Global asymptotic stability for predator-prey models with environmental time-variations

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Abstract

This paper considers a Lotka-Volterra predator-prey model with predator receiving an environmental time-variation. For such a system, a unique interior equilibrium is shown to be globally asymptotically stable if the time-variation is bounded and weakly integrally positive. Our result tells that the equilibrium can be stabilized even by nonnegative functions that make the limiting system structurally unstable. Numerical simulations are also shown to illustrate the result and to suggest that cases with time-variation acting on predator have larger-scale convergence to the equilibrium than population dynamics with time-variation acting on prey.

Key words: Global asymptotic stability; Predator-prey systems; Weakly integrally positive; Time-variation
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1. Introduction

Theoretical study on predator-prey systems in mathematical ecology has a long history starting with the pioneering work of Lotka and Volterra. Their model is described by ordinary differential equations for a prey with population density $N(t)$ and a predator with population density $P(t)$ as follows:

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

where the prime denotes d/dt and parameters a, b, c, and d are assumed to be positive. This model has a single positive equilibrium point $(c/d, a/b)$, which is a center, i.e., a “neutrally stable” equilibrium surrounded by a family of periodic orbits whose amplitudes depend on the initial population sizes.

A time-variational component of the environment is one of the processes that the Lotka-Volterra equations ignore. Realistically, constant per capita birth and mortality rates are highly unlikely for most natural populations; rather they are usualy subject to environmerntal fluctuations. Supposing that predators have a carrying capacity and are more effective to receive time-variation of the environment than their prey, we may discuss a general version of model

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(LV) in which $-c$ is modified to $-c = \xi(t) - \eta(t)P$, where $\xi(t)$ and $\eta(t)$ are continuous functions with $\eta(t) \geq 0$. In a simplest way, we will consider the following modified system of (LV)

$$\begin{aligned} N' &= (a - bP)N, \\ P' &= (-\,c + ah(t) - bh(t)P + dN)P, \end{aligned} \tag{E}$$

where $h(t)$ is continuous and nonnegative for $t \geq 0$. Because of some technical setting, the modified model (E) still has the same interior equilibrium $(c/d, a/b)$ uniquely. Let, for example, $h(t) = 1/(1+t)$. Then, what behavior of solutions is expected for system (E)? Noting that the limiting equations of (E) becomes (LV), will we observe a long-time behavior of the solution which converges to periodic orbits surrounding the point $(c/d, a/b)$ or not?

In this paper, we give answer for this question in a more general way. For this purpose, 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 $I = \displaystyle\bigcup_{n=1}^{\infty}[\tau_n, \sigma_n]$ such that $\tau_n + \delta < \sigma_n < \tau_{n+1} \leq \sigma_n + \Delta$ 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 [3, 4, 5, 11, 12, 13]). It is easy to see that the family of weakly integrally positive functions includes certain nonnegative functions which converge to 0 as $t \to \infty$; e.g., it includes the decreasing function with this property.

Needless to say, we consider model (E) in the first quadrant $\{(N, P) \colon N > 0 \text{ and } P > 0\}$, and then 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 the interior equilibrium of (E) is stable, then it is said to be *globally asymptotically stable*. We have the following:

Theorem 1. *Suppose that $h(t)$ is bounded and nonnegative for $t \geq 0$. 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 nonnegative functions that make the limiting system of (E) equal to (LV).

The organization of this paper is as follows. In Section 2, we introduce a Lyapunov function to prove stability on the interior equilibrium and examine properties of certain functions which will be used in proving our main theorem. We prove global attraction on the interior equilibrium in Section 3. In [14], based on the same model (LV), the authors have considered a predator-prey model where only prey (not predators) receive time-variation of the environment to obtain the same type of result as Theorem 1. Using numerical simulations, in Section 4, we illustrate Theorem 1 and suggest that the time-variation acting on predator has larger-scale convergence to the equilibrium as compared with the case of a time-variation acting on prey. We summarize our findings in Section 5.

2. Lyapunov's function

Let $x = -\log(bP/a)$ and $y = -\log(dN/c)$. Then, our model (E) can be transformed into the system

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

The interior equilibrium $(c/d, a/b)$ of (E) corresponds to the zero solution $(x(t), y(t)) \equiv (0,0)$ of (1). To prove Theorem 1, we have only to show two conclusions:

(i) the zero solution of (1) is stable;
(ii) all solutions of (1) tend to the origin $(0,0)$ as time increases.

Define

$$f(z) = e^{-z} + z - 1 \quad \text{and} \quad g(z) = |1 - e^{-z}|$$

for $z \in \mathbb{R}$. Note that

$$g(z) = \left| \frac{d}{dz} f(z) \right|.$$

It is easy to check that $f(0) = 0$ and $f(-z) > f(z)$ for $z > 0$. Hence, it turns out that

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

with $\alpha > 0$. The function $f(z)$ is increasing for $z \ge 0$ and decreasing for $z \le 0$. Let $w = \hat{f}(z) \overset{\text{def}}{=} f(z)\mathrm{sgn} z$ and denote the inverse function by $\hat{f}^{-1}(z)$. Then, we see that

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

It is also clear that $g(z)$ is increasing for $z \ge 0$ and decreasing for $z \le 0$ with $g(0) = 0$, $\lim_{z\to\infty} g(z) = 1$, $\lim_{z\to-\infty} g(z) = \infty$ and $g(-z) > g(z)$ for $z > 0$. Hence, it follows that

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

and

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

with α positive.

As a suitable Lyapunov function for system (1), we adopt

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

Obviously, $V(x,y)$ is positive definite and $V(0,0) = 0$. Differentiating $V(x,y)$ along any solution of (1) gives

$$\dot{V}_{(1)}(t,x,y) = -a^2 h(t) g^2(x(t))$$

on $[0,\infty) \times \mathbb{R}^2$. Hence, by means of a well-known Lyapunov-type theorem, we have the following result (as to the Lyapunov-type theorem, see Theorem 1.7 in [10, p. 14] or to Theorem 8.2 in [15, p. 32]).

Proposition 2. *If* $h(t)$ *is nonnegative for* $t \ge t_0$, *then the zero solution of* (1) *is uniformly stable.*

We obtained the first conclusion that we desired. In the next section, we will show the second conclusion, that is, the global attraction of solutions of (1).

3. Global attraction

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

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

for $t \geq t_0$. Then, we obtain

$$v'(t) = -a^2 h(t) g^2(x(t)) \leq 0,$$

and therefore, $v(t)$ is nonincreasing for $t \geq t_0$ and it has a limiting value $v_0 \geq 0$. Hence, there exists a $T \geq t_0$ such that

$$v_0 \leq v(t) \leq 2v_0 \quad \text{for} \;\; t \geq T. \tag{7}$$

From (6) and the property that $f(z) \to 0$ as $z \to 0$, we conclude that all solutions of (1) tend to $(0, 0)$ as $t \to \infty$ if and only if $v_0 = 0$. Assuming additional conditions on $h(t)$, we can show that the case in which $v_0 > 0$ does not occur.

Proposition 3. *In addition to the assumptions in Proposition* 2, *if* $h(t)$ *is bounded and weakly integrally positive, then all solutions of* (1) *tend to the origin* $(0, 0)$ *as time increases.*

Before proving Proposition 3, we examine the property of the first component of the solution $(x(t), y(t))$ of (1).

Lemma 4. *If* $h(t)$ *is bounded and* v_0 *is positive, then* $x(t)$ *does not converge to zero as* $t \to \infty$.

Proof. Suppose that $x(t)$ converges to zero as $t \to \infty$. Then, for a sufficiently small $\varepsilon > 0$, there exists a $T_1 \geq T$ such that

$$|x(t)| < \varepsilon \quad \text{for} \;\; t \geq T_1. \tag{8}$$

Hence, it follows from (2) that $0 \leq f(x(t)) \leq f(-\varepsilon)$ for $t \geq T_1$. By this inequality with (6) and (7), we obtain

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

for $t \geq T_1$. Since v_0 is positive and ε is small enough, we may consider that $v_0 - af(-\varepsilon)$ is positive. Let $u_0 = (v_0 - af(-\varepsilon))/c > 0$. Then, there are two cases that we should consider: (a) $y(t) \geq \hat{f}^{-1}(u_0) > 0$ for $t \geq T_1$; (b) $y(t) \leq \hat{f}^{-1}(-u_0) < 0$ for $t \geq T_1$. Since $h(t)$ is bounded, there exists a $\overline{h} > 0$ such that $|h(t)| \leq \overline{h}$ for $t \geq 0$. We first consider the case (a). From (5), we see that

$$\begin{aligned} x'(t) &= c\bigl(1 - e^{-y(t)}\bigr) - ah(t)\bigl(1 - e^{-x(t)}\bigr) \\ &\geq c\bigl(1 - e^{-y(t)}\bigr) - a\overline{h}g(x(t)) \\ &\geq c\Bigl(1 - \exp\Bigl(-\hat{f}^{-1}(u_0)\Bigr)\Bigr) - a\overline{h}g(-\varepsilon) \overset{\text{def}}{=} \lambda_1 \end{aligned}$$

for $t \geq T_1$. Since u_0 is positive and ε is small enough, λ_1 is a positive number. This contradicts the assumption that $x(t)$ converges to zero as $t \to \infty$. We next consider the case (b). Similarly, we obtain

$$\begin{aligned} x'(t) &\leq c\bigl(1 - e^{-y(t)}\bigr) + a\overline{h}g(x(t)) \\ &\leq -c\Bigl(\exp\Bigl(-\hat{f}^{-1}(-u_0)\Bigr) - 1\Bigr) + a\overline{h}g(-\varepsilon) \overset{\text{def}}{=} -\lambda_2 \end{aligned}$$

for $t \geq T_1$, where $\lambda_2 > 0$. This is also a contradiction. The lemma is thus proved. $\square$

We are now ready to prove Proposition 3.

Proof of Proposition 3. As mentioned in the top paragraph of Section 3, $v(t)$ has a limiting value v_0. We will show that $v_0 = 0$. By way of contradiction, we suppose that $v_0 > 0$. It follows from (6) and (7) that $f(x(t)) \leq 2v_0/a$. Taking account of (3), we see that

$$|x(t)| \leq \hat{f}^{-1}(2v_0/a) \quad \text{for} \;\; t \geq T. \tag{9}$$

Hence, there exist the lower limit and the upper limit of $|x(t)|$.

If the lower limit of $|x(t)|$ is positive, then we can find a $\gamma > 0$ and a $T_2 \geq T$ such that $|x(t)| > \gamma$ for $t \geq T_2$. Hence, it follows from (4) that $g^2(x(t)) \geq g^2(\gamma)$ for $t \geq T_2$. Using this inequality, we have

$$v'(t) = -a^2h(t)g^2(x(t)) \leq -a^2g^2(\gamma)h(t)$$

for $t \geq T_2$. Taking into account that $v'(t) \leq 0$ for $t_0 \leq t \leq T_2$, we obtain

$$-v(t_0) \leq v(t) - v(t_0) = \int_{t_0}^{t} v'(s)ds \leq -a^2g^2(\gamma)\int_{T_2}^{t} h(s)ds.$$

On the other hand, since $h(t)$ is weakly integrally positive,

$$\int_{T_2}^{t} h(s)ds \to \infty \quad \text{as} \;\; t \to \infty.$$

This is a contradiction. Thus, we see that $\liminf_{t\to\infty} |x(t)| = 0$.

Combining the conclusion of Lemma 4 and the above fact, we see that the upper limit of $|x(t)|$ is positive. Let $\mu = \limsup_{t\to\infty} |x(t)|$. Recall that $|h(t)| \leq \overline{h}$ for $t \geq 0$. We choose ε to be small enough as follows: $0 < \varepsilon < \min\{\mu/2, -\hat{f}^{-1}(-v_0/a)\}$;

$$\frac{a\overline{h}}{c}g(-\varepsilon) < 1 - \exp\biggl(-\hat{f}^{-1}\biggl(\frac{v_0 - af(-\varepsilon)}{c}\biggr)\biggr); \tag{10}$$

and

$$\frac{a\overline{h}}{c}g(-\varepsilon) < \exp\biggl(-\hat{f}^{-1}\biggl(\frac{af(-\varepsilon) - v_0}{c}\biggr)\biggr) - 1. \tag{11}$$

Since $g(-\varepsilon)$ approaches zero and the right-hand sides of (10) and (11) approach positive numbers as $\varepsilon \to 0$, such an ε exists. Let $w_0 = (v_0 - af(-\varepsilon))/c$. Then, w_0 is positive, because $0 < \varepsilon < -\hat{f}^{-1}(-v_0/a)$.

Since $\liminf_{t\to\infty} |x(t)| = 0 < \mu = \limsup_{t\to\infty} |x(t)|$, we can find two sequences of intervals $[\tau_n, \sigma_n]$ and $[t_n, s_n]$ with $[t_n, s_n] \subset [\tau_n, \sigma_n]$, $T < \tau_n$ and $\tau_n \to \infty$ as $n \to \infty$ such that $|x(\tau_n)| = |x(\sigma_n)| = \varepsilon$, $|x(t_n)| = \mu/2$, $|x(s_n)| = 3\mu/4$ and

$$|x(t)| > \varepsilon \quad \text{for} \;\; \tau_n < t < \sigma_n, \tag{12}$$

$$|x(t)| < \varepsilon \quad \text{for} \;\; \sigma_n < t < \tau_{n+1}, \tag{13}$$

$$\frac{1}{2}\mu < |x(t)| < \frac{3}{4}\mu \quad \text{for} \;\; t_n < t < s_n. \tag{14}$$

Using (13) instead of (8) and following the same process as in the proof of Lemma 4, we conclude that there exists a $\nu > 0$ such that

$$|x'(t)| \geq \nu \quad \text{for} \;\; \sigma_n \leq t \leq \tau_{n+1}.$$

Hence, together with (9), we can estimate that

$$\begin{aligned} 2\hat{f}^{-1}(2v_0/a) \geq |x(\tau_{n+1})| + |x(\sigma_n)| &\geq \left| \int_{\sigma_n}^{\tau_{n+1}} x'(t)dt \right| \\ &= \int_{\sigma_n}^{\tau_{n+1}} |x'(t)|dt \geq \nu\,(\tau_{n+1} - \sigma_n), \end{aligned}$$

namely, $\tau_{n+1} \leq \sigma_n + \Delta$ for $n \in \mathbb{N}$, where $\Delta = 2\hat{f}^{-1}(2v_0/a)/\nu$.

It follows from (4) and (12) that

$$g(x(t)) \geq g(\varepsilon) > 0 \quad \text{for} \;\; \tau_n \leq t \leq \sigma_n.$$

Since $h(t)$ is nonnegative for $t \geq 0$, we see that

$$\begin{aligned} v_0 - v(t_0) &= \int_{t_0}^{\infty} v'(t)dt \\ &= -a^2 \int_{t_0}^{\infty} h(t) g^2(x(t))dt \leq -a^2 g^2(\varepsilon) \sum_{n=1}^{\infty} \int_{\tau_n}^{\sigma_n} h(t)dt. \end{aligned}$$

Hence, we obtain

$$\sum_{n=1}^{\infty} \int_{\tau_n}^{\sigma_n} h(t)dt \leq \frac{v(t_0) - v_0}{a^2 g^2(\varepsilon)} < \infty. \tag{15}$$

If there exists a $\delta > 0$ such that $\sigma_n - \tau_n > \delta$ for $n \in \mathbb{N}$, then

$$\sum_{n=1}^{\infty} \int_{\tau_n}^{\sigma_n} h(t)dt = \infty$$

because $h(t)$ is weakly integrally positive and $\tau_{n+1} \leq \sigma_n + \Delta$ for $n \in \mathbb{N}$. This contradicts (15). Thus, 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

$$\liminf_{n\to\infty}(s_n - t_n) = 0. \tag{16}$$

Using (3), (6) and (7) again, we obtain

$$|y(t)| \leq \hat{f}^{-1}(2v_0/c) \quad \text{for} \;\; t \geq T.$$

From this estimation and (5), we see that

$$g(y(t)) \leq g\Big(-\hat{f}^{-1}(2v_0/c)\Big) \quad \text{for} \;\; t \geq T. \tag{17}$$

By (5) and (15), we also estimate that

$$g(x(t)) \leq g(-3\lambda/4) \quad \text{for} \;\; t_n \leq t \leq s_n.$$

Hence, together with (17), we get

$$|x'(t)| \le cg(y(t)) + a\overline{h}g(x(t)) \\ \le cg\Big(-\hat{f}^{-1}(2v_0/c)\Big) + a\overline{h}g(-3\lambda/4) \overset{\text{def}}{=} \rho$$

for $t_n \le t \le s_n$. This yields that

$$0 < \frac{1}{4}\mu = |x(s_n)| - |x(t_n)| \le |x(s_n) - x(t_n)| \\ = \left|\int_{t_n}^{s_n} x'(s)ds\right| \le \int_{t_n}^{s_n} |x'(s)|ds \le \rho(s_n - t_n)$$

for $n \in \mathbb{N}$, which contradicts (16). This contradiction was caused because it had been assumed that v_0 was positive. We therefore conclude that $v_0 = 0$.

The proof of Proposition 3 is then complete. ☐

As mentioned in Section 2, our model (E) is equivalent to system (1) by the transformation $x = -\log(bP/a)$ and $y = -\log(dN/c)$. Hence, Theorem 1 is obtained from Propositions 2 and 3.

4. Numerical results

To give numerical results on the main theorem for system (E), we first use a set of parameter values $a = 1$, $b = 0.1$, $c = 1$, and $d = 0.08$. Choose

$$h(t) = \frac{\beta}{1+t}, \qquad \beta \ge 0.$$

This $h(t)$ converges to 0 as $t \to \infty$ but is weakly integrally positive if $\beta > 0$. Then, the interior equilibrium is $(12.5, 10)$ and, from Theorem 1, it is globally asymptotically stable if $\beta > 0$. Figure 1 shows phase-plane plots of prey versus predator for $\beta = 1$, where spiral convergence is observed. Note that the initial data is $(N(0), P(0)) = (20, 1)$. If $\beta = 0$, we have periodic orbits whose amplitudes depend on the initial population sizes (see dotted lines in Figs. 1 and 2 for the same initial data).

In [14], the authors discussed another modified system of (LV) as follows:

$$\begin{aligned} N' &= (a + ch(t) - dh(t)N - bP)N, \\ P' &= (-c + dN)P \end{aligned} \tag{18}$$

to show that a unique interior equilibrium is globally asymptotically stable if the time-variation $h(t)$ is bounded and weakly integrally positive, which is the same type of result as Theorem 1 here. To run simulations for comparison of the result in [14] with Theorem 1, choose the same parameters $a = 1$, $b = 0.1$, $c = 1$, and $d = 0.08$ and the same function $h(t) = 1/(1+t)$ as Figure 1. Using the same initial data $(N(0), P(0)) = (20, 1)$, we obtain spiral convergence to the equilibrium in phase-plane plots of prey versus predator (see Fig. 2). As shown in Figs. 1 and 2, the former looks larger-scale than the latter in the solution convergence.

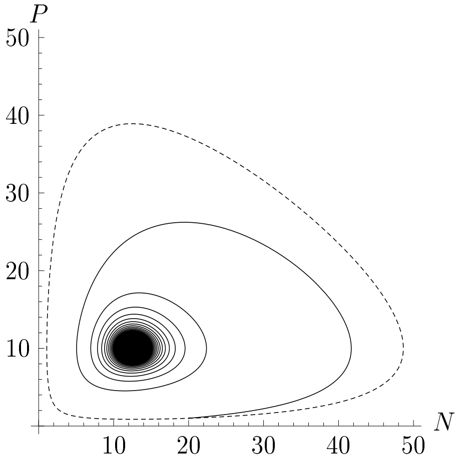

Figure 1. An illustration on the stabilizing effect of $h(t)$ for system (E) with $a = 1$, $b = 0.1$, $c = 1$, and $d = 0.08$. A solid line is plotted for $h(t) = 1/(1 + t)$, while a dotted line is plotted for $h(t) = 0$.

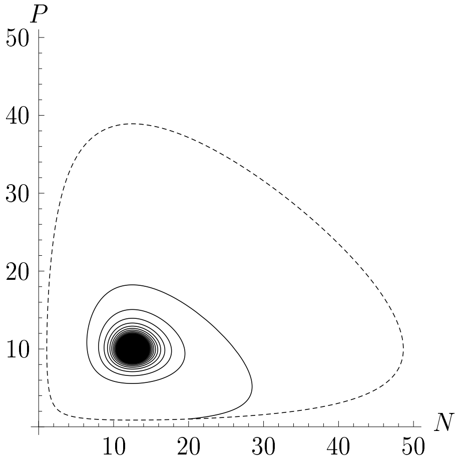

Figure 2. An illustration on the stabilizing effect of $h(t)$ for system (18) with $a = 1$, $b = 0.1$, $c = 1$, and $d = 0.08$. A solid line is plotted for $h(t) = 1/(1 + t)$, while a dotted line is plotted for $h(t) = 0$.

Next, in order to illustrate how the weak integral positiveness of $h(t)$ is sufficient in Theorem 1, we will show an example. Use another set of parameter values $a = b = c = d = 1$ for system (E). In this case, the interior equilibrium is $(1, 1)$. Choosing a function which is not weakly integrally positive, for example, given as $h(t) = 1/(1 + t)^2$, we observe a solution that evolves slowly to a periodic solution and the interior equilibrium is not globally asymptotically stable (see Fig. 3 for the initial data $(N(0), P(0)) = (1, 2)$).

5. Concluding remarks

The neutral stability of (LV) implies that the population state once changed by an external factor cannot return to the original one. Also, the slightest change to the (LV)'s structure typically results in qualitatively different behavior (see [2]). For these mathematical facts, (LV) is called *structurally unstable*. However, it is desirable that models describing periodical population behavior observed in nature involve robust properties such that population states

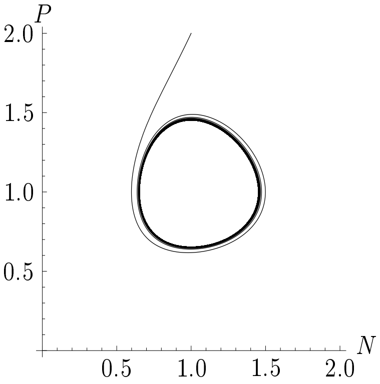

Figure 3. An illustration that an interior equilibrium is not globally asymptotically stable if $h(t)$ is not weakly integrally positive, $a = b = c = d = 1$, and $h(t) = 1/(1+t)^2$. This positive solution converges to a periodic orbit surrounding the interior equilibrium $(1, 1)$.

strayed away from the orbit will return to the original orbit as time passes. In fact, predator-prey systems in nature apparently persist stably (in spite of being affected by external factors). 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, [1, 6, 7, 8, 9]).

Realistic models should take account of a time-variational component of the environment, which is one of the processes that the Lotka-Volterra equations ignore. Our result of this paper presents an example that population dynamics can be stabilized for one of simplest situations in which only predators have a carrying capacity and predators are more effective to receive time-variation of the environment than their prey. What we mention here is that the global stabilization of the equilibrium is realized even for nonnegative time-variational functions that make the limiting system structurally unstable. We also numerically suggested difference in the solution convergence between systems (E) and (18). We ran additional simulations for the numerical work, with various combinations of parameters (data not shown). From these results, it might be a qualitative structure present in a predator-prey pair that time-variation acting on predator leads larger-scale convergence to equilibrium than time-variation acting on prey.

As a simplest way for the growth of predator receiving an environmental time-variation, we put the same $h(t)$ into per capita birth and mortality rates in system (E). Our result here is greatly indebted to such a technical setting which makes the modified model still have a unique interior equilibrium point $(c/d, a/b)$. It is a more biologically practical scenario to develop these considerations into a model that provides different time-variational functions on per capita birth and mortality rates of the predator, which will be left for future work.

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