of (b) is obvious, we omit it here.

For the rest, we only need to prove (c). Given any solution $u(k)$ of (3.1), let $v(k) = bu(k)$, then from (3.1), we have

$$\begin{aligned} v(k + 1) &= bu(k) \exp\{a(k) - bu(k)\} = v(k) \exp\{a(k) - v(k)\} \\ &\leq v(k) \exp\{(a(k))^M - v(k)\}. \end{aligned} \tag{3.3}$$

Consider the auxiliary equation

$$V(k + 1) = V(k) \exp\{(a(k))^M - V(k)\}. \tag{3.4}$$

It is easy to show that Eq. (3.4) is a population model, notice that $v(0) = bu(0) > 0$, then by Theorem 2.1, we have $\lim_{k \rightarrow \infty} V(k) = (a(k))^M$. Thus $(a(k))^M < 1$ implies all solutions of Eq. (3.4) are less than 1 when k is sufficiently large. Then from Lemma 2.2, we know that $bu(k) \leq 1$ for k sufficiently large. This complete the proof. \square

Theorem 3.1. *Assume that (H1), (H2), and*

$$(b_2(k))^M < 1 \tag{3.5}$$

hold. Then system (2.4) is permanent.

To prove this theorem, we need the following several propositions. For the rest of this paper, we consider the solution of (2.4) with initial conditions (2.5). For the definition of semicycle and other related concepts, we refer to the monograph [1]. And in what follows, for $\sum_{i=m}^n f(i)$, we define its value as zero if $n < m$.

Proposition 3.1. *There exists a positive constant K_1 such that*

$$\limsup_{k \rightarrow \infty} N_1(k) \leq K_1.$$

Proof. Given any positive solution $(N_1(k), N_2(k))$ of (2.4), from the first equation of (2.4), we have

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

Let $x(k) = \ln(N_1(k))$, then

$$x(k+1) - x(k) \leq b_1(k) - a_1(k) \exp\{x(k - [\tau_1])\},$$

thus

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

that is,

$$x(k) - \sum_{i=k-[\tau_1]}^{k-1} b_1(i) \leq x(k - [\tau_1]),$$

hence

$$\begin{aligned} N_1(k - [\tau_1]) &= \exp\{x(k - [\tau_1])\} \\ &\geq \exp\left\{x(k) - \sum_{i=k-[\tau_1]}^{k-1} b_1(i)\right\} = N_1(k) \exp\left\{-\sum_{i=k-[\tau_1]}^{k-1} b_1(i)\right\}. \end{aligned}$$

Therefore

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

Consider the following auxiliary equation:

$$z(k+1) = z(k) \exp\left\{b_1(k) - a_1(k)z(k) \exp\left\{-\sum_{i=k-[\tau_1]}^{k-1} b_1(i)\right\}\right\}, \quad (3.6)$$

by Lemma 3.1, Eq. (3.6) has at least one positive ω -periodic solution, denoted as $z^*(k)$.

Let

$$y(k) = \ln(z^*(k)), \quad (3.7)$$

then

$$\begin{aligned}
 x(k+1) - x(k) &\leq b_1(k) - a_1(k) \exp\left\{-\sum_{i=k-[\tau_1]}^{k-1} b_1(i)\right\} \exp\{x(k)\}, \\
 y(k+1) - y(k) &= b_1(k) - a_1(k) \exp\left\{-\sum_{i=k-[\tau_1]}^{k-1} b_1(i)\right\} \exp\{y(k)\}.
 \end{aligned}$$

Denote $u(k) = x(k) - y(k)$, then

$$u(k+1) - u(k) \leq -a_1(k) \exp\left\{-\sum_{i=k-[\tau_1]}^{k-1} b_1(i)\right\} \exp\{y(k)\} [\exp\{u(k)\} - 1]. \tag{3.8}$$

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

$$N_1(k) < z^*(k) \leq (z^*(k))^M.$$

Either if the former holds, then by (3.8), we have $u(k+1) < u(k)$, which means that $u(k)$ is eventually decreasing, also in terms of its positivity, we obtain that $\lim_{k \rightarrow \infty} u(k)$ exists. Then (3.8) leads to $\lim_{k \rightarrow \infty} u(k) = 0$, this implies

$$\limsup_{k \rightarrow \infty} N_1(k) \leq (z^*(k))^M.$$

Now we assume that $u(k)$ oscillates about zero, by (3.8), we know that if $u(k) > 0$, then $u(k+1) \leq u(k)$. Thus, if we let $\{u(l)\}$ be a subsequence of $\{u(k)\}$ in which $u(l)$ will be the first element of the l th positive semicycle of $\{u(k)\}$, then $\limsup_{k \rightarrow \infty} u(k) = \limsup_{l \rightarrow \infty} u(l)$. From

$$\begin{aligned}
 u(l) &\leq u(l-1) \\
 &\quad - a_1(l-1) \exp\left\{-\sum_{i=l-1-[\tau_1]}^{l-2} b_1(i)\right\} \exp\{y(l-1)\} [\exp\{u(l-1)\} - 1],
 \end{aligned}$$

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

$$\begin{aligned}
 u(l) &\leq a_1(l-1) \exp\left\{-\sum_{i=l-1-[\tau_1]}^{l-2} b_1(i)\right\} \exp\{y(l-1)\} [1 - \exp\{u(l-1)\}] \\
 &\leq a_1(l-1) \exp\left\{-\sum_{i=l-1-[\tau_1]}^{l-2} b_1(i)\right\} \exp\{y(l-1)\} \\
 &\leq \left(a_1(l-1) \exp\left\{-\sum_{i=l-1-[\tau_1]}^{l-2} b_1(i)\right\} \exp\{y(l-1)\}\right)^M.
 \end{aligned}$$

Therefore

$$\limsup_{k \rightarrow \infty} u(l) \leq \left(a_1(l-1) \exp\left\{-\sum_{i=l-1-[\tau_1]}^{l-2} b_1(i)\right\} \exp\{y(l-1)\}\right)^M.$$

By the medium of (3.7), we have $\limsup_{k \rightarrow \infty} N_1(k) \leq K_1$, where

$$K_1 = (z^*(k))^M \exp \left\{ \left(a_1(k) z^*(k) \exp \left\{ - \sum_{i=k-\lceil \tau_1 \rceil}^{k-1} b_1(i) \right\} \right)^M \right\}. \quad \square$$

Proposition 3.2. *Under the condition (H1), there exists a positive constant k_1 such that*

$$\liminf_{k \rightarrow \infty} N_1(k) \geq k_1.$$

Proof. Given any positive solution $(N_1(k), N_2(k))$ of (2.4), from the first equation of (2.4), we have

$$N_1(k+1) \geq N_1(k) \exp \left\{ b_1(k) - \frac{\alpha_1(k)}{2m} - a_1(k) N_1(k - \lceil \tau_1 \rceil) \right\}.$$

Let $x(k) = \ln(N_1(k))$. Then

$$x(k+1) - x(k) \geq b_1(k) - \frac{\alpha_1(k)}{2m} - a_1(k) \exp\{x(k - \lceil \tau_1 \rceil)\},$$

thus

$$\sum_{i=k-\lceil \tau_1 \rceil}^{k-1} (x(i+1) - x(i)) \geq \sum_{i=k-\lceil \tau_1 \rceil}^{k-1} \left(b_1(i) - \frac{\alpha_1(i)}{2m} - a_1(i) K_1 \right),$$

that is,

$$x(k - \lceil \tau_1 \rceil) \leq x(k) - \sum_{i=k-\lceil \tau_1 \rceil}^{k-1} \left(b_1(i) - \frac{\alpha_1(i)}{2m} - a_1(i) K_1 \right),$$

then

$$\begin{aligned} N_1(k - \lceil \tau_1 \rceil) &= \exp\{x(k - \lceil \tau_1 \rceil)\} \\ &\leq \exp \left\{ x(k) - \sum_{i=k-\lceil \tau_1 \rceil}^{k-1} \left(b_1(i) - \frac{\alpha_1(i)}{2m} - a_1(i) K_1 \right) \right\} \\ &= N_1(k) \exp \left\{ - \sum_{i=k-\lceil \tau_1 \rceil}^{k-1} \left(b_1(i) - \frac{\alpha_1(i)}{2m} - a_1(i) K_1 \right) \right\}. \end{aligned}$$

Therefore

$$\begin{aligned} N_1(k+1) &\geq N_1(k) \exp \left\{ b_1(k) - \frac{\alpha_1(k)}{2m} \right. \\ &\quad \left. - N_1(k) a_1(k) \exp \left\{ - \sum_{i=k-\lceil \tau_1 \rceil}^{k-1} \left(b_1(i) - \frac{\alpha_1(i)}{2m} - a_1(i) K_1 \right) \right\} \right\}. \end{aligned}$$

Consider the following auxiliary equation:

$$z(k+1) = z(k) \exp \left\{ b_1(k) - \frac{\alpha_1(k)}{2m} - z(k) a_1(k) \exp \left\{ - \sum_{i=k-\lceil \tau_1 \rceil}^{k-1} \left(b_1(i) - \frac{\alpha_1(i)}{2m} - a_1(i) K_1 \right) \right\} \right\}, \tag{3.9}$$

by Lemma 3.1, Eq. (3.9) has at least one positive ω -periodic solution, denoted as $z_1^*(k)$.

Let

$$y(k) = \ln(z_1^*(k)), \tag{3.10}$$

then

$$x(k+1) - x(k) \geq b_1(k) - \frac{\alpha_1(k)}{2m} - a_1(k) \exp \left\{ - \sum_{i=k-\lceil \tau_1 \rceil}^{k-1} \left(b_1(i) - \frac{\alpha_1(i)}{2m} - a_1(i) K_1 \right) \right\} \exp\{x(k)\},$$

and

$$y(k+1) - y(k) = b_1(k) - \frac{\alpha_1(k)}{2m} - a_1(k) \exp \left\{ - \sum_{i=k-\lceil \tau_1 \rceil}^{k-1} \left(b_1(i) - \frac{\alpha_1(i)}{2m} - a_1(i) K_1 \right) \right\} \exp\{y(k)\}.$$

Denote $u(k) = x(k) - y(k)$, then

$$u(k+1) - u(k) \geq -a_1(k) \exp \left\{ - \sum_{i=k-\lceil \tau_1 \rceil}^{k-1} \left(b_1(i) - \frac{\alpha_1(i)}{2m} - a_1(i) K_1 \right) \right\} \times \exp\{y(k)\} [\exp\{u(k)\} - 1]. \tag{3.11}$$

If $u(k)$ does not oscillate, then by a similar analysis as that in Proposition 3.1, we have

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

Either if $u(k)$ oscillates about zero, by (3.11), we know that if $u(k) < 0$, then $u(k+1) \geq u(k)$. Thus, if we let $\{u(l)\}$ be a subsequence of $\{u(k)\}$ in which $u(l)$ will be the first element of the l th negative semicycle of $\{u(k)\}$, then $\liminf_{k \rightarrow \infty} u(k) = \liminf_{l \rightarrow \infty} u(l)$. From

$$u(l) \geq u(l-1) - a_1(l-1) \exp \left\{ - \sum_{i=l-1-\lceil \tau_1 \rceil}^{l-2} \left(b_1(i) - \frac{\alpha_1(i)}{2m} - a_1(i) K_1 \right) \right\} \times \exp\{y(l-1)\} [\exp\{u(l-1)\} - 1]$$

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

$$\begin{aligned}
u(l) &\geq a_1(l-1) \exp\left\{-\sum_{i=l-1-[\tau_1]}^{l-2} \left(b_1(i) - \frac{\alpha_1(i)}{2m} - a_1(i)K_1\right)\right\} \\
&\quad \times \exp\{y(l-1)\}[1 - \exp\{u(l-1)\}] \\
&\geq -a_1(l-1) \exp\left\{-\sum_{i=l-1-[\tau_1]}^{l-2} \left(b_1(i) - \frac{\alpha_1(i)}{2m} - a_1(i)K_1\right)\right\} \exp\{y(l-1)\} \\
&\geq \left(-a_1(l-1)z_1^*(l-1) \exp\left\{-\sum_{i=l-1-[\tau_1]}^{l-2} \left(b_1(i) - \frac{\alpha_1(i)}{2m} - a_1(i)K_1\right)\right\}\right)^L.
\end{aligned}$$

Therefore

$$\begin{aligned}
\liminf_{l \rightarrow \infty} u(l) &\geq \left(-a_1(l-1)z_1^*(l-1)\right. \\
&\quad \left. \times \exp\left\{-\sum_{i=l-1-[\tau_1]}^{l-2} \left(b_1(i) - \frac{\alpha_1(i)}{2m} - a_1(i)K_1\right)\right\}\right)^L.
\end{aligned}$$

By the medium of (3.10), we have

$$\begin{aligned}
\liminf_{k \rightarrow \infty} N_1(k) &\geq (z_1^*(k))^L \exp\left\{\left(-a_1(l-1)z_1^*(l-1)\right.\right. \\
&\quad \left.\left. \times \exp\left\{-\sum_{i=l-1-[\tau_1]}^{l-2} \left(b_1(i) - \frac{\alpha_1(i)}{2m} - a_1(i)K_1\right)\right\}\right)^L\right\},
\end{aligned}$$

therefore $\liminf_{k \rightarrow \infty} N_1(k) \geq k_1$, where

$$\begin{aligned}
k_1 &= (z_1^*(k))^L \exp\left\{\left(-a_1(k)z_1^*(k)\right.\right. \\
&\quad \left.\left. \times \exp\left\{-\sum_{i=k-[\tau_1]}^{k-1} \left(b_1(i) - \frac{\alpha_1(i)}{2m} - a_1(i)K_1\right)\right\}\right)^L\right\}. \quad \square
\end{aligned}$$

Proposition 3.3. *If (3.5), then there exists a positive constant K_2 such that*

$$\limsup_{k \rightarrow \infty} N_2(k) \leq K_2.$$

Proof. Given any positive solution $(N_1(k), N_2(k))$ of (2.4), let $N_2(k) = 1/w(k)$, from the second equation of (2.4), we have

$$w(k+1) = w(k) \exp\left\{b_2(k) - \frac{\alpha_2(k)N_1^2(k - [\tau_2])w^2(k - [\tau_2])}{N_1^2(k - [\tau_2])w^2(k - [\tau_2]) + m^2}\right\},$$

then

$$w(k+1) \geq w(k) \exp\{b_2(k) - \alpha_2(k)\}, \tag{3.12}$$

and by the inequality $a^2 + b^2 \geq 2ab$, we have

$$w(k + 1) \geq w(k) \exp \left\{ b_2(k) - \frac{\alpha_2(k)K_1 w(k - [\tau_2])}{2m} \right\}. \tag{3.13}$$

Let $y(k) = \ln(w(k))$, then from (3.12), we have

$$y(k + 1) - y(k) \geq b_2(k) - \alpha_2(k),$$

thus

$$\sum_{i=k-[\tau_2]}^{k-1} (y(i + 1) - y(i)) \geq \sum_{i=k-[\tau_2]}^{k-1} (b_2(i) - \alpha_2(i)),$$

which is equivalent to

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

then

$$\begin{aligned} w(k - [\tau_2]) = \exp\{y(k - [\tau_2])\} &\leq \exp \left\{ y(k) - \sum_{i=k-[\tau_2]}^{k-1} (b_2(i) - \alpha_2(i)) \right\} \\ &= w(k) \exp \left\{ - \sum_{i=k-[\tau_2]}^{k-1} (b_2(i) - \alpha_2(i)) \right\}. \end{aligned}$$

Therefore by (3.13), we have

$$\begin{aligned} w(k + 1) &\geq w(k) \exp \left\{ b_2(k) - \frac{\alpha_2(k)K_1}{2m} \exp \left\{ - \sum_{i=k-[\tau_2]}^{k-1} (b_2(i) - \alpha_2(i)) \right\} \right\} \\ &\geq w(k) \exp \left\{ b_2(k) - \left(\frac{\alpha_2(k)K_1}{2m} \exp \left\{ - \sum_{i=k-[\tau_2]}^{k-1} (b_2(i) - \alpha_2(i)) \right\} \right)^M w(k) \right\}. \end{aligned}$$

Consider the following auxiliary equation:

$$z(k + 1) = z(k) \exp \left\{ b_2(k) - \left(\frac{\alpha_2(k)K_1}{2m} \exp \left\{ - \sum_{i=k-[\tau_2]}^{k-1} (b_2(i) - \alpha_2(i)) \right\} \right)^M z(k) \right\}, \tag{3.14}$$

by Lemma 3.1, Eq. (3.14) has at least one positive ω -periodic solution, denoted as $z_3^*(k)$.

Also in view of (3.5), by Lemma 2.2 and part (c) of Lemma 3.1, we know $w(k) \geq z_3^*(k)$. Therefore

$$\liminf_{k \rightarrow \infty} w(k) \geq (z_3^*(k))^L.$$

If we choose

$$K_2 = \frac{1}{(z_3^*(k))^L},$$

then by the medium of $N_2(k) = 1/w(k)$, we have $\limsup_{k \rightarrow \infty} N_2(k) \leq K_2$. \square

Proposition 3.4. *Under the condition (H2), there exists a positive constant k_2 such that*

$$\liminf_{k \rightarrow \infty} N_2(k) \geq k_2.$$

Proof. Given any positive solution $(N_1(k), N_2(k))$ of (2.4), from the second equation of (2.4), we have

$$\begin{aligned} N_2(k+1) &= N_2(k) \exp \left\{ -b_2(k) + \frac{\alpha_2(k)N_1^2(k - [\tau_2])}{N_1^2(k - [\tau_2]) + m^2N_2^2(k - [\tau_2])} \right\} \\ &= N_2(k) \exp \left\{ \alpha_2(k) - b_2(k) \right. \\ &\quad \left. + \alpha_2(k) \left[\frac{N_1^2(k - [\tau_2])}{N_1^2(k - [\tau_2]) + m^2N_2^2(k - [\tau_2])} - 1 \right] \right\} \\ &= N_2(k) \exp \left\{ \alpha_2(k) - b_2(k) \right. \\ &\quad \left. - \alpha_2(k) \left[\frac{m^2N_2^2(k - [\tau_2])}{N_1^2(k - [\tau_2]) + m^2N_2^2(k - [\tau_2])} \right] \right\}, \end{aligned}$$

by the inequality $a^2 + b^2 \geq 2ab$, we have

$$N_2(k+1) \geq N_2(k) \exp \left\{ \alpha_2(k) - b_2(k) - \frac{\alpha_2(k)mN_2(k - [\tau_2])}{2k_1} \right\}. \quad (3.15)$$

In view of

$$\begin{aligned} N_2(k+1) &= N_2(k) \exp \left\{ -b_2(k) + \frac{\alpha_2(k)N_1^2(k - [\tau_2])}{N_1^2(k - [\tau_2]) + m^2N_2^2(k - [\tau_2])} \right\} \\ &\geq N_2(k) \exp \{-b_2(k)\}, \end{aligned}$$

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

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

that is,

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

then

$$\begin{aligned} N_2(k - [\tau_2]) &= \exp\{y(k - [\tau_2])\} \leq \exp\left\{y(k) + \sum_{i=k-[\tau_2]}^{k-1} (b_2(i))\right\} \\ &= N_2(k) \exp\left\{\sum_{i=k-[\tau_2]}^{k-1} (b_2(i))\right\}. \end{aligned}$$

Therefore from (3.15), we have

$$N_2(k + 1) \geq N_2(k) \exp\left\{\alpha_2(k) - b_2(k) - N_2(k) \frac{\alpha_2(k)m}{2k_1} \exp\left\{\sum_{i=k-[\tau_2]}^{k-1} (b_2(i))\right\}\right\}.$$

Consider the auxiliary equation

$$z(k + 1) = z(k) \exp\left\{\alpha_2(k) - b_2(k) - z(k) \frac{\alpha_2(k)m}{2k_1} \exp\left\{\sum_{i=k-[\tau_2]}^{k-1} (b_2(i))\right\}\right\}, \quad (3.16)$$

by Lemma 3.1 and (H2), Eq. (3.16) has at least one positive ω -periodic solution, denoted as $z_2^*(k)$.

Let

$$x(k) = \ln(z_2^*(k)), \quad (3.17)$$

then

$$\begin{aligned} y(k + 1) - y(k) &\geq \alpha_2(k) - b_2(k) - \frac{\alpha_2(k)m}{2k_1} \exp\left\{\sum_{i=k-[\tau_2]}^{k-1} (b_2(i))\right\} \exp\{y(k)\}, \\ x(k + 1) - x(k) &= \alpha_2(k) - b_2(k) - \frac{\alpha_2(k)m}{2k_1} \exp\left\{\sum_{i=k-[\tau_2]}^{k-1} (b_2(i))\right\} \exp\{x(k)\}. \end{aligned}$$

Denote $u(k) = y(k) - x(k)$, then

$$u(k + 1) - u(k) \geq -\frac{\alpha_2(k)m}{2k_1} \exp\left\{\sum_{i=k-[\tau_2]}^{k-1} (b_2(i))\right\} \exp\{x(k)\} [\exp\{u(k)\} - 1]. \quad (3.18)$$

If $u(k)$ does not oscillate, then by a similar analysis as that in Proposition 3.1, we have

$$\liminf_{k \rightarrow \infty} N_2(k) \geq (z_2^*(k))^L.$$

Either if $u(k)$ oscillates about zero, by (3.18), we know that if $u(k) < 0$, then $u(k + 1) \geq u(k)$. Thus, if we let $\{u(l)\}$ be a subsequence of $\{u(k)\}$ in which $u(l)$ will be the first element of the l th negative semicycle of $\{u(k)\}$, then $\liminf_{k \rightarrow \infty} u(k) = \liminf_{l \rightarrow \infty} u(l)$. From

$$\begin{aligned} u(l) &\geq u(l - 1) - \frac{\alpha_2(l - 1)m}{2k_1} \exp\left\{\sum_{i=l-1-[\tau_2]}^{l-2} (b_2(i))\right\} \\ &\quad \times \exp\{x(l - 1)\} [\exp\{u(l - 1)\} - 1], \end{aligned}$$

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

$$\begin{aligned} u(l) &\geq \frac{\alpha_2(l-1)m}{2k_1} \exp\left\{\sum_{i=l-1-[\tau_2]}^{l-2} (b_2(i))\right\} \exp\{x(l-1)\} [1 - \exp\{u(l-1)\}] \\ &\geq -\frac{\alpha_2(l-1)m}{2k_1} \exp\left\{\sum_{i=l-1-[\tau_2]}^{l-2} (b_2(i))\right\} \exp\{x(l-1)\} \\ &\geq \left(-\frac{m\alpha_2(l-1)z_2^*(l-1)}{2k_1} \exp\left\{\sum_{i=l-1-[\tau_2]}^{l-2} (b_2(i))\right\}\right)^L. \end{aligned}$$

Therefore

$$\liminf_{l \rightarrow \infty} u(l) \geq \left(-\frac{m\alpha_2(l-1)z_2^*(l-1)}{2k_1} \exp\left\{\sum_{i=l-1-[\tau_2]}^{l-2} (b_2(i))\right\}\right)^L.$$

By the medium of (3.17), we have

$$\liminf_{k \rightarrow \infty} N_1(k) \geq (z_2^*(k))^L \exp\left\{\left(-\frac{m\alpha_2(l-1)z_2^*(l-1)}{2k_1} \exp\left\{\sum_{i=l-1-[\tau_2]}^{l-2} (b_2(i))\right\}\right)^L\right\},$$

therefore $\liminf_{k \rightarrow \infty} N_1(k) \geq k_2$, where

$$k_2 = (z_2^*(k))^L \exp\left\{\left(-\frac{m\alpha_2(k)z_2^*(k)}{2k_1} \exp\left\{\sum_{i=k-[\tau_2]}^{k-1} (b_2(i))\right\}\right)^L\right\}. \quad \square$$

Proof of Theorem 3.1. From the Propositions 3.1–3.4, we can easily know that system (2.4) is permanent. The proof is complete. \square

4. Discussion

In what above we have obtained sufficient conditions for the permanence of Eq. (2.4) in which the coefficients are periodic. For the system with the corresponding continuous system, in [27], Wang and Li established verifiable criteria for the permanence of the periodic system (1.3) and found that for (1.3), the criteria for the permanence is exactly the same as that for the existence of the positive periodic solution. But for the corresponding discrete system (2.4), to make the system be permanent, the death rate of the predator must not be too large except that the conditions for the existence of the positive periodic solution hold true. Just as pointed out in [10], even if the coefficients are constants, the asymptotical behavior of the discrete system is rather complex and contains more rich dynamics than the continuous one. Our investigation gives an affirmative explanation for this point of view. By intuition, we should believe that when the death rate of the predator is rather small as well as the intrinsic growth rate of the prey is relatively large, the two species could coexist in the long run. The conclusion we obtain here exactly confirm this.

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