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GLOBAL ASYMPTOTIC STABILITY FOR PREDATOR-PREY SYSTEMS WHOSE PREY RECEIVES TIME-VARIATION OF THE ENVIRONMENT

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ABSTRACT. A predator-prey model with prey receiving time-variation of the environment is considered. Such a system is shown to have a unique interior equilibrium that is globally asymptotically stable if the time-variation is bounded and weakly integrally positive. In particular, the result tells that the equilibrium point can be stabilized even by nonnegative functions that make the limiting system structurally unstable. The method that is used to obtain the result is an analysis of asymptotic behavior of the solutions of an equivalent system to the predator-prey model.

1. Introduction

Predator-prey systems in nature apparently persist stably while the most basic models and experiments show their instability (see, for example, [8, 17, 23, 31]). This gap suggests that our insight is not enough to understand mechanisms acting in nature which stabilize population dynamics. To resolve the gap, theoreticians and experimentalists have made a long list of such processes (see, the books [6, 14, 18, 21]).

The basic theoretical tool in these investigations is the system of Lotka-Volterra equations for a prey with population density $N(t)$ and a predator with population density $P(t)$:

$$(LV) \qquad \begin{aligned} N' &= (a - bP)N, \\ P' &= (-\,c + dN)P, \end{aligned}$$

where the prime denotes d/dt and parameters a, b, c, and d are assumed to be positive. This model is often criticized because its single positive equilibrium point is a center, i.e., a "neutrally stable" equilibrium surrounded by a family of periodic orbits whose amplitudes depend on the initial population sizes. Also, the slightest change to the model's structure typically results in qualitatively different behavior. For example, if a decreases linearly with prey density the equilibrium point is stable; on the other hand, introducing a saturating (Type II) functional response turns the equilibrium into an unstable spiral point (see [9]). This structural instability means

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that the model cannot make any predictions that are robust enough to be tested. After all, we know that model (LV) does not adequately describe even the most highly controlled experiments.

Structural instability can, however, be used to our advantage. In effect, it allows us to use the Lotka-Volterra equations as an exquisitely sensitive balance, with which we can determine the effects of the processes that it ignores. So, when we say that a Type II functional response is destabilizing, we mean that it destabilizes the equilibrium point in model (LV). Similarly, when we say that the presence of a carrying capacity for the prey tends to be stabilizing, we mean that it stabilizes the equilibrium point. There is a long tradition of using the Lotka-Volterra equations in this way (see [22]).

A time-variational component of the environment is one of the processes that the Lotka-Volterra equations ignore. Realistic models should take account of seasonal effect. Constant per capita birth and mortality rates are highly unlikely for most natural populations; rather thay are usually subject to seasonal fluctuations. Supposing that prey have a carrying capacity and are more effective to receive time-variation of the environment than their predators, we may discuss a general version of model (LV) where only a is modified to $a = \beta(t) - \delta(t)N$ with continuous and nonnegative functions $\beta(t)$ and $\delta(t)$.

In this paper, in a simplest way, we consider a predator-prey model of the form

$$(E) \qquad \begin{aligned} N' &= (a + ch(t) - dh(t)N - bP)N, \\ P' &= (-\,c + dN)P, \end{aligned}$$

where $h(t)$ is continuous and nonnegative for $t \ge 0$ and a, b, c, and d are positive constants. It is clear that the modified model (E) still has a unique interior equilibrium point $(c/d, a/b)$. Needless to say, we only have to consider model (E) in the first quadrant $\{(N,P)\colon N > 0 \text{ and } P > 0\}$. Hence, the initial data is in the first quadrant. The interior equilibrium of (E) is said to be *globally attractive* if it attracts any solution of (E) with the initial data. Moreover, if interior equilibrium of (E) is stable, then it is said to be *globally asymptotically stable*.

To state our main result, we define a family of functions. We say a nonnegative function ϕ is *weakly integrally positive* if

$$\int_I \phi(t)dt = \infty$$

for every set $I = \bigcup_{n=1}^{\infty}[\tau_n, \sigma_n]$ such that $\tau_n + \delta < \sigma_n < \tau_{n+1} \le \sigma_n + \Delta$ for some $\delta > 0$ and $\Delta > 0$. A simple example of weakly integrally positive function is $\sin^2 t$, $1/(1+t)$, or $\sin^2 t/(1+t)$ (see [12, 13, 27–29]). It is easy to see that the family of weakly integrally positive functions includes nonnegative functions which converge to 0 as $t \to \infty$.

Theorem 1. *Suppose there exists an $\overline{h}$ such that $0 \le h(t) \le \overline{h}$ for $t \ge 0$. If $h(t)$ is weakly integrally positive, then the interior equilibrium $(c/d, a/b)$ of (E) is globally asymptotically stable.*

Theorem 1 tells that the equilibrium point of (E) can be stabilized even by such nonnegative functions that make the limiting system of (E) structurally unstable.

The organization of this paper is as follows. In Section 2, we introduce a transformation and establish a proposition on Lyapunov's stability. Also, we eximane properties of certain functions which will be used in proving our main theorem. We prove the main theorem in Section 3 and summarize our findings in Section 4.

2. Transformation

Changing variables

$$x = -\log(bP/a) \quad \text{and} \quad y = -\log(dN/c),$$

we can transform model (E) into the system

$$\begin{aligned} x' &= c(1-e^{-y}), \\ y' &= -a(1-e^{-x}) - ch(t)(1-e^{-y}). \end{aligned} \tag{1}$$

System (1) has the zero solution $(x(t), y(t)) \equiv (0,0)$, which corresponds to the interior equilibrium $(c/d, a/b)$ of (E). The above transformation is a one-to-one correspondence from the first quadrant $\{(N,P): N>0 \text{ and } P>0\}$ to the whole real plane $\{(x,y): x \in \mathbb{R} \text{ and } y \in \mathbb{R}\}$. Hence, the interior equilibrium $(c/d, a/b)$ of (E) is globally attractive if and only if every solution $(x(t), y(t))$ of (1) tends to $(0,0)$ as time t increases.

To prove Theorem 1, we have to derive two conclusions: the zero solution of (1) is stable; any solution of (1) approaches the origin $(0,0)$. It is easy to show the stability of the zero solution of (1) by using a Lyapunov-type theorem. For details about the direct method of Lyapunov, see the books [1, 4, 10, 11, 16, 19, 20, 26, 33, 34] for example.

Proposition 2. *If $h(t)$ is nonnegative for $t \geq 0$, then the zero solution of* (1) *is uniformly stable.*

Proof. As a suitable Lyapunov function, we choose

$$V(x,y) = af(x) + cf(y),$$

where $f(z) = e^{-z} + z - 1$ for $z \in \mathbb{R}$. Since

$$\frac{d}{dz} f(z) = -e^{-z} + 1,$$

$f(z)$ is increasing for $z \geq 0$ and decreasing for $z \leq 0$. Hence, $f(z) > 0 = f(0)$ for $z \neq 0$. This means that $V(x,y)$ is positive definite and decrescent. Differentiate $V(x,y)$ along any solution of (1) to obtain

$$\dot{V}_{(1)}(t,x,y) = -c^2 h(t)\left(1-e^{-y}\right)^2 \leq 0$$

on $[0,\infty)\times\mathbb{R}^2$. We therefore conclude that the zero solution of (1) is uniformly stable by using a Lyapunov-type theorem due to Persidski [25] (refer also to Theorem 1.7 in [26, p. 14] or to Theorem 8.2 in [33, p. 32]). □

In order to prove the attraction of any solution of (1), it is helpful to describe the properties of functions $f(z)$ and

$$g(z) = \left|1 - e^{-z}\right|$$

for $z \in \mathbb{R}$. It is clear that the inequality $f(-z) \geq f(z)$ holds for $z \geq 0$, with equality if and only if $z = 0$. Hence, we see that

$$0 \leq f(z) \leq f(-\alpha) \quad \text{for} \ \ |z| \leq \alpha \tag{2}$$

with α positive. Let $f^{-1}(w)$ be the inverse function of $w = f(z)\text{sgn}z$. Then, $f^{-1}(w)$ is increasing for $w \in \mathbb{R}$ and $f^{-1}(0) = 0$. Hence, $f^{-1}(w)$ is positive for $w > 0$ and negative for $w < 0$. Since $f(-z) > f(z) > 0$ for $z > 0$, we see that

$$0 < -f^{-1}(-w) < f^{-1}(w) \quad \text{for} \ \ w > 0. \tag{3}$$

Also, $f^{-1}(w)$ tends to ∞ as $w \to \infty$ and it tends to $-\infty$ as $w \to -\infty$. Since

$$\frac{d}{dz}g(z) = \begin{cases} e^{-z} & \text{if} \ \ z \geq 0 \\ -\, e^{-z} & \text{if} \ \ z \leq 0, \end{cases}$$

$g(z)$ is increasing for $z \geq 0$ and decreasing for $z \leq 0$. Hence, $g(z) > 0 = g(0)$ for $z \neq 0$. It is easy to check that $\lim_{z\to\infty} g(z) = 1$, $\lim_{z\to-\infty} g(z) = \infty$ and the inequality $g(-z) \geq g(z)$ holds for $z \geq 0$, with equality if and only if $z = 0$. Hence, we see that

$$g(z) \geq g(\alpha) > 0 \quad \text{for} \ \ |z| \geq \alpha \tag{4}$$

and

$$0 \leq g(z) \leq g(-\alpha) \quad \text{for} \ \ |z| \leq \alpha \tag{5}$$

with α positive.

3. Proof of the main result

We are now ready to prove Theorem 1.

Proof of Theorem 1. By means of Proposition 2, we conclude that the zero solution of (1) is stable. We will prove that every solution of (1) tends to the origin.

Let $(x(t), y(t))$ be any solution of (1) with the initial time $t_0 \geq 0$ and let

$$v(t) = V(x(t), y(t)) = af(x(t)) + cf(y(t)). \tag{6}$$

Then, we have

$$v'(t) = -c^2h(t)g^2(y(t)) \leq 0 \quad \text{for} \ \ t \geq t_0,$$

namely, $v(t)$ is nonincreasing for $t \geq t_0$. Hence, $v(t)$ has a limiting value $v_0 \geq 0$. If $v_0 = 0$, then from (6) we see that the solution $(x(t), y(t))$ tends to $(0, 0)$ as $t \to \infty$. This completes the proof. Thus, we need consider only the case in which $v_0 > 0$. We will show that this case does not occur.

Since $v(t)$ tends to a positive value v_0 as $t \to \infty$, there exists a $T_1 \geq t_0$ such that

$$0 < v_0 \leq v(t) \leq 2v_0 \quad \text{for} \ \ t \geq T_1. \tag{7}$$

Hence, by (6), we have

$$f(y(t)) \leq \frac{2v_0}{c},$$

namely,

$$f^{-1}(-2v_0/c) \leq y(t) \leq f^{-1}(2v_0/c)$$

for $t \geq T_1$. From (3), we see that

$$|y(t)| \leq f^{-1}(2v_0/c) \quad \text{for} \ \ t \geq T_1. \tag{8}$$

Since $|y(t)|$ is bounded, it has an inferior limit and a superior limit. First, we will show that the inferior limit of $|y(t)|$ is zero, and we will then show that the superior limit of $|y(t)|$ is also zero.

Suppose that $\liminf_{t\to\infty}|y(t)|>0$. Then, there exist a $\gamma>0$ and a $T_2\ge t_0$ such that $|y(t)|>\gamma$ for $t\ge T_2$. It follows from (4) that $g^2(y(t))\ge g^2(\gamma)$ for $t\ge T_2$. Hence, we have

$$v'(t)=-c^2h(t)g^2(y(t))\le -c^2g^2(\gamma)h(t)$$

for $t\ge T_2$. Integrating this inequality from t_0 to t, we obtain

$$-v(t_0)\le v(t)-v(t_0)=\int_{t_0}^t v'(s)ds\le -c^2g^2(\gamma)\int_{T_2}^t h(s)ds,$$

which tends to $-\infty$ as $t\to\infty$ because $h(t)$ is weakly integrally positive. This is a contradiction. Thus, we see that $\liminf_{t\to\infty}|y(t)|=0$.

Suppose that $\limsup_{t\to\infty}|y(t)|>0$. Let $\lambda=\limsup_{t\to\infty}|y(t)|$. Let ε be so small that $0<\varepsilon<-f^{-1}(-v_0/c)$,

$$\frac{c\overline{h}}{a}g(-\varepsilon)<1-\exp\left(-f^{-1}\left(\frac{v_0-cf(-\varepsilon)}{a}\right)\right) \tag{9}$$

and

$$\frac{c\overline{h}}{a}g(-\varepsilon)<\exp\left(-f^{-1}\left(\frac{cf(-\varepsilon)-v_0}{a}\right)\right)-1. \tag{10}$$

Since $g(-\varepsilon)$ approaches zero and the right-hand sides of (9) and (10) approach positive numbers as $\varepsilon\to 0$, we can find such a positive number ε. Also, we may assume without loss of generality that $\varepsilon<\lambda/2$.

As proved above, the inferior limit of $y(t)$ is zero. Hence, we can choose two intervals $[\tau_n,\sigma_n]$ and $[t_n,s_n]$ with $[t_n,s_n]\subset[\tau_n,\sigma_n]$, $T_1<\tau_n$ and $\tau_n\to\infty$ as $n\to\infty$ such that $|y(\tau_n)|=|y(\sigma_n)|=\varepsilon$, $|y(t_n)|=\lambda/2$, $|y(s_n)|=3\lambda/4$ and

$$|y(t)|\ge\varepsilon \quad \text{for } \tau_n<t<\sigma_n, \tag{11}$$

$$|y(t)|\le\varepsilon \quad \text{for } \sigma_n<t<\tau_{n+1}, \tag{12}$$

$$\frac{1}{2}\lambda<|y(t)|<\frac{3}{4}\lambda \quad \text{for } t_n<t<s_n. \tag{13}$$

By (2), (6), (7) and (12), we have

$$af(x(t))=v(t)-cf(y(t))\ge v_0-cf(-\varepsilon)$$

for $\sigma_n\le t\le\tau_{n+1}$. For the sake of brevity, let $w_0=v_0-cf(-\varepsilon)$. Then, w_0 is positive, because $0<\varepsilon<-f^{-1}(-v_0/c)$. There are two cases to consider: (a) $x(t)\ge f^{-1}(w_0/a)>0$ for $\sigma_n\le t\le\tau_{n+1}$; (b) $x(t)\le f^{-1}(-w_0/a)<0$ for $\sigma_n\le t\le\tau_{n+1}$. In case (a), using the second equation in system (1) with (5) and (12), we obtain

$$\begin{aligned}y'(t)&=-a\big(1-e^{-x(t)}\big)-ch(t)\big(1-e^{-y(t)}\big)\\&\le -a\big(1-e^{-x(t)}\big)+c\overline{h}g(y(t))\\&\le -a\big(1-\exp\big(-f^{-1}(w_0/a)\big)\big)+c\overline{h}g(-\varepsilon)\overset{\text{def}}{=}-\mu_1\end{aligned}$$

for $\sigma_n \le t \le \tau_{n+1}$. From (9), we see that μ_1 is positive. Note that μ_1 is independent of n. Similarly, in case (b), we have

$$\begin{aligned} y'(t) &= -a\bigl(1 - e^{-x(t)}\bigr) - ch(t)\bigl(1 - e^{-y(t)}\bigr) \\ &\ge -a\bigl(1 - e^{-x(t)}\bigr) - c\overline{h}g(y(t)) \\ &\ge a\bigl(\exp\bigl(-f^{-1}(-w_0/a)\bigr) - 1\bigr) - c\overline{h}g(-\varepsilon) \overset{\text{def}}{=} \mu_2 \end{aligned}$$

for $\sigma_n \le t \le \tau_{n+1}$. From (10), we see that μ_2 is also positive and independent of n. Let $\mu(\varepsilon) = \min\{\mu_1, \mu_2\} > 0$. Then, in either case, we get

$$|y'(t)| \ge \mu \quad \text{for} \ \ \sigma_n \le t \le \tau_{n+1}.$$

Using this inequality and (8), we can estimate that

$$\begin{aligned} 2f^{-1}(2v_0/c) \ge |y(\tau_{n+1})| + |y(\sigma_n)| &\ge \left| \int_{\sigma_n}^{\tau_{n+1}} y'(t)dt \right| \\ &= \int_{\sigma_n}^{\tau_{n+1}} |y'(t)|dt \ge \mu\,(\tau_{n+1} - \sigma_n), \end{aligned}$$

or $\tau_{n+1} \le \sigma_n + \Delta$ for $n \in \mathbb{N}$, where $\Delta = 2f^{-1}(2v_0/c)/\mu$.

Let $I = \displaystyle\bigcup_{n=1}^{\infty}[\tau_n, \sigma_n]$. Then, it follows from (11) that $|y(t)| \ge \varepsilon$ for $t \in I$. Hence, by (4), we have

$$g(y(t)) \ge g(\varepsilon) > 0 \quad \text{for} \ \ t \in I,$$

and therefore,

$$\int_{t_0}^{\infty} v'(t)dt = -c^2 \int_{t_0}^{\infty} h(t)g^2(y(t))dt \le -c^2 g^2(\varepsilon) \int_I h(t)dt.$$

Since

$$\int_{t_0}^{\infty} v'(t)dt = \lim_{t\to\infty} v(t) - v(t_0) = v_0 - v(t_0),$$

we obtain

$$\int_I h(t)dt \le \frac{v(t_0) - v_0}{c^2 g^2(\varepsilon)} < \infty.$$

Hence, from the assumption that $h(t)$ is weakly integrally positive and the estimation that $\tau_{n+1} \le \sigma_n + \Delta$ for $n \in \mathbb{N}$, we see that $\liminf_{n\to\infty}(\sigma_n - \tau_n) = 0$. Since $[t_n, s_n] \subset [\tau_n, \sigma_n]$, it turns out that

$$\liminf_{n\to\infty}(s_n - t_n) = 0. \tag{14}$$

By (6) and (7), we have

$$f(x(t)) \le \frac{2v_0}{a},$$

namely,

$$f^{-1}(-2v_0/a) \le x(t) \le f^{-1}(2v_0/a)$$

for $t \ge T_1$. From (3), we see that

$$|x(t)| \le f^{-1}(2v_0/a) \quad \text{for} \ \ t \ge T_1.$$

Hence, by (5), we obtain

$$g(x(t)) \le g\bigl(-f^{-1}(2v_0/a)\bigr) \quad \text{for} \ \ t \ge T_1. \tag{15}$$

Using (5) and (13), we have

$$g(y(t)) \le g(-3\lambda/4) \quad \text{for } t_n \le t \le s_n.$$

Hence, together with (15), we get

$$\begin{aligned}|y'(t)| &\le ag(x(t)) + c\bar{h}g(y(t)) \\ &\le ag\big(-f^{-1}(2v_0/a)\big) + c\bar{h}g(-3\lambda/4)\end{aligned}$$

for $t_n \le t \le s_n$. Letting $\nu = ag(-f^{-1}(2v_0/a)) + c\bar{h}g(-3\lambda/4)$ and integrating this inequality from t_n to s_n, we obtain

$$\begin{aligned}\frac{1}{4}\lambda &= |y(s_n)| - |y(t_n)| \le |y(s_n) - y(t_n)| \\ &= \left|\int_{t_n}^{s_n} y'(s)ds\right| \le \int_{t_n}^{s_n} |y'(s)|ds \le \nu(s_n - t_n).\end{aligned}$$

This contradicts (14). We therefore conclude that $\limsup_{t\to\infty} |y(t)| = \lambda = 0$.

In summary, $y(t)$ tends to zero as $t \to \infty$. Hence, there exists a $T_3 \ge T_1$ such that

$$|y(t)| < \varepsilon \quad \text{for } t \ge T_3. \tag{16}$$

Using (16) instead of (12) and following the same process as in the above argument, we see that

$$|y'(t)| \ge \mu \quad \text{for } t \ge T_3.$$

This inequality yields

$$|y(t) - y(T_3)| = \left|\int_{T_3}^{t} y'(s)ds\right| = \int_{T_3}^{t} |y'(s)|ds \ge \mu(t - T_3),$$

which tends to ∞ as $t \to \infty$. This contradicts the fact that $y(t)$ tends to zero as $t \to \infty$. Thus, the case of $v_0 > 0$ cannot happen.

The proof of Theorem 1 is now complete. □

4. Discussion

System (1) is rewritten as a quasi-linear system of the form

$$\mathbf{x}' = A(t)\mathbf{x} + \mathbf{f}(t, \mathbf{x}),$$

where

$$\mathbf{x} = \begin{pmatrix} x \\ y \end{pmatrix}, \qquad A(t) = \begin{pmatrix} 0 & c \\ -a & -ch(t) \end{pmatrix}$$

and

$$\mathbf{f}(t, \mathbf{x}) = \mathbf{f}(t, x, y) = \begin{pmatrix} c(1 - y - e^{-y}) \\ -a(1 - x - e^{-x}) - ch(t)(1 - y - e^{-y}) \end{pmatrix}.$$

The nonlinear part $\mathbf{f}(t, x, y)$ is a higher-order term with respect to x and y, and the linear approximation for system (1) is

$$\mathbf{x}' = A(t)\mathbf{x}. \tag{17}$$

It is known that under all of the assumptions in Theorem 1, the zero solution of (17) is asymptotically stable, but it is not always uniformly asymptotically stable. For example, if $h(t) = \sin^2 t$, then the zero solution of (17) is uniformly asymptotically stable. On the other hand, if $h(t) = 1/(1 + t)$ or $h(t) = \sin^2 t/(1 + t)$, then the zero solution of (17) is asymptotically stable, but it is not uniformly asymptotically stable (for details, see [2, 13, 28]).

If the zero solution of a linear system is uniformly asymptotically stable, then the zero solution of the corresponding quasi-linear system is also uniformly asymptotically stable. As Perron [24] has proved, however, the asymptotic stability of the zero solution of a linear system does not necessarily imply that the zero solution of the corresponding quasi-linear system is asymptotically stable. As to Perron's example, see the books [3, pp. 42–43], [4, pp. 169–170], [5, p. 71], [30, pp. 92–93], [32, pp. 315–317], etc.

Therefore, needless to say, even if the zero solution of (17) is asymptotically stable, we cannot show that the zero solution of (1) is globally asymptotically stable. In this paper, we exhibited a sufficient condition for the zero solution of (1) to be globally asymptotically stable as Theorem 1. An advantage of Theorem 1 is here.

The same $h(t)$ put into per capita birth and mortality rates for prey in (E) is a technical setting that makes the modified model still have a unique interior equilibrium point $(c/d, a/b)$. From a biological point of view, however, they should be different. Developing these considerations into a model that provides different time-variational functions on per capita birth and mortality rates of the prey, which is a more biologically practical scenario, will be left for future work.

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