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EXTINCTION, PERSISTENCE AND GLOBAL STABILITY IN MODELS OF POPULATION GOWTH

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Abstract. First, we systematize earlier results on the global stability of discrete model $A_{n+1} = \lambda A_n + F(A_{n-m})$ of population growth. Second, we invent the effect of delay m when F is unimodal. New, deep and strong results are discussed in Section 4, although theorems 3-5 (Section 3) are still freshly new. This paper may be considered as discrete version of our earlier work on the model $\dot{x}(t) = -\mu x(t) + f(x(t-\tau))$ [1]. We are mainly using ω-limit set of persistent solution, which is discussed in more general by P. Walters [7].

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Introduction

Earlier, several authors study delay models $\dot{x}(t) = -\mu x(t) + f(x(t-\tau))$ and $A_{n+1} = \lambda A_n + F(A_{n-m})$ of population growth. They find several conditions for the global stability without effect of delay. Recently, we just invent the effect of delay in the continuous time model $\dot{x}(t) = -\mu x(t) + f(x(t-\tau))$ [1]. In this paper we will study the delay-effect in the model $A_{n+1} = \lambda A_n + F(A_{n-m})$. But first we should systematize earlier results of several authors involving this model.

1. The extinction

Consider the difference equation

$$A_{n+1} = \lambda A_n + F(A_{n-m}) \qquad 1.1$$

for $n = 0, 1, 2, \cdots$, where $F : [0, \infty) \to [0, \infty)$ is a continuous function, and $m \geq 0$ is a fixed integer. The positive initial values $A_{-m}, A_{-m+1}, \cdots, A_0$ are given. And $\lambda \in (0, 1)$ is given parameter. The constant variation formula is read as

$$A_{n+1} = \lambda^{n+1} A_0 + \sum_{i=0}^{n} \lambda^{n-i} F(A_{i-m}) \qquad \text{for } n = 0, 1, 2, \cdots. \qquad 1.2$$

This is proved very easily by using induction according to n. The following theorem gives a sufficient and necessary condition for extinctive populations.

THEOREM 1 ( ) $F(u) <$
$(1-\lambda)u$ $u > 0$

Remark. Theorem 1 may be read in [2] with other proof. Our proof looks simpler, so we present here for the sake of complete.

2. The Persistence and the Periodicity

A positive solution $\{A_n\}_n$ is called persistent if

$$0 < \liminf_{n\to\infty} A_n \leq \limsup_{n\to\infty} A_n < \infty.$$

The following theorem gives a sufficient condition for persistent (non-extinctive) populations.

THEOREM 2 $F(x) = H(x,x)$ $H(x,y) : [0,\infty)\times[0,\infty) \to [0,\infty)$ x y $H(x,y) > 0$ $x, y > 0$

$$\limsup_{x,y\to\infty} \frac{H(x,y)}{x} < 1-\lambda, \tag{2.1}$$

$$\liminf_{x,y\to 0+0} \frac{H(x,y)}{x} > 1-\lambda. \tag{2.2}$$

$\{A_n\}_{n=-m}^{\infty}$ ( )

Remark. Theorem 2 may be found in [3] with some restrictions on the function F. Our proof is good for larger class of function F so we present here for the sake of complete.

For a persistent solution $\{A_n\}$ we let $\omega(A) \subset R_+^{m+1}$ be the set of all limit-points of the sequence of vectors $\{\underline{v}_n = (A_{n-m}, A_{n-m+1}, \cdots, A_n)\}_n$. This set is compact and invariant under the map $T : R_+^{m+1} \to R_+^{m+1}$ defining by $T\underline{v}_0 = \underline{v}_1$. Here, v_0 is vector of initial data, which is running in the positive quarter of R^{m+1}. The map T takes the initial data to the next data. This map is well-defined. If the solution $\{A_n\}$ is periodic, the ω-limit set $\omega(A)$ is of finite points. Conversely, if the ω-limit set is of finite points, itself should be a periodic solution [7]. Moreover, the map T maps $\omega(A)$ (surjectively) itself. Hence, there are two sequences $\{P_n\}_{n=-\infty}^{\infty}$ and $\{Q_n\}_{n=-\infty}^{\infty}$ (the initial values are chosen from the ω-limit set) satisfying equation (1.1) for all n such that

$$\limsup_{n\to\infty} A_n = P_0 \qquad \liminf_{n\to\infty} A_n = Q_0$$

and

$$Q_0 \le P_s \le P_0, \qquad Q_0 \le Q_s \le P_0 \quad (-\infty < s < \infty).$$

We have

$$P_0 = \lambda P_{-1} + F(P_{-m-1}), \qquad Q_0 = \lambda Q_{-1} + F(Q_{-m-1})$$

and consequently,

$$P_0 \le \frac{F(P_{-m-1})}{1-\lambda}, \qquad Q_0 \ge \frac{F(Q_{-m-1})}{1-\lambda}.$$

From this formula it follows that

$$\frac{1}{1-\lambda}\cdot \inf_{x>0} F(x) \le \liminf_{n\to\infty} A_n \le \limsup_{n\to\infty} A_n \le \frac{1}{1-\lambda}\cdot \sup_{x>0} F(x).$$

Several authors mention the sequences $\{P_n\}_{n=-\infty}^{\infty}$ and $\{Q_n\}_{n=-\infty}^{\infty}$ as full limiting sequences [3]. We are better calling them as full time solutions, because they remind us to the past time (the ancestors of population in our model). We are mainly using them in the following sections, so we emphasize that the existence of them is well-known in references. Here, we just outline the proof via ω-limit set for the sake of complete.

3. Stability with all delay

From now we always assume that the algebraic equation

$$x = \lambda x + F(x)$$

has unique solution $x = \overline{x}$ in $(0, \infty)$. Authors call $\overline{x}$ the only positive equilibrium of our model.

THEOREM 3 $F(x)$

$$\limsup_{x \to \infty} \frac{F(x)}{x} < 1 - \lambda, \tag{3.1}$$

$$\liminf_{x \to 0} \frac{F(x)}{x} > 1 - \lambda. \tag{3.2}$$

$\{A_n\}$ $\overline{x}$

THEOREM 4 $F(x)$

$$f(x) = \frac{F(x)}{1 - \lambda}.$$

$$\alpha = f(\beta), \qquad \beta = f(\alpha)$$

$\alpha = \beta = \overline{x}$ $\{A_n\}$

$\overline{x}$.

From now we assume that for some $y_0 > 0$, we have

$$F(y_0) = \max_{y \geq 0} F(x)$$

and $F(x)$ is increasing in $[0, y_0]$ and decreasing in (y_0, ∞). This function $F(x)$ is called unimodal. Let

$$f(x) = \frac{F(x)}{(1 - \lambda)}.$$

Suppose further that $\{A_n\}$ is a persistent solution of 1.1. Let $\{P_n\}_{n=-\infty}^{\infty}$ and $\{Q_n\}_{n=-\infty}^{\infty}$ be the full limiting sequences satisfying equation 1.1 for all n such that

$$\limsup_{n\to\infty} A_n = P_0, \qquad Q_0 \leq P_s \leq P_0. \tag{3.6}$$

Hence,

$$P_0 \leq \frac{F(P_{-m-1})}{1-\lambda} \leq \frac{F(y_0)}{1-\lambda} = f(y_0). \tag{3.7}$$

THEOREM 5 $f(y_0) \leq y_0$
$\{A_n\}_{n=-m}^{\infty}$ $\lim_{n\to\infty} A_n = \overline{x}$

From now we assume that $f(y_0) > y_0$. Let I be the interval $[0, f(y_0)]$. Clearly, the function f maps I into itself. From (3.7) we have $A_n \in I$ for all but finite n. Let f^n denote the nth iteration of f. These facts give

LEMMA 1 $\lim_{n\to\infty} f^n(x) = \overline{x}$ $x \in I$
$\overline{x}$.

LEMMA 2 $| f'(\overline{x}) | \leq 1$

$$Sf(x) = \frac{f'''(x)}{f'(x)} - \frac{3}{2}\left(\frac{f''(x)}{f'(x)}\right)^2$$

f $I - \{\overline{x}\}$ $\lim_{n\to\infty} f^n(x) = \overline{x}$ $x \in I$ The proof of this Lemma can be found in [5 and 6]. Lemmas 1 and 2 together give

THEOREM 6 $| f'(\overline{x}) | \leq 1$

$$Sf(x) = \frac{f'''(x)}{f'(x)} - \frac{3}{2}\left(\frac{f''(x)}{f'(x)}\right)^2$$

f $I - \{\overline{x}\}$
$\overline{x}$

4. Effect of delay on the convergence and the periodicity

In this section we will study the effect of delay on the global stability. Recall that f is unimodal function and $f(y_0) = \max_{x\geq 0} f(x) > y_0$. This implies that $\overline{x} > y_0$.

PROPOSITION 1 $\{A_n\}$

$$\lambda^{m+1}\overline{x} < \liminf_{n\to\infty} A_n \leq \overline{x} \leq \limsup_{n\to\infty} A_n \leq f(y_0).$$

To invent the effect of delay, we suppose further that

$$0 \le f(x) - \overline{x} \le L_1(\overline{x} - x) \quad \text{for all } x \in [\lambda^{m+1}\overline{x}, \overline{x}],$$
$$0 \le \overline{x} - f(x) \le L_2(x - \overline{x}) \quad \text{for all } x \in [\overline{x}, f(y_0)].$$

We will prove that the global stability still holds in this case, if m is small enough.

THEOREM 7

$$\lambda^{m+1} > 1 - \frac{1}{\sqrt{L_1 L_2}}.$$

$\{A_n\}$ $\overline{x}$

Now we investigate the periodicity of our model. We have

PROPOSITION 2 $m_0 \ge 0$

$$\lambda^{m_0+1} > 1 - \frac{1}{\sqrt{L_1 L_2}}.$$

$m > m_0$ ( ) $\{A_n\}$ 1.1

$m - m_0$

Remark. It follows directly from this proposition that no divisor of the $m-m_0$ could be a period of a periodic solution.

5. Application

Consider the following model of the bobwhite quail population

$$A_{n+1} = \lambda A_n + \frac{\mu A_{n-m}}{1 + A_{n-m}^k} \qquad (0 < \lambda < 1; \quad \mu, k > 0).$$

Here,

$$F(x) = \frac{\mu x}{1 + x^k}, \qquad f(x) = \frac{F(x)}{1 - \lambda}.$$

If $\lambda + \mu \le 1$, using Theorem 1, we have $\lim A_n = 0$. From now let $\lambda + \mu > 1$. Put

$$H(x, y) = \frac{\mu x}{1 + y^k}.$$

Using Theorem 2, we have

$$0 < \liminf A_n \le \limsup A_n < \infty.$$

On the other hand,

$$F'(x) = \mu \cdot \frac{1 + (1-k)x^k}{(1+x^k)^2},$$

so if $k \leq 1$, we have $F'(x) > 0$ and $F(x)$ is increasing. Further, conditions 3.1 and 3.2 of Theorem 3 are satisfied, so

$$\lim A_n = \overline{x},$$

where the positive equilibrium

$$\overline{x} = \sqrt[k]{\frac{\lambda + \mu - 1}{1 - \lambda}}.$$

Now let $k > 1$. In this case using Theorem 4, we compute

$$y_0 = \sqrt[k]{\frac{1}{k-1}}, \qquad F(y_0) = \frac{(k-1)\mu}{k} y_0$$

and we obtain that if

$$k \leq \frac{\mu}{\lambda + \mu - 1},$$

then $F(y_0) \leq (1-\lambda) y_0$ and consequently, $\lim A_n = \overline{x}$. From now let

$$k > \frac{\mu}{\lambda + \mu - 1}.$$

To apply Theorem 6, first we compute

$$f'(\overline{x}) = \frac{1}{\mu}\{\mu - k(\lambda + \mu - 1)\}.$$

This should be no greater than 1 in absolute value. This holds exactly with

$$k \leq \frac{2\mu}{\lambda + \mu - 1}.$$

We show that for $k \geq 2$, the Schwarzian Sf is negative on the interval $[0, f(y_0)]$. Elementary computation gives

$$Sf(x) = -\frac{k(k-1)x^k\{(k-1)(k-2)x^k + 2(k+1)\}}{2x^2\{(k-1)x^k - 1\}^2}.$$

Therefore, $Sf(x) < 0$ for all $x > 0$ if $k \geq 2$. Hence, every positive solution converges to $\overline{x}$ if

$$k \in \left(0, \frac{\mu}{\lambda + \mu - 1}\right] \cup \left[2, \frac{2\mu}{\lambda + \mu - 1}\right].$$

Note that in case $1 < k < 2$, we must assume further that

$$\frac{\mu}{1 - \lambda} \leq \sqrt[k]{\frac{2(k+1)}{2-k}} \cdot \frac{k}{k-1}$$

in order to get the global asymptotical stability of $\overline{x}$.

To invent the effect of delay, we find a positive number L such that

$$|f(x) - \overline{x}| \le L|x - \overline{x}| \qquad \text{for all } x \in [0, f(y_0)].$$

An elementary calculus give

$$L_1 = L_2 = L = \frac{\mu}{1-\lambda} \cdot \frac{(k-1)^2}{4k}$$

satisfying (4.1). Hence, if

$$\lambda^{m+1} > 1 - \frac{1}{L}$$

and if $f(\lambda^{m+1}\overline{x}) \ge \overline{x}$, i.e., if

$$\frac{\lambda + \mu - 1}{1 - \lambda} \ge \frac{1 - \lambda^{m+1}}{\lambda^{m+1} - \lambda^{(m+1)k}},$$

then we have $\lim_{n\to\infty} A_n = \overline{x}$ for every positive solution $\{A_n\}$.

In [4] the authors proved that if

$$k < \frac{2}{1-\lambda} \cdot \frac{\mu}{\lambda + \mu - 1},$$

then the positive equilibrium $\overline{x}$ is locally asymptotically stable. Our result is global asymptotic stability so it requires more conditions on parameters.

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