

Study on periodic solutions for a class of ecological models

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Abstract: We consider a non-autonomous predator-prey model with nonmonotonic functional response in a periodic environment. Some new sufficient conditions are obtained for the nonexistence of periodic solutions and the global existence of at least one or two positive periodic solutions. Our method is based on Mawhin's coincidence degree and novel estimation techniques for the priori bounds of unknown solutions.

Key words: periodic solution; coincidence degree; predator-prey model; nonmonotonic functional response

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1 Introduction

The dynamic relationship between predators and their preys has been and will continue to be one of the dominant themes in both ecology and mathematical ecology due to its universal importance^[1-4]. In modelling different predator-prey systems, Holling^[5] proposed three types of monotonic functional responses $g(x) = \frac{x}{m+x}$, $\frac{x^2}{m+x^2}$. Monotonic response functions are appropriate in many predator-prey models. However there are experiments that indicate that nonmonotonic responses occur for example in the cases of 'inhibition' in microbial dynamics and group defence in population dynamics^[6-9]. Unlike monotonic responses, nonmonotonic responses are humped and decline at high prey density x . Indeed, the so-called Holling type IV functional response $g(x) = \frac{x}{a+x+\frac{x^2}{m}}$ (which is not monotone) has been proposed and used to model the inhibitory effect at high concentrations^[7]. In [9] the authors have also considered a special predator-prey model with type IV functional response.

$$\begin{cases} \frac{dx(t)}{dt} = rx \left[1 - \frac{x(t)}{K} \right] - m \frac{x(t)y(t)}{1 + bx(t) + ax^2(t)} \\ \frac{dy(t)}{dt} = y(t) \left[-d + \frac{cmx(t)}{1 + bx(t) + ax^2(t)} \right] \end{cases}, \quad (1)$$

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where the nonmonotonic functional response is $\frac{x(t)y(t)}{1+bx(t)+ax^2(t)}$. They have investigated a series of bifurcations that system (1) undergoes including the saddle-node bifurcation, the supercritical and subcritical Hopf bifurcations as well as the homoclinic bifurcation. It is interesting that they found that the unique equilibrium is a cusp of codimension 3 (a degenerate Bogdanov-Takens bifurcation point) been carried out on the following predator-prey system with 'group' defense using the nonmonotonic functional response $g(x) = xe^{-\beta x}$ (see [10])

$$\begin{cases} \frac{dx(t)}{dt} = rx \left[1 - \frac{x(t)}{K} \right] - c x(t) y(t) e^{-\beta x(t)} \\ \frac{dy(t)}{dt} = y(t) [-d + \alpha x(t) e^{-\beta x(t)}] \end{cases} \quad (2)$$

As we know, the variation of the environment plays an important role in many biological and ecological dynamic systems. To incorporate the periodicity of the environment (e.g. seasonal effects of weather, food supplies, mating habits, etc.) it is reasonable to assume periodicity of the parameters in the system. For this reason, Chen^[11] has considered the following predator-prey system with Holling type IV functional response in a periodic environment

$$\begin{cases} \frac{dx(t)}{dt} = x(t) \left[b_1(t) - a_1(t) x(t - \tau_1(t)) \right] - \frac{c(t) x(t) y(t)}{\frac{x^2(t)}{m} + x(t) + a} \\ \frac{dy(t)}{dt} = y(t) \left[-b_2(t) + \frac{a_2(t) x(t - \tau_2(t))}{\frac{x^2(t - \tau_2(t))}{m} + x(t - \tau_2(t)) + a} \right] \end{cases}, \quad (3)$$

where $a_i(t)$, $b_i(t)$ and $\tau_i(t)$ ($i=1, 2$) are all positive periodic continuous functions with period $\omega > 0$ and m, μ are positive real constants. By applying the method of coincidence degree and the bounds for solutions to an operator equation, some sufficient conditions have been obtained for the global existence of at least two periodic solutions of system (3). By employing the theory of coincidence degree and some novel estimation techniques for the priori bounds of unknown solutions to $Lz = \lambda Nz$, Xia et al^[12-13] obtained some sufficient conditions for the discrete model and the stage-structured model with nonmonotonic functional response respectively.

Coincidence degree theory recently introduced by Gaines and Mawhin^[14] is a powerful tool to investigate periodic non-autonomous systems. It has gained increasing interest in many applications to biological systems (see [11-15]). Motivated by aforementioned discussions, in the present paper we propose the following more general nonautonomous models with nonmonotonic functional response g :

$$\begin{cases} \dot{x}(t) = x(t) [a(t) - b(t)x(t)] - c(t)g(x(t))y(t) \\ \dot{y}(t) = y(t) [-d(t) + e(t)g(x(t))] \end{cases}, \quad (4)$$

and

$$\begin{cases} \dot{x}(t) = x(t) [a(t) - b(t)x(t - \tau_1(t))] - c(t)g(x(t))y(t) \\ \dot{y}(t) = y(t) [-d(t) + e(t)g(x(t - \tau_2(t)))] \end{cases}, \quad (5)$$

where $x(t)$ and $y(t)$ represent prey and predator densities, respectively. $a(t)$, $b(t)$, $c(t)$, $d(t)$, $e(t)$, $\pi_1(t)$ and $\tau_2(t)$ are all nonnegative periodic continuous functions with period $\omega > 0$. We assume the functional response $g: [0, \infty) \rightarrow [0, \infty)$ is continuous and satisfies the (NM) ('nonmonotonic') condition:

- (i) $g(0) = 0$;
- (ii) there exists a constant $M > 0$ such that $(x - M)g'(x) < 0$ for $x \neq M$.

Clearly g is increasing on $[0, M]$, decreasing on (M, ∞) and $g(x) \leq g(M)$ for $x \geq 0$. Also it is easy to see that the functions

$$g(x) = \frac{x}{m^2 + x^2}, \quad g(x) = xe^{-\beta x} \quad \text{and} \quad g(x) = \frac{x}{\frac{x^2}{m} + x + a}$$

appearing in (1) – (3) satisfy conditions (i) – (ii). Obviously, the systems (1) – (3) are special cases of system (4) or (5).

Throughout, if $f(t)$ is an ω -periodic function, we shall set

$$\bar{f} = \frac{1}{\omega} \int_0^\omega f(t) dt.$$

Clearly $\bar{f} > 0$ if $f(t) > 0$ a. e. $t \in [0, \omega]$. We also set

$$D = \frac{\bar{d}}{e}.$$

From the point of view of mathematical biology, we choose $\mathbb{R}_+^2 = \{(x, y)^T \in \mathbb{R}^2 : x > 0, y > 0\}$ as the state space for (4) and (5).

We shall study the global existence of ω -periodic solutions of (4) and (5) using $D = \frac{\bar{d}}{e}$ as the bifurcation parameter. Some new and interesting sufficient conditions are obtained for the *nonexistence* of periodic solutions, global existence of at least one positive periodic solution and global existence of at least two positive periodic solutions. When system (F) reduces to the particular case (3), our results generalize the previous results in [11]. Our method is based on Mawhin's coincidence degree and novel estimation techniques for the a priori bounds of unknown solutions. We will introduce some novel estimation techniques for the a priori bounds of unknown solutions to $Lz = \lambda Nz$, which are much different from the arguments used in the existing literature^[11-15].

2 Nonexistence

We shall first give a necessary condition for the existence of periodic positive solutions of the system (4).

Theorem 2.1 If the system (4) has a positive ω -periodic solution, then $g(M) \geq D$.

Proof We make the change of variables

$$x(t) = \exp\{u(t)\} \quad \text{and} \quad y(t) = \exp\{v(t)\}. \tag{6}$$

Then, system (4) becomes

$$\begin{cases} \dot{u}(t) = a(t) - b(t) \exp\{u(t)\} - c(t) g(\exp\{u(t)\}) \exp\{v(t) - u(t)\} \\ \dot{v}(t) = -d(t) + e(t) g(\exp\{u(t)\}) \end{cases} \tag{7}$$

Obviously, system (4) is equivalent to system (7) on \mathbb{R}_+^2 . Suppose system (7) has an ω -periodic solution $(u(t), v(t))^T$, i. e. $u(t + \omega) = u(t)$ and $v(t + \omega) = v(t)$. An integration of the second equation of (7) over $[0, \omega]$ leads to

$$v(\omega) - v(0) = \int_0^\omega [-d(t) + e(t) g(\exp\{u(t)\})] dt,$$

or

$$0 = -\bar{d}\omega + \int_0^\omega e(t) g(\exp\{u(t)\}) dt. \quad (8)$$

Since $g(M)$ is the maximum of $g(x)$, it follows from (6) that

$$\bar{d}\omega = \int_0^\omega e(t) g(\exp\{u(t)\}) dt \leq g(M) \bar{e}\omega,$$

which implies

$$g(M) \geq \frac{\bar{d}}{\bar{e}} = D.$$

This completes the proof of Theorem 2.1.

The following is immediate from Theorem 2.1.

Theorem 2.2 If $g(M) < D$ then the system (4) has no positive ω -periodic solution.

3 Existence of one periodic solution

In this section, we shall apply the continuation theorem of Mawhin's coincidence degree theory to establish the global existence of at least one positive periodic solution. We first summarize a few concepts from the book by Gaines and Mawhin^[14].

Let X, Y be real normed vector spaces. $L: \text{Dom}L \subset X \rightarrow Y$ be a linear mapping and $N: X \rightarrow Y$ be a continuous mapping. The mapping L is called a Fredholm mapping of index zero if $\dim \text{Ker}L = \text{codim Im}L < \infty$ and $\text{Im}L$ is closed in Y . If L is a Fredholm mapping of index zero, there exist continuous projectors $P: X \rightarrow X$ and $Q: Y \rightarrow Y$ such that $\text{Im}P = \text{Ker}L$, $\text{Ker}Q = \text{Im}L = \text{Im}(I - Q)$. It follows that $L|_{\text{Dom}L \cap \text{Ker}P}: (I - P)X \rightarrow \text{Im}L$ is invertible. Let the inverse of that map be denoted by K_p . If Ω is an open bounded subset of X , the mapping N will be called L -compact on $\bar{\Omega}$ if $QN(\bar{\Omega})$ is bounded and $K_p(I - Q)N: \bar{\Omega} \rightarrow X$ is compact. Since $\text{Im}Q$ is isomorphic to $\text{Ker}L$, there exists an isomorphism $J: \text{Im}Q \rightarrow \text{Ker}L$.

Lemma 3.1 (Continuation theorem^[14]) Let L be a Fredholm mapping of index zero and N be L -compact on $\bar{\Omega}$. Suppose

- (a) for each $\lambda \in (0, 1)$, every solution z of $Lz = \lambda Nz$ is such that $z \notin \partial\Omega$;
- (b) $QNz \neq 0$ for each $z \in \partial\Omega \cap \text{Ker}L$ and $\deg\{JQN, \Omega \cap \text{Ker}L, 0\} \neq 0$.

Then, the operator equation $Lz = Nz$ has at least one solution lying in $\text{Dom}L \cap \bar{\Omega}$.

Theorem 3.1 Assume that

- (H₁) $g(M) = D$;
- (H₂) $\bar{a} > \bar{b}M \exp\{(|\bar{a}| + \bar{a})\omega\}$.

Then, system (4) has at least one positive ω -periodic solution.

Proof We shall consider system (7) (equivalent to (4)). Take

$$X = Y = \{z = (u(t), p(t))^T \in C(\mathbb{R}, \mathbb{R}^2) : z(t + \omega) = z(t)\}$$

and define

$$\|z\| = \max_{t \in [0, \omega]} |u(t)| + \max_{t \in [0, \omega]} |v(t)|, z = (u, p)^T \in X \text{ or } Y,$$

where $|\cdot|$ denotes the Euclidean norm. Then X and Y are Banach spaces with the norm $\|\cdot\|$. For any $z = (u, p)^T \in X$, by means of the periodicity assumption, we can easily check that

$$\begin{aligned} \Delta_1(z, t) &:= a(t) - b(t) \exp\{u(t)\} - c(t) g(\exp\{u(t)\}) \exp\{v(t) - u(t)\}, \\ \Delta_2(z, t) &:= -d(t) + e(t) g(\exp\{u(t)\}) \end{aligned}$$

are ω -periodic. Define L on $\text{Dom}L \cap X$, where $\text{Dom}L = \{(u(t), p(t))^T \in C^1(\mathbb{R}, \mathbb{R}^2)\}$, by

$$L \begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} \frac{du(t)}{dt} \\ \frac{dv(t)}{dt} \end{pmatrix},$$

and also define $N: X \rightarrow X$ P and Q on X as following:

$$N \begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} \Delta_1(z, t) \\ \Delta_2(z, t) \end{pmatrix},$$

$$P \begin{pmatrix} u \\ v \end{pmatrix} = Q \begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} \frac{1}{\omega} \int_0^\omega u(t) dt \\ \frac{1}{\omega} \int_0^\omega v(t) dt \end{pmatrix}.$$

It is not difficult to show that

$$\begin{aligned} \text{Ker}L &= \{z \in X: z = C_0, C_0 \in \mathbb{R}^2\}, \\ \text{Im}L &= \{z \in Y: \int_0^\omega z(t) dt = 0\} \text{ is closed in } Y, \\ \dim \text{Ker}L &= \text{codim Im } L = 2, \end{aligned}$$

P and Q are continuous projectors such that

$$\text{Im}P = \text{Ker}L, \text{Ker}Q = \text{Im}L = \text{Im}(I - Q).$$

It follows that L is a Fredholm mapping of index zero. Furthermore, the generalized inverse (to L) $K_p: \text{Im}L \rightarrow \text{Dom}L \cap \text{Ker}P$ exists and is given by

$$K_p(z) = \int_0^t z(s) ds - \frac{1}{\omega} \int_0^\omega \int_0^t z(s) ds dt.$$

Then $QN: X \rightarrow Y$ and $K_p(I - Q)N: X \rightarrow X$ are defined by

$$QNz = \begin{pmatrix} \frac{1}{\omega} \int_0^\omega \Delta_1(z, t) dt \\ \frac{1}{\omega} \int_0^\omega \Delta_2(z, t) dt \end{pmatrix} \text{ and } K_p(I - Q)Nz = \begin{pmatrix} \Psi_1(z, t) \\ \Psi_2(z, t) \end{pmatrix},$$

where

$$\Psi_i(z, t) = \int_0^t \Delta_i(z, s) ds - \frac{1}{\omega} \int_0^\omega \int_0^t \Delta_i(z, s) ds dt - \left(\frac{t}{\omega} - \frac{1}{2}\right) \int_0^\omega \Delta_i(z, s) ds \quad i = 1, 2.$$

Clearly QN and $K_p(I - Q)N$ are continuous. By using the Arzela - Ascoli Theorem, it is not difficult to prove that $\overline{K_p(I - Q)N(\overline{\Omega})}$ is compact for any open bounded set $\Omega \subset X$. Moreover, $QN(\overline{\Omega})$ is bounded. Therefore, N is L -compact on $\overline{\Omega}$ for any open bounded set $\Omega \subset X$.

Now we need to search for an appropriate open bounded subset Ω for the application of Lemma 3.1.

Corresponding to the operator equation $Lz = \lambda Nz$, where $\lambda \in (0, 1)$, we have

$$\begin{cases} \dot{u}(t) = \lambda [a(t) - b(t) \exp\{u(t)\} - c(t) g(\exp\{u(t)\}) \exp\{v(t) - u(t)\}] \\ \dot{v}(t) = \lambda [-d(t) + e(t) g(\exp\{u(t)\})] \end{cases}, \quad (9)$$

Suppose that $z = (u(t), v(t))^T \in X$ is a solution of (9) for a certain $\lambda \in (0, 1)$. An integration of (9) over $[0, \omega]$ leads to

$$\begin{cases} \int_0^{\omega} [a(t) - b(t) \exp\{u(t)\} - c(t) g(\exp\{u(t)\}) \exp\{v(t) - u(t)\}] dt = 0 \\ \int_0^{\omega} [-d(t) + e(t) g(\exp\{u(t)\})] dt = 0 \end{cases},$$

or

$$\int_0^{\omega} b(t) \exp\{u(t)\} dt + \int_0^{\omega} c(t) g(\exp\{u(t)\}) \exp\{v(t) - u(t)\} dt = \bar{a}\omega, \quad (10)$$

$$\int_0^{\omega} e(t) g(\exp\{u(t)\}) dt = \bar{d}\omega. \quad (11)$$

By the mean value theorem, there exists a $\xi \in (0, \omega)$ such that

$$\int_0^{\omega} e(t) g(\exp\{u(t)\}) dt = g(\exp\{u(\xi)\}) \int_0^{\omega} e(t) dt.$$

Since $g(M) = D = \frac{\bar{d}}{e}$, it follows from (11) that

$$\exp\{u(\xi)\} = M \quad \text{or} \quad u(\xi) = \ln M. \quad (12)$$

On the other hand, from the first equation of (9) and (10), we have

$$\begin{aligned} \int_0^{\omega} |\dot{u}(t)| dt &= \lambda \int_0^{\omega} |a(t) - b(t) \exp\{u(t)\} - c(t) g(\exp\{u(t)\}) \exp\{v(t) - u(t)\}| dt < \\ &|\bar{a}| \omega + \int_0^{\omega} b(t) \exp\{u(t)\} dt + \int_0^{\omega} c(t) g(\exp\{u(t)\}) \exp\{v(t) - u(t)\} dt = \\ &(|\bar{a}| + \bar{a}) \omega. \end{aligned} \quad (13)$$

Similarly, from the second equation of (9) and (10), it is not difficult to derive that

$$\int_0^{\omega} |\bar{v}(t)| dt < (|\bar{d}| + \bar{d}) \omega. \quad (14)$$

It follows from (12) and (13) that

$$u(t) \leq u(\xi) + \int_0^{\omega} |\dot{u}(t)| dt < \ln M + (|\bar{a}| + \bar{a}) \omega =: A_1 \quad (15)$$

and

$$u(t) \geq u(\xi) - \int_0^{\omega} |\dot{u}(t)| dt > \ln M - (|\bar{a}| + \bar{a}) \omega =: B_1. \quad (16)$$

Since $(u(t), v(t))^T \in X$, there exist $\delta, \eta \in [0, \omega]$ such that

$$v(\delta) = \min_{t \in [0, \omega]} v(t) \quad \text{and} \quad v(\eta) = \max_{t \in [0, \omega]} v(t). \quad (17)$$

Note that $g(M) = D$ is the maximum of g . Then it follows from (10), (15), (16), (17) and (H_2) that

$$\bar{b}\omega \exp\{A_1\} + \bar{c}D\omega \exp\{v(\eta) - B_1\} \geq \bar{a}\omega,$$

or

$$v(\eta) \geq \ln \frac{\bar{a} \exp\{B_1\} - \bar{b} \exp\{A_1 + B_1\}}{\bar{c}D} = \ln \frac{(\bar{a} - \bar{b}M \exp\{(|\bar{a}| + \bar{a}) \omega\}) M}{\bar{c}D \exp\{(|\bar{a}| + \bar{a}) \omega\}}. \quad (18)$$

This, combined with (14), gives

$$v(t) \geq v(\eta) - \int_0^{\omega} |\dot{v}(t)| dt > \ln \frac{(\bar{a} - \bar{b}M \exp\{(|\bar{a}| + \bar{a}) \omega\})}{\bar{c}D \exp\{(|\bar{a}| + \bar{a}) \omega\}} - (|\bar{d}| + \bar{d}) \omega =: A_2. \quad (19)$$

Note that $\exp\{B_1\} < M$ and $\exp\{A_1\} > M$. Since g is increasing on $[0, M)$ and decreasing on (M, ∞) , we have

$$g(\exp\{u(t)\}) \geq \min\{g(\exp\{B_1\}), g(\exp\{A_1\})\} \quad \mu(t) \in (B_1, A_1).$$

This, together with (10), (15), (16) and (17), leads to

$$\bar{c}\omega \min\{g(\exp\{B_1\}), g(\exp\{A_1\})\} \exp\{v(\delta) - A_1\} \leq \bar{a}\omega,$$

or

$$v(\delta) \leq \ln \frac{\bar{a}\exp\{A_1\}}{\min\{g(\exp\{B_1\}), g(\exp\{A_1\})\} \bar{c}}. \tag{20}$$

Coupled with (14) it yields

$$v(t) \leq v(\delta) + \int_0^\omega |v'(t)| dt < \ln \frac{\bar{a}\exp\{A_1\}}{\min\{g(\exp\{B_1\}), g(\exp\{A_1\})\} \bar{c}} + (|\bar{d}| + \bar{d})\omega = B_2. \tag{21}$$

Let

$$A = \max\{|A_1|, |B_1|\} \quad \text{and} \quad B = \max\{|A_2|, |B_2|\}.$$

Then from (15), (16), (19) and (20), we have $|u(t)| < A$ and $|v(t)| < B$. Clearly $A_i, B_i (i = 1, 2)$ are independent of λ .

Now consider the equation $QNz = 0$ where $z = (u, v)^T \in \mathbb{R}^2$, i. e.,

$$QN \begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} \bar{a} - \bar{b}\exp\{u\} - \bar{c}g(\exp\{u\}) \exp\{v - u\} \\ -\bar{d} + \bar{e}g(\exp\{u\}) \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}. \tag{22}$$

In view of (H_2) , we have $\bar{a} - \bar{b}M > 0$. Together with (H_1) , it is easy to show that the above system has a unique solution

$$(u^*, v^*)^T = \left(\ln M, \ln \frac{M\bar{e}(\bar{a} - \bar{b}M)}{\bar{c}\bar{d}} \right)^T.$$

Let $C > 0$ be such that

$$\|(u^*, v^*)^T\| = |u^*| + |v^*| < C.$$

Define

$$\Omega = \{z \in X : \|z\| < A + B + C\}.$$

It is clear that Ω satisfies condition (a) of Lemma 3.1. When $z = (u, v)^T \in \partial\Omega \cap \text{Ker}L = \partial\Omega \cap \mathbb{R}^2$, z is a constant vector in \mathbb{R}^2 with $\|z\| = A + B + C$, and it is clear that $QNz \neq 0$. Furthermore, let $J: \text{Im}Q \rightarrow \text{Ker}L$ be the identity mapping. In view of the assumptions in Theorem 3.1, it is easy to see that

$$\deg\{JQN, \Omega \cap \text{Ker}L, \rho\} = \text{sgndet} \begin{bmatrix} W & -\bar{c}g(\exp\{u\}) \exp\{v - u\} \\ \bar{e}g'(\exp\{u\}) \exp\{u\} & 0 \end{bmatrix} = \text{sgn}\{-\bar{c}\bar{e}g'(\exp\{u\}) \exp\{u\} \exp\{v\}\} \neq 0,$$

where $\deg(\cdot)$ is the Brouwer degree and

$$W = -\bar{b}\exp\{u\} - \bar{c}g'(\exp\{u\}) \exp\{v\} + \bar{c}g(\exp\{u\}) \exp\{v - u\}.$$

By now we have proved that Ω satisfies all the requirements of Lemma 3.1. Thus it follows that $Lz = Nz$ (i. e., system (7)) has at least one solution in $\text{Dom}L \cap \bar{\Omega}$. The proof is completed.

4 Existence of two periodic solutions

In this section we shall study system (E) under the assumption $g(M) > D$. From the (NM) condition it is easy to see that if $g(M) > D$, then the equation $g(x) = D$ has two positive solutions r_1 and r_2 such that

$$g(r_1) = g(r_2) = D \quad \text{and} \quad 0 < r_1 < M < r_2.$$

Theorem 4.1 Assume that

(H_3) $g(M) > D$;

$$(H_4) \quad \bar{a} > \bar{b}r_2 \exp\{(|\bar{a}| + \bar{a})\omega\};$$

$$(H_5) \quad r_1 \exp\{(|\bar{a}| + \bar{a})\omega\} \leq M \text{ and } r_2 \geq M \exp\{(|\bar{a}| + \bar{a})\omega\}.$$

Then the system (E) has at least two positive ω -periodic solutions.

Proof In order to prove the existence of two periodic solutions, our most important task is to search for at least two appropriate open bounded subsets Ω_1 and Ω_2 in X for the application of Lemma 3.1. Let X, Y, L, N, P and Q be defined as in the proof of Theorem 3.1 and let $z = (u(t), v(t))^T \in X$ be a solution of $Lz = \lambda Nz$ for a certain $\lambda \in (0, 1)$. As in the proof of Theorem 3.1, we have

$$\int_0^\omega b(t) \exp\{u(t)\} dt + \int_0^\omega c(t) g(\exp\{u(t)\}) \exp\{v(t) - u(t)\} dt = \bar{a}\omega, \quad (23)$$

$$\int_0^\omega e(t) g(\exp\{u(t)\}) dt = \bar{d}\omega, \quad (24)$$

and

$$\int_0^\omega |\dot{u}(t)| dt < (|\bar{a}| + \bar{a})\omega, \quad \int_0^\omega |\dot{v}(t)| dt < (|\bar{d}| + \bar{d})\omega. \quad (25)$$

Since $z = (u(t), v(t))^T \in X$, there exist $\varepsilon, \chi \in [0, \omega]$ such that

$$v(\varepsilon) = \min_{t \in [0, \omega]} v(t) \quad \text{and} \quad v(\chi) = \max_{t \in [0, \omega]} v(t). \quad (26)$$

Note that $u(t) \neq \ln M$ for $t \in [0, \omega]$, otherwise it follows from (4.2) that $\bar{d} = \bar{e}g(M)$, which is a contradiction to (H_3) . Therefore, either $u(t) \in (-\infty, \ln M)$ or $u(t) \in (\ln M, \infty)$.

Case 1 $u(t) < \ln M$ $t \in [0, \omega]$. From (24), (H_3) and the (NM) condition, there exists a $\theta_1 \in [0, \omega]$ such that

$$\bar{d}\omega = \bar{e}\omega g(\exp\{u(\theta_1)\}),$$

or

$$\exp(u(\theta_1)) = g^{-1}(D) \in (0, M) = r_1.$$

This, combined with (25) and (H_5) , gives

$$u(t) \leq u(\theta_1) + \int_0^\omega |\dot{u}(t)| dt < \ln r_1 + (|\bar{a}| + \bar{a})\omega \leq \ln M \quad (27)$$

and

$$u(t) \geq u(\theta_1) - \int_0^\omega |\dot{u}(t)| dt > \ln r_1 - (|\bar{a}| + \bar{a})\omega =: B_1^*. \quad (28)$$

It follows from (27) and (28) that

$$u(t) \in (B_1^*, \ln M). \quad (29)$$

On the other hand, from (23), (26) and (29), we find

$$\bar{c}\omega g(\exp\{B_1^*\}) \exp\{v(\varepsilon) - \ln M\} \leq \bar{a}\omega,$$

or

$$v(\varepsilon) \leq \ln \frac{\bar{a}M}{g(\exp\{B_1^*\})\bar{c}}. \quad (30)$$

This, together with (25), leads to

$$v(t) \leq v(\varepsilon) + \int_0^\omega |\dot{v}(t)| dt < \ln \frac{\bar{a}M}{g(\exp\{B_1^*\})\bar{c}} + (|\bar{d}| + \bar{d})\omega =: A_2^*. \quad (31)$$

From (H_4) and (H_5) , it is not difficult to show that $\bar{a} - \bar{b}M > 0$. It follows from (23), (26) and (29) that

$$\bar{b}\omega \exp\{\ln M\} + \bar{c}\omega g(M) \exp\{v(\chi) - B_1^*\} \geq \bar{a}\omega,$$

or

$$v(\chi) \geq \ln \frac{(\bar{a} - \bar{b} M) \exp\{B_1^*\}}{\bar{c}g(M)} = \ln \frac{(\bar{a} - \bar{b} M) r_1}{\bar{c}g(M) \exp\{(|\bar{a}| + \bar{a})\omega\}}. \tag{32}$$

Coupled with (25) ,this suggests

$$v(t) \geq v(\chi) - \int_0^\omega |\dot{v}(t)| dt > \ln \frac{(\bar{a} - \bar{b} M) r_1}{\bar{c}g(M) \exp\{(|\bar{a}| + \bar{a})\omega\}} - (|\bar{d}| + \bar{d})\omega = B_2^*. \tag{33}$$

Therefore from (31) and (33) ,we have

$$\max_{t \in [0, \omega]} |v(t)| < \max\{|A_2^*|, |B_2^*|\} = B^* \text{ for } u(t) \in (B_1^*, \ln M). \tag{34}$$

Case 2 $u(t) > \ln M \ t \in [0, \omega]$. From (24) ,(H₃) and the (NM) condition ,there exists a $\theta_2 \in [0, \omega]$ such that

$$\bar{d}\omega = \bar{e}\omega g(\exp\{u(\theta_2)\}) , \text{ or } \exp(u(\theta_2)) = g^{-1}(D) \in (M, \infty) = r_2.$$

This ,combined with (25) and (H₃) gives

$$u(t) \leq u(\theta_2) + \int_0^\omega |\dot{u}(t)| dt < \ln r_2 + (|\bar{a}| + \bar{a})\omega = A_1^+ \tag{35}$$

and

$$u(t) \geq u(\theta_2) - \int_0^\omega |\dot{u}(t)| dt > \ln r_2 - (|\bar{a}| + \bar{a})\omega \geq \ln M. \tag{36}$$

It follows from (35) and (36) that

$$u(t) \in (\ln M, A_1^+). \tag{37}$$

Since $g(x)$ is decreasing for $x \in (M, \infty)$,it follows from (23) ,(26) and (37) that

$$\bar{c}\omega g(\exp\{A_1^+\}) \exp\{v(\varepsilon) - A_1^+\} \leq \bar{a}\omega ,$$

or

$$v(\varepsilon) \leq \ln \frac{\bar{a}\exp\{A_1^+\}}{g(\exp\{A_1^+\})\bar{c}}. \tag{38}$$

Together with (25) ,we get

$$v(t) \leq v(\varepsilon) + \int_0^\omega |\dot{v}(t)| dt < \ln \frac{\bar{a}\exp\{A_1^+\}}{g(\exp\{A_1^+\})\bar{c}} + (|\bar{d}| + \bar{d})\omega = A_2^+. \tag{39}$$

On the other hand ,it follows from (23) ,(26) ,(37) and condition (H₄) that

$$\bar{b}\omega \exp\{A_1^+\} + \bar{c}\omega g(M) \exp\{v(\chi) - \ln M\} \geq \bar{a}\omega ,$$

or

$$v(\chi) \geq \ln \frac{(\bar{a} - \bar{b} \exp\{A_1^+\}) M}{\bar{c}g(M)} = \ln \frac{(\bar{a} - \bar{b} r_2 \exp\{(|\bar{a}| + \bar{a})\omega\}) M}{\bar{c}g(M)}. \tag{40}$$

This ,combined with (25) gives

$$v(t) \geq v(\chi) - \int_0^\omega |\dot{v}(t)| dt > \ln \frac{(\bar{a} - \bar{b} \exp\{A_1^+\}) M}{\bar{c}g(M)} - (|\bar{d}| + \bar{d})\omega = B_2^+. \tag{41}$$

Therefore from (39) and (41) ,we get

$$\max_{t \in [0, \omega]} |v(t)| < \max\{|A_2^+|, |B_2^+|\} = B^+ \text{ for } u(t) \in (\ln M, A_1^+). \tag{42}$$

Obviously $r_1, r_2, \ln M, B_1^*, A_1^+, B^*$ and B^+ are independent of λ .

Now ,let us consider the equation $QNz = 0$, where $z = (u, p)^T \in \mathbb{R}^2$.i. e. ,(22) . Noting the (NM) condition ,(H₃) and (H₄) ,we can easily show that (22) has two distinct solutions.

$$(\tilde{u}, \tilde{v})^T = (\ln r_1, \ln\{\frac{(\bar{a} - \bar{b}r_1)\bar{e}r_1}{\bar{c}\bar{d}}\}) \quad \text{and} \quad (\hat{u}, \hat{v})^T = (\ln r_2, \ln\{\frac{(\bar{a} - \bar{b}r_2)\bar{e}r_2}{\bar{c}\bar{d}}\}).$$

Choose $C_0 > 0$ such that

$$\max\{|\ln\{\frac{(\bar{a} - \bar{b}r_1)\bar{e}r_1}{\bar{c}\bar{d}}\}|, |\ln\{\frac{(\bar{a} - \bar{b}r_2)\bar{e}r_2}{\bar{c}\bar{d}}\}|\} < C_0. \tag{43}$$

Define

$$\Omega_1 = \{z = (u, v)^T \in X: u(t) \in (B_1^*, \ln M), \max_{t \in [0, \omega]} |v(t)| < B^* + C_0\}$$

and

$$\Omega_2 = \{z = (u, v)^T \in X: u(t) \in (\ln M, A_1^+), \max_{t \in [0, \omega]} |v(t)| < B^+ + C_0\}.$$

Both Ω_1 and Ω_2 are bounded open subsets of X . It follows from the (NM) condition (34) and (42) that $(\tilde{u}, \tilde{v})^T \in \Omega_1$ and $(\hat{u}, \hat{v})^T \in \Omega_2$. In view of (34) and (42) it is easy to see that $\Omega_1 \cap \Omega_2 = \emptyset$ and Ω_i satisfies condition (a) of Lemma 3.1 for $i = 1, 2$. Moreover, $QNz \neq 0$ for $z \in \partial\Omega_i \cap \text{Ker}L = \partial\Omega_i \cap \mathbb{R}^2$. A direct computation gives

$$\text{deg}\{JQN, \Omega_i \cap \text{Ker}L, \emptyset\} = \text{sgn}\{-\bar{c}\bar{e}g'(\exp\{u\})_u g(\exp\{u\}) \exp\{v\}\} = (-1)^{i+1} \neq 0.$$

Here J is taken as the identity mapping since $\text{Im}Q = \text{Ker}L$. We have proved that Ω_i satisfies all the conditions in Lemma 3.1. Hence $Lz = Nz$ (i.e., system (7)) has at least two ω -periodic solutions $z^* = (u^*, v^*)^T$ and $z^+ = (u^+, v^+)^T$ with $z^* \in \text{Dom}L \cap \bar{\Omega}_1$ and $z^+ \in \text{Dom}L \cap \bar{\Omega}_2$.

Obviously z^* and z^+ are different. By using (6),

$$(\exp\{u^*(t)\}, \exp\{v^*(t)\})^T \quad \text{and} \quad (\exp\{u^+(t)\}, \exp\{v^+(t)\})^T$$

are two different positive ω -periodic solutions of (4). This ends the proof.

We are now ready to tackle the system (5). With the change of variables in (6), system (5) becomes

$$\begin{cases} \dot{u}(t) = a(t) - b(t) \exp\{u(t - \tau_1(t))\} - c(t) g(\exp\{u(t)\}) \exp\{v(t) - u(t)\} \\ \dot{v}(t) = -d(t) + e(t) g(\exp\{u(t - \tau_2(t))\}) \end{cases} \tag{7}$$

The arguments used in the proof of Theorem 2.1 will still be valid. As for the analog of Theorem 3.1, corresponding to (11) we have

$$\int_0^\omega e(t) g(\exp\{u(t - \tau_2(t))\}) dt = \bar{d}\omega. \tag{11}$$

By the mean value theorem, there exists a $\xi_0 \in (0, \omega)$ such that

$$\int_0^\omega e(t) g(\exp\{u(t - \tau_2(t))\}) dt = g(\exp\{u(\xi_0 - \tau_2(\xi_0))\}) \int_0^\omega e(t) dt.$$

Since u is ω -periodic, there exists a $\xi \in [0, \omega]$ such that

$$u(\xi_0 - \tau_2(\xi_0)) = u(\xi).$$

Thus, we have

$$\int_0^\omega e(t) g(\exp\{u(t - \tau_2(t))\}) dt = g(\exp\{u(\xi)\}) \int_0^\omega e(t) dt$$

and the rest of the arguments in the proof of Theorem 3.1 follows. We have the following result for the system (5).

Theorem 4.2 Theorem 2.1, Theorem 2.2 and Theorem 3.1 and Theorem 4.1 are also valid for the delayed system (5).

Remark We have introduced some novel estimation techniques for the priori bounds of unknown solu-

tions to $Lz = \lambda Nz$, which are much different from the arguments used in [11 – 15]. In addition, we have studied the diversity of the periodic solutions including non-existence of periodic solutions at least one periodic solution and at least two periodic solutions. However, the existing literature only gave some sufficient conditions for one of the three cases.

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一类生态模型的周期解研究

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摘 要: 考虑了周期环境中带有非单调功能反应的非自治捕食者食饵模型,得到了不存在周期解、至少存在一个或两个周期解的新的充分条件,所用方法主要基于 Mawhin 的适合度理论及估计先验界的新技巧。

关键词: 周期解; 适合度; 捕食者 – 食饵模型; 非单调功能反应

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