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Permanence of a stage-structured predator-prey system with a class of functional responses[☆]

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ABSTRACT

A stage-structured predator-prey system incorporating a class of functional responses is presented in this article. By analyzing the system and using the standard comparison theorem, the sufficient conditions are derived for permanence of the system and non-permanence of predators.

1. Introduction

The past decades have witnessed an enormous interest in predator-prey systems, with most of them focusing on homogeneous populations [1–5]. In fact, no natural population is truly homogeneous, many organisms undergo radical changes in many aspects such as the rates of survival, maturation, reproduction and predation while while they are processing their life history. Therefore, stage-structured predator-prey systems have received much attention recently [6–21].

However, these works [7–21] are largely using constant coefficient systems and have stage structures on only one of the interactive species. The research objectives mainly include the stability and permanence of the system, often with one particular type of functional response. In this article, we propose the following variable coefficient predator-prey system with time delays and stage structures for both interactive species, as well as different functional responses, Specifically, we will consider the condition for the permanence of the two species and the non-permanence condition for predators to become extinct:

$$\begin{aligned}
\dot{x}_1(t) &= r_1(t)x_2(t) - d_{11}x_1(t) - r_1(t)e^{-d_{11}\tau_1}x_2(t-\tau_1)\\
\dot{x}_2(t) &= r_1(t)e^{-d_{11}\tau_1}x_2(t-\tau_1) - d_{12}x_2(t) - b_1(t)x_2^2\\
&\quad - c_1(t)\varphi(x_2(t))x_2(t)y_2(t)\\
\dot{y}_1(t) &= r_2(t)y_2(t) - d_{22}y_1(t) - r_2(t)e^{-d_{22}\tau_2}y_2(t-\tau_2)\\
\dot{y}_2(t) &= r_2(t)e^{-d_{22}\tau_2}y_2(t-\tau_2) - d_{21}y_2(t) - b_2(t)y_2^2\\
&\quad + c_2(t)\varphi(x_2(t))x_2(t)y_2(t)
\end{aligned} \tag{1}$$

where $x_1(t)$ and $x_2(t)$ denote the immature and mature densities of the prey at time t, respectively. $y_1(t)$ and $y_2(t)$ denote the immature and mature densities of the predator at time t, respectively. $r_i(t)$, $b_i(t)$, $c_i(t)$ $(i = 1, 2)$ are positive and continuous functions for all $t \geq 0$.

The above system assumes that the mature predators only feed on the mature prey population, the immature are produced by the mature populations. The birth rate of prey and predators ($r_i(t) > 0$; $i = 1, 2$) is proportional to the existing mature population sizes.

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The other parameters have the following biological meanings: $c_1(t)$ denotes the capturing rate of mature predators at time t, and $c_2(t)/c_1(t)$ is the rate of conversion of nutrients from the mature prey into the reproduction of the mature predator; $b_i(t) > 0$ $(i = 1, 2)$ represents the intraspecific competition rate of mature prey and predators at time t, respectively; d_{11} and d_{12} are the death rate of immature and mature population of prey respectively, d_{22} and d_{21} are the death rate of immature and mature population of predator respectively; $\tau_i > 0 (i = 1, 2)$ is the length of time from the birth to maturity of the species i. The term $r_1(t)e^{-d_{11}\tau}{}_1 x_2(t-\tau_1)$ represents the survived prey population born at time $t-\tau_1$, that is, the transition from the immature to mature prey. The term $r_2(t)e^{-d_{22}\tau}{}_2 y_2(t-\tau_2)$ denotes the survived predator population born at time $t-\tau_2$, that is, the transition from the immature to mature predator.

The term $\varphi(x_2)x_2$, the number of prey captured per predator per unit time, is called the predator functional response and satisfies the following assumptions

$$0 < \varphi(x_2) < L < +\infty, \quad \frac{\mathrm{d}}{\mathrm{d}x_2}\big(\varphi(x_2)x_2\big) \geq 0 (x_2 > 0). \tag{2}$$

The initial conditions of system (1) are given by

$$\begin{aligned} &x_i(\theta) = \varphi_i(\theta) > 0, \quad y_i(\theta) = \psi_i(\theta) > 0, \quad \varphi_i(0) > 0, \\ &\psi_i(0) > 0 \quad (i = 1, 2), \quad \theta \in [-\tau, 0], \\ &\tau = \max\{\tau_1, \tau_2\}. \end{aligned} \tag{3}$$

For the continuity of initial conditions, we require further that

$$\begin{aligned} x_1(0) &= \int_{-\tau_1}^{0} r_1(s)\varphi_2(s)\,\mathrm{d}s, \\ y_1(0) &= \int_{-\tau_2}^{0} r_2(s)\psi_2(s)\,\mathrm{d}s. \end{aligned} \tag{4}$$

Again, we define that

$$\begin{aligned} &r_k^s = \sup_{t \geq 0} r_k(t) > 0, c_k^s = \sup_{t \geq 0} c_k(t) > 0, b_k^s = \sup_{t \geq 0} b_k(t) > 0, \\ &r_k^i = \inf_{t \geq 0} r_k(t) > 0, c_k^i = \inf_{t \geq 0} c_k(t) > 0, b_k^i = \inf_{t \geq 0} b_k(t) > 0 \\ &\quad (k = 1, 2). \end{aligned} \tag{5}$$

2. Positivity and boundedness

Theorem 2.1. *Solutions of system (1) with initial conditions (3) and (4)are positive and bounded for all $t \geq 0$.*

Proof. First we show $x_2(t) > 0$ for all $t \geq 0$. Otherwise, noticing that $x_2(t) = \varphi_2(t) > 0$ for all $-\tau_1 < t < 0$.

Then there exists a $t^* > 0$, such that $x_2(t^*) = 0$.

Now denoting $t_0 = \inf\{t > 0 \mid x_2(t) = 0\}$.

Then $t_0 > 0$ and from system (1), we have

$$0 \leq t_0 \leq \tau_1 \Rightarrow \dot{x}_2(t_0) = r_1(t_0)e^{-d_{11}\tau_1}\varphi_2(t_0 - \tau_1) > 0.$$

$$t_0 > \tau_1 \Rightarrow \dot{x}_2(t_0) = r_1(t_0)e^{-d_{11}\tau_1}x_2(t_0 - \tau_1) > 0.$$

Hence $\dot{x}_2(t_0) > 0$. By the definition of t_0, we have $\dot{x}_2(t_0) \leq 0$. A contradiction.

Thus $x_2(t) > 0$ for all $t > 0$.

Again, considering the following equation

$$\begin{aligned} &\dot{u}(t) = -d_{11}u(t) - r_1(t)e^{-d_{11}\tau_1}u(t-\tau_1) \\ &u(0) = x_2(0) \end{aligned} \tag{6}$$

We can easily obtain that

$$u(t) = e^{-d_{11}t}\left[\varphi_2(0) - \int_0^t r_1(s)\varphi_2(s)\,\mathrm{d}s\right].$$

and

$$x_1(t) > u(t) (0 \leq t < \tau_1).$$

From the initial conditions (3), we have $u(\tau_1) = 0$, then $x_1(t) > u(t) > 0$ for $0 \leq t < \tau_1$.

By induction, we can show $x_1(t) > 0$ for all $t \geq 0$.

Similarly, we can prove that $y_1(t) > 0$ and $y_2(t) > 0$ for all $t \geq 0$.

Next, we will prove the boundedness of the solutions of system (1).

Defining the function

$$V(t) = c_2^s x_1(t) + c_2^s x_2(t) + c_1^i y_1(t) + c_1^i y_2(t).$$

The derivative of $V(t)$ along the positive solutions of system (1) is

$$\begin{aligned} \dot{V}(t) &= c_2^s\dot{x}_1(t) + c_2^s\dot{x}_2(t) + c_1^i\dot{y}_1(t) + c_1^i\dot{y}_2(t) \\ &\leq (c_2^s r_1^s - c_2^s d_{12})x_2(t) - c_2^s b_1^i x_2^2(t) - c_2^s d_{11}x_1(t) \\ &\quad + (c_1^i r_2^s - c_1^i d_{21})y_2(t) - c_1^i b_2^i y_2^2(t) - c_1^i d_{22}y_1(t). \end{aligned}$$

For a positive constant $d \leq \min\{d_{11}, d_{22}\}$, then

$$\begin{aligned} \dot{V}(t) + dV(t) &\leq c_2^s(r_1^s - d_{12} + d)x_2(t) - c_2^s b_1^i x_2^2(t) \\ &\quad + c_1^i(r_2^s - c_1^i d_{21} + d)y_2(t) - c_1^i b_2^i y_2^2(t). \end{aligned}$$

Hence there exists a positive number M, such that $\dot{V}(t) + dV(t) \leq M$. Then we get

$$V(t) \leq Md^{-1} + (V(0) - Md^{-1})e^{-dt}.$$

Therefore, the positive solutions of system (1) are bounded. This completes the Proof. □

3. Permanence and non-permanence

Definition 3.1. If there exist positive constants m_x, M_x, m_y and M_y, such that each solution $(x_1(t), x_2(t), y_1(t), y_2(t))$ of system (1) satisfies

$$0 < m_x \leq liminf_{\,t\to+\infty}x_i(t) \leq limsup_{\,t\to+\infty}x_i(t) \leq M_x \quad (i = 1, 2),$$

$$0 < m_y \leq liminf_{\,t\to+\infty}y_i(t) \leq limsup_{\,t\to+\infty}y_i(t) \leq M_y \quad (i = 1, 2).$$