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Analysis of a Holling-Tanner Predator-Prey System With Birth Pulse and Harvesting Effect

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Abstract The permanence and harvesting policy of a Holling-Tanner predator-prey model with birth pulse and harvesting effect is investigated. First, by the stroboscopic map, we obtain an exact periodic solution of the system which has Ricker function or Beverton-Holt function. Further, by the Floquet theorem, we prove the boundary periodic solution is always unstable. And by the comparison theorem of impulsive differential equation, we obtain the condition for permanence of the system. At last, we gain the maximum harvesting effort for the system.

Key words Holling-Tanner predator-prey system, birth pulse, extinction, permanence, the maximum harvesting effort
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一个具有收获和生育脉冲效应的 Holling-Tanner捕食者——食饵系统分析

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[摘要] 研究了一个具有收获和生育脉冲效应的 Holling-Tanner捕食者——食饵系统的持久性和收获策略. 首先, 利用频闪映射, 得到了带有 Ricker和 Beverton-Holt函数的脉冲系统准确的周期解. 进而, 通过 Floquet定理, 证明了边界周期解总是不稳定的, 利用脉冲比较定理, 得到了系统持续生存的条件. 最后, 得到了系统的最大收获努力量.

[关键词] Holling-Tanner捕食者——食饵系统, 生育脉冲, 灭绝, 持续生存, 最大收获努力量

0 Introduction

Predator-prey systems have been studied in many literatures[1-3]. Generally, the Holling-Tanner predator-prey model is described as

$$\begin{cases} \dot{x} = x(B(x) - d) - \dfrac{cxy}{A + x}, \\ \dot{y} = y\left(s - h\dfrac{y}{x}\right), \end{cases} \tag{1}$$

where x, y stand for prey and predator density, respectively. $\dfrac{cx}{A+x}$ is Holling-II functional response; $d > 0$ is the death rate constant, and $B(x)x$ is a birth rate function of the prey population, with $B(x)$ satisfying the following

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basic assumptions for $x \in (0, \infty)$: (1) $B(x) > 0$; (2) $B(x)$ is continuously differentiable with $B'(x) < 0$; (3) $B(0^+) > d + E > B(\infty)$. Examples of birth functions $B(x)$ found in the biological literature [4] are: (1) $B_1(x) = b e^{-ax}$, with $a > 0$, $b > 0$; (2) $B_2(x) = \frac{p}{q + x^m}$, with $p, q, m > 0$. Functions B_1 and B_2 with $m = 1$ are used in fisheries, and are known as the Richer function and Beverton-Holt function, respectively.

1 Model

Model (1) invariably assumes that the prey species reproduce throughout the year, whereas it is often the case that births are seasonal or occur in regular pulses. Thus the continuous reproduction of population is then removed from the traditional models and replaced with a birth pulse[4], that is, reproduction takes place in a relatively short period each year. Consequently, impulsive differential equations (hybrid dynamical systems) provide a natural description of such phenomenon. Recently, the impulsive equations are found in almost every domain of applied sciences. Numerous examples are given in Bainov's and his collaborators' books[5]. In this paper, we introduce a Holling-Tanner predator-prey model with prey birth pulse and ratio harvest as follows

$$\begin{cases} \dot{x} = -dx - \dfrac{cxy}{A + x} - Ex, & \\ & t \neq n, \\ \dot{y} = y\left(s - h\dfrac{y}{x}\right), & \\ x(t^+) = x(t) + B(x(t))x(t), & t = n, \end{cases} \tag{2}$$

where $n \in \mathbf{N}$, the period of impulsive effect is 1, E is the harvesting effort.

In this paper, our main purpose is to study the extinction and permanence of system (2). The organizations of the paper are as follows. In next section, using the discrete dynamical system determined by the stroboscopic map, we obtain an exact periodic solution of the system which has Ricker function or Beverton-Holt function. Moreover, by the Floquet theory and a comparison theorem, we establish the sufficient conditions under which the boundary periodic solution is always unstable and system is permanent. In the last section, we obtain the maximum harvesting effort for the system.

2 Extinction and Permanence

Let $\tilde{y} = hy$, $\tilde{c} = h^{-1}c$, we can write system (2) in the following form

$$\begin{cases} \dot{x} = -(d + E)x - \dfrac{cxy}{A + x}, & \\ & t \neq n, \\ \dot{y} = y\left(s - \dfrac{y}{x}\right), & \\ x(t^+) = x(t) + B(x(t))x(t), & t = n. \end{cases} \tag{3}$$

In the absence of the predator, system (3) reduces to

$$\begin{cases} \dot{x} = -(d + E)x, & t \neq n, \\ x(t^+) = x(t) + B(x(t))x(t), & t = n. \end{cases} \tag{4}$$

We solve the prey population in system (4) between pulses,

$$x(t) = x_n e^{-(d+E)(t-n)}, \quad n < t \leqslant n + 1, \tag{5}$$

where $x_n \doteq x(n^+)$ is the initial population at time n. Using the second equation of system (4), we deduce the stroboscopic map such that

$$x_{n+1} = x_n e^{-(d+E)}\left(1 + B\left(x_n e^{-(d+E)}\right)\right) \doteq F(x_n),$$

where $F(x) = x e^{-(d+E)}\left(1 + B\left(x e^{-(d+E)}\right)\right)$.

If $B_1(x) = b e^{-x}$, then

$$x_{n+1} = x_n e^{-(d+E)}\left(1 + b e^{-x_n e^{-(d+E)}}\right). \tag{6a}$$

If $B_2(x)=\dfrac{p}{q+x^m}$, then

$$x_{n+1}=x_n e^{-(d+E)}\left(1+\frac{p}{q+(x_n e^{-(d+E)})^m}\right). \tag{6b}$$

Differential equations (6a) and (6b) describe the numbers of prey population at a pulse in terms of values at the previous pulse. We are, in other words, stroboscopically sampling at its pulsing period. The dynamical behaviors of (6a) and (6b), coupled with (5), determines the dynamical behavior of system (4). In the following, we will focus our attention on systems (6a) and (6b). We will focus here on b for the Ricker function and p for the Beverton-Holt function, and document the changes in the qualitative dynamics of (6a) (or (6b)) as b (or p) varies. First, the trivial equilibrium $x_e^*=0$ is always a solution for equation (6a) (or (6b)). For the Ricker function, when b is small enough, that is $b_0=e^{d+E}-1$, $b\in(0,b_0)$, $x_e^*=0$ is globally asymptotically stable. And when $b>b_0$, equation (6a) has stable positive equilibrium $x_s^*=e^{d+E}\ln\left(\dfrac{b}{e^{d+E}-1}\right)$. For the Beverton-Holt function, when $p<p_0=q(e^{d+E}-1)$, $x_e^*=0$ is globally asymptotically stable. And when $p>p_0$, equation (6a) has stable positive equilibrium $x_s^*=e^{d+E}\left(\dfrac{p}{e^{d+E}-1}-q\right)^{\frac{1}{m}}$. Obviously, x_s^* satisfies $x_s^*>F(x)>x$ if $x_s^*>x>0$, $x>F(x)>x_s^*$ if $x>x_s^*$. From [4], x_s^* is globally asymptotically stable. Therefore, we have the following lemma.

Lemma 1 Let $x(t)$ be a solution of system (4) with initial condition $x(0)>0$.

(i) For $B_1(x)=be^{-x}$, if $b<b_0$, then $x(t)\to 0$ as $t\to\infty$. If $b>b_0$, then system (4) has unique asymptotically stable positive solution

$$\tilde{x}_s(t)=e^{d+E}\ln\left(\frac{b}{e^{d+E}-1}\right)e^{-(d+E)(t-n)},\quad n<t\leqslant n+1.$$

(ii) For $B_2(x)=\dfrac{p}{q+x^m}$, if $p<p_0$, $x(t)\to 0$ as $t\to\infty$. If $p>p_0$, system (4) has unique asymptotically stable positive solution

$$\tilde{x}_s(t)=e^{d+E}\left(\frac{p}{e^{d+E}-1}-q\right)^{\frac{1}{m}}e^{-(d+E)(t-n)},\quad n<t\leqslant n+1.$$

From the above, we know that if $b>b_0$ (or $p>p_0$), there exists the boundary periodic solution $(\tilde{x}_s(t),0)$ of system (3). Next, we will discuss that $(\tilde{x}_s(t),0)$ is always unstable.

Theorem 1 For system (3), the boundary periodic solution $(\tilde{x}_s(t),0)$ is always unstable.

Proof Defining $x(t)=u(t)+\tilde{x}_s(t)$, $y(t)=v(t)$, there may be written

$$\begin{pmatrix}u(t)\\v(t)\end{pmatrix}=\Phi(t)\begin{pmatrix}u(0)\\v(0)\end{pmatrix},$$

where $\Phi(t)$ satisfies

$$\frac{d\Phi}{dt}=\begin{pmatrix}-d-E & -\dfrac{c\tilde{x}_s(t)}{A+\tilde{x}_s(t)}\\ 0 & s\end{pmatrix}\Phi(t)$$

and $\Phi(0)=I$, the identity matrix. The linearization of impulsive subsystem (3) becomes

$$\begin{pmatrix}u(n^+)\\v(n^+)\end{pmatrix}=\begin{pmatrix}1+B(x_s^*)+x_s^*B'(x_s^*) & 0\\ 0 & 1\end{pmatrix}\begin{pmatrix}u(n)\\v(n)\end{pmatrix}.$$

We denote that

$$\boldsymbol{M}=\begin{pmatrix}1+B(x_s^*)+x_s^*B'(x_s^*) & 0\\ 0 & 1\end{pmatrix}\Phi(1).$$

The eigenvalues of the matrix $\boldsymbol{M}$ are $\mu_1=(1+B(x_s^*)+x_s^*B'(x_s^*))e^{-(d+E)}<1$, $\mu_2=e^s>1$. Notice that $\mu_2=$

$e^s > 1$, the boundary periodic solution $(\tilde{x}_s(t), 0)$ of system (3) is always unstable. The proof is complete.

Theorem 2 (i) For $B_1(x) = b e^{-x}$, system (3) is permanent provided $b > e^{d+E+csx_s^*} - 1$ holds true, here $x_s^* = e^{d+E} \ln \frac{b}{e^{d+E} - 1}$; (ii) For $B_2(x) = \frac{p}{q + x^m}$, system (3) is permanent provided $p > q(e^{d+E+csx_s^*} - 1)$ holds true, here $x_s^* = e^{d+E}(\frac{p}{e^{d+E} - 1} - q)^{\frac{1}{m}}$.

Proof Let $(x(t), y(t))$ is any solution of system (3) with initial values $x(0^+) > 0$, $y(0^+) > 0$.

(i) For $B_1(x) = b e^{-x}$, since $b > e^{d+E+csx_s^*} - 1$, it is easy to know $b > e^d - 1$. At the same time, we can choose a sufficiently small ε such that

$$b > e^{d+E+cs\sigma} - 1,$$

here $\sigma = x_s^* + \varepsilon$. From the first equation of system (3), we have $\dot{x} < -(d+E)x$, and then consider the comparison system (4). By Lemma 1, it is obvious that for the chosen $\varepsilon > 0$, there exists a sufficiently large t_1 such that

$$x(t) \leqslant \tilde{x}_s(t) + \varepsilon < e^{d+E} \ln \frac{b}{e^{d+E} - 1} + \varepsilon = x_s^* + \varepsilon \doteq \sigma, \quad n < t \leqslant n+1, \quad t > t_1.$$

(ii) For $B_2(x) = \frac{p}{q + x^m}$, by the same method, we have

$$x(t) \leqslant \tilde{x}_s(t) + \varepsilon < e^{d+E}(\frac{p}{e^{d+E} - 1} - q)^{\frac{1}{m}} + \varepsilon = x_s^* + \varepsilon \doteq \sigma, \quad n < t \leqslant n+1, \quad t > t_1.$$

Considering the comparison system

$$\frac{dy}{dt} = \frac{y}{\sigma}(s\sigma - y),$$

which has asymptotically stable solution $y = s\sigma$, we know there is a $t_2 > t_1$ such that $y < s\sigma$ for $t > t_2$; that is $y(t) \to 0$ with $t \to \infty$. Hence, there exists a constant $M = \max\{\sigma, s\sigma\} > 0$ such that $x(t) \leqslant M$, $y(t) \leqslant M$ for any solution $(x(t), y(t))$ of system (3) with $t > t_2$.

Next, we shall prove that there exist $m_1 > 0$, $m_2 > 0$ such that for any solution $(x(t), y(t))$ of system (3), $x(t) \geqslant m_1$, $y(t) \geqslant m_2$.

From the first equation of system (3), we have $\dot{x} \geqslant -(d + \frac{cs\sigma}{A})x \doteq -\delta_1 x$, then we consider the following comparison system with pulse:

$$\begin{cases} \dot{x} = -\delta_1 x, & t \neq n, \\ x(t^+) = x(t) + B(x(t))x(t), & t = n. \end{cases} \tag{7}$$

By Lemma 1 and the comparison theorem[5], there exists $t_3 > t_2$ such that

(1) for $B_1(x) = b e^{-x}$,

$$x(t) \geqslant \tilde{x}(t) - \varepsilon > \ln(\frac{b}{e^{\delta_1} - 1}) - \varepsilon \doteq m_1 > 0, \quad n < t \leqslant n+1, \quad t > t_3,$$

where

$$\tilde{x}(t) = e^{\delta_1} \ln(\frac{b}{e^{\delta_1} - 1}) e^{-\delta_1(t-n)}$$

is the periodic solution of system (7);

(2) for $B_2(x) = \frac{p}{q + x^m}$,

$$x(t) \geqslant \tilde{x}(t) - \varepsilon > (\frac{p}{e^{\delta_1} - 1} - q)^{\frac{1}{m}} - \varepsilon \doteq m_1 > 0, \quad n < t \leqslant n+1, \quad t > t_3,$$

where

$$\tilde{x}(t) = e^{\delta_1}(\frac{p}{e^{\delta_1} - 1} - q)^{\frac{1}{m}} e^{-\delta_1(t-n)}$$

is the periodic solution of system (7).

We are left to prove there exist $m_2>0$ and a sufficiently large t_0 such that $y(t)\geqslant m_2$ for all $t>t_0$. The probative process can be divided into the following two steps.

Step 1 (1) For $B_1(x)=be^{-x}$, if $b>e^{d+E}-1$, we can choose $0<m'_2<s\sigma$ such that for the chosen $\varepsilon>0$, $s\eta-m'_2>0$, where $\eta=\ln(\frac{b}{e^{\delta_2}-1})-\varepsilon$.

(2) For $B_2(x)=\frac{p}{q+x^m}$, if $p>q(e^{d+E}-1)$, likewise, we can choose $0<m'_2<s\sigma$ such that for the chosen $\varepsilon>0$, $s\eta-m'_2>0$, where $\eta=(\frac{p}{e^{\delta_2}-1}-q)^{\frac{1}{m}}-\varepsilon$.

We are sure that there exists a $t_4>t_3>0$ such that $y(t_4)\geqslant m'_2$. Otherwise, if $y(t)<m'_2$ for all $t>t_3$, from the first equation of system (3), we have $\dot{x}>-(d+E+\frac{\sigma m'_2}{A})x\doteq-\delta_2 x$. Considering the following comparison system

$$\begin{cases}\dot{x}=-\delta_2 x, & t\neq n,\\ x(t^+)=x(t)+B(x(t))x(t), & t=n.\end{cases}\tag{8}$$

By the same method as (7), we obtain there exists $t'>t_3>0$ such that

(1) for $B_1(x)=be^{-x}$,

$$x(t)\geqslant\tilde{x}(t)-\varepsilon>\ln(\frac{b}{e^{\delta_2}-1})-\varepsilon\doteq\eta,\quad n<t\leqslant n+1,\quad t>t',$$

where

$$\tilde{x}(t)=e^{\delta_2}\ln(\frac{b}{e^{\delta_2}-1})e^{-\delta_2(t-n)}$$

is the periodic solution of system (8);

(2) for $B_2(x)=\frac{p}{q+x^m}$,

$$x(t)\geqslant\tilde{x}(t)-\varepsilon>(\frac{p}{e^{\delta_2}-1}-q)^{\frac{1}{m}}-\varepsilon\doteq\eta,\quad n<t\leqslant n+1,\quad t>t',$$

where

$$\tilde{x}(t)=e^{\delta_2}(\frac{p}{e^{\delta_2}-1}-q)^{\frac{1}{m}}e^{-\delta_2(t-n)}$$

is the periodic solution of system (8).

From the second equation of system (3), we have

$$\dot{y}>y(s-\frac{m'_2}{\eta})>0,\quad \text{for } t>t'.$$

Hence, $y(t)\to\infty$ as $t\to\infty$. It is contrary to $y(t)<m'_2$ for all $t>t_3$. Upon that, we accomplish there exists a $t_4>0$ such that $y(t_4)\geqslant m'_2$.

Step 2 By the above step, we are left to consider two cases.

Case 1 If $y(t)\geqslant m'_2$ for all large t, then the proof is complete, here $m_2=m'_2$.

Case 2 If $y(t)$ oscillates about m'_2 for all large t, we can choose constants $h>0$ and $t_0>\max\{t',t_4\}$ (t_0 is demanded be sufficiently large) such that $y(t)\leqslant m'_2$, $y(t_0)=y(t_0+h)=m'_2$ and $x(t)>\eta$ for $t\in[t_0,t_0+h]$. Thus, there exists a $t^*\in(t_0,t_0+h)$ such that $y(t)\geqslant\frac{m'_2}{2}$ for $t\in[t_0,t^*]$. Assuming $t^*\in(n_1,n_1+1]$, $n_1\in\mathbf{Z}_+$, $\mathbf{Z}_+=1,2,\cdots$, we shall discuss the following two cases.

(i) If $n_1+1\geqslant t_0+h$, from the second equation of system (3), we have $\dot{y}>-\frac{m'_2}{\eta}y$. Then $y(t)\geqslant y(t^*)$

$\exp(-\frac{m_2'}{\eta}(t_0+h-t^*))>\frac{m_2'}{2}\exp(-\frac{m_2'}{\eta})\doteq\zeta$, for $t\in[t^*, t_0+h]$.

(ii) If $n_1+1<t_0+h$, we obtain that $y(t)>y(t^*)\exp(-\frac{m_2'}{\eta}(n_1+1-t^*))>\frac{m_2'}{2}\exp(-\frac{m_2'}{\eta})\doteq\zeta$, for $t\in[t^*, n_1+1]$. For $t\in[n_1+1, t_0+h]$, there exists $t^{**}\in(n_1+1, t_0+h)$ such that $y(t)\geqslant\frac{\zeta}{2}$ for $t\in[n_1+1, t^{**}]$. Assuming $t^{**}\in(n_2, n_2+1]$, $n_2>n_1$, $n_2\in\mathbf{Z}_+$. By the same method, it is not difficult to obtain that if $n_2+1\geqslant t_0+h$, for $t\in[t^{**}, t_0+h]$, $y(t)>\frac{m_2'}{2^2}\exp(-\frac{2m_2'}{\eta})$; if $n_2+1<t_0+h$, for $t\in[t^{**}, n_2+1]$, $y(t)>y(t^*)>\frac{m_2'}{2^2}\exp(-\frac{2m_2'}{\eta})$. For $t\in[n_2+1, t_0+h]$, we repeat the above process. Because h is limited, consequentially, there exist $t_l>0$ and $n_l\in\mathbf{Z}_+$ such that $t_l\in(n_l, n_l+1]$ and $n_l+1\geqslant t_0+h$, then we can deduce $y(t)>\frac{m_2'}{2^l}\exp(-\frac{lm_2'}{\eta})$.

Owing to the randomicity of t_0, we can conclude there exists $m_2\doteq\frac{m_2'}{2^l}\exp(-\frac{lm_2'}{\eta})$ such that $y(t)\geqslant m_2$ for all $t>t_0$. The proof is complete.

3 Harvesting Policy and Discussion

The optimal management of renewable resources, which has a direct relationship to sustainable development, has been studied extencively by many authors. Economic and biological aspects of renewable resources management have been considered by Clark[6]. From the point of views of ecological managers, it may be desirable for the system to be globble stability or permance of even globally attractive, in order to plan harvesting strategies and keep a sustainable development of the ecosystem. Anothers, as well known, 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, one of those theories is Holling-Tanner predator-prey model, which can be roughly stated as that more preys should be keeped on more predators. Hence it is important for us to study Holling-Tanner predator-prey model with birth pulse and harvesting effect.

In this paper, firstly, by using the Floquet theorem and small amplitude perturbation skills, we have proved the boundary periodic solution $(\widetilde{x_s}(t), 0)$ of the system which has Ricker function or Beverton-Holt function is always unstable when $b>b_0$ (or $p>p_0$). Moreover, by using comparison method, we have obtained the system is permanent when $b>b_0$ (or $p>p_0$). Based on the above results, we can develope the following results.

(1) For $B_1(x)=be^{-x}$, if $b>b_0:=e^d-1$. Then if $0\leqslant E<E_{\max}$ (the maximum harvesting effort to keep the system permant), system (3) is permanent, where $z=E_{\max}$ is the positive root of the following equation

$$\ln(b+1)=d+z+cse^{d+z}\ln\frac{b}{e^{d+z}-1}.$$

(2) For $B_2(x)=\frac{p}{q+x^m}$, if $p>p_0:=q(e^d-1)$. Then if $0\leqslant E<E_{\max}$ (the maximum harvesting effort to keep the system permant), system (3) is permanent, where $z=E_{\max}$ is the positive root of the following equation

$$\ln\left(\frac{p}{q}+1\right)=d+z+cse^{d+z}\left(\frac{p}{e^{d+z}-1}-q\right)^{\frac{1}{m}}.$$

Therefore, in order to keep system (3) permanent, $0\leqslant E<E_{\max}$ is a harvesting threshold for the prey population. From the point of view of ecological managers, it may be desirable to plan harvesting strategies and keep sustainable development of the ecosystem. In system (3), fix $d=0.8$, $c=1$, $s=0.3$, $A=0.6$. For $B_2(x)=\frac{p}{q+x^m}$, fix $q=0.8$, $m=1$. Some maximum harvesting efforts $E_{\max}$ to keep the system permant are listed in

Table 1.

Table 1　The maximum harvesting effort E_{max} to keep system permance

	b or p	E_{max}	b or p	E_{max}
be^{-x}	80	3.594 449 155	600	5.598 594 935
	120	3.995 790 546	2 000	6.801 402 335
	300	4.907 110 265	20 000	9.103 537 551
$\frac{p}{q+x^m}$	80	3.582 379 277	600	5.597 017 268
	120	3.987 806 362	2000	6.800 930 012
	300	4.907 110 265	20 000	9.103 490 357

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