

STABILITY, DELAY, AND CHAOTIC BEHAVIOR IN A LOTKA-VOLTERRA PREDATOR-PREY SYSTEM

S. NAKAOKA, Y. SAITO AND Y. TAKEUCHI

Department of Systems Engineering, Faculty of Engineering, Shizuoka University
Johoku 3-5-1, Hamamatsu, Shizuoka 432-8561, Japan

ABSTRACT. We consider the following Lotka-Volterra predator-prey system with two delays:

$$\begin{cases} x'(t) = x(t) [r_1 - ax(t - \tau_1) - by(t)] \\ y'(t) = y(t) [-r_2 + cx(t) - dy(t - \tau_2)]. \end{cases} \quad (\text{E})$$

We show that a positive equilibrium of system (E) is globally asymptotically stable for small delays. Critical values of time delay through which system (E) undergoes a Hopf bifurcation are analytically determined. Some numerical simulations suggest an existence of subcritical Hopf bifurcation near the critical values of time delay. Further system (E) exhibits some chaotic behavior when τ_2 becomes large.

1. Introduction. An extensive literature deals with various aspects of Lotka-Volterra delay systems. Many studies concern permanence, persistence and the stability of a positive equilibrium. Permanence and persistence for Lotka-Volterra delay systems are extensively studied, for example, by Cao and Gard [2], Saito [22], Wang and Ma [30], and Burton and Hutson [1] and Hale and Waltman [6]. In studying the stability of a positive equilibrium, one often classifies systems under consideration in two types. One type of systems contains undelayed (or instantaneous) intraspecific competitions which dominate both delayed intraspecific and interspecific interactions. Another type of systems contains only delayed intraspecific competitions. For the former class, Lu and Wang [16] obtained a necessary and sufficient condition under which a positive equilibrium of a two-dimensional Lotka-Volterra system without any intraspecific time delay is globally asymptotically stable. Hofbauer and So [11] generalized the result in [16] to an arbitrary n -dimensional system. In both cases, it was shown that delays incorporated in the system are harmless under some appropriate condition, called a *weakly diagonally dominant condition* (see Hofbauer and Sigmund [12] for the definition of WDD). The other generalization of [16] was given by Saito [21], [23], in which a necessary and sufficient condition for a global asymptotic stability of positive equilibrium for a Lotka-Volterra system with intraspecific time delay is also given. It was pointed out by Kuang [13] that more realistic models should consist of delay differential systems without instantaneous intraspecific competitions, since instantaneous responses are rare or weak relative to delayed response in real-life interactions. Lotka-Volterra

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systems without instantaneous intraspecific competitions are often called “pure-delay-type” systems. Pure-delay-type systems have been extensively studied by He [7], [9], [10], Lu and Takeuchi [15], Ma and Takeuchi [17], Zhen and Ma [31], etc. Gopalsamy and He [4], He [8] and Kuang [13] improved existing results for the global attractivity of various Lotka-Volterra systems by assuming that an interaction matrix has the form of M -matrix. Recently 2/3-type criteria for the global attractivity of pure-delay-type systems were obtained by Tang et al. [28] [29], and similar types of criteria for the asymptotic stability of linear delay systems are given by So et al [25], [26]. Each also assumes that an interaction matrix has the form of M -matrix.

On the other hand, it is known that time delays destabilize the system. Shibata and Saito [24] considered a pure-delay-type Lotka-Volterra competitive model with two delays and showed that complicated chaotic dynamics appear when time delays become large. Also, differential equations with two delays have been well studied by Li et al. [14] and Ruan and Wei ([19], [20]), in which a Hopf bifurcation due to the effect of time delay is observed.

In this paper, we consider the following Lotka-Volterra prey-predator system with distributed delays:

$$\begin{cases} x'(t) = x(t) \left[r_1 - a \int_{-\tau_1}^0 x(t+s) d\mu_1(s) - by(t) \right], \\ y'(t) = y(t) \left[-r_2 + cx(t) - d \int_{-\tau_2}^0 y(t+s) d\mu_2(s) \right] \end{cases} \quad (1.1)$$

with the initial condition

$$x(s) = \phi(s) > 0 \text{ and } y(s) = \psi(s) > 0 \text{ for } -\max_{i=1,2} \tau_i \leq s \leq 0. \quad (1.2)$$

Here, $x(t)$ and $y(t)$ denote the population densities of prey and predator, respectively; τ_i is nonnegative and the rest of parameters are positive. Further, $\mu_i : [-\tau_i, 0] \rightarrow \mathbf{R}$ is nondecreasing on $[-\tau_i, 0]$, continuous to the left on $(-\tau_i, 0)$ and satisfies $\int_{-\tau_i}^0 d\mu_i(s) = 1$, ($i = 1, 2$).

Throughout the remainder of this paper we assume that

$$cr_1 - ar_2 > 0. \quad (1.3)$$

Then system (1.1) has a unique positive equilibrium (x^*, y^*) :

$$x^* = \frac{dr_1 + br_2}{ad + bc}, \quad y^* = \frac{cr_1 - ar_2}{ad + bc}.$$

As a special case, system (1.1) contains the following predator-prey system with discrete delays:

$$\begin{cases} x'(t) = x(t)[r_1 - ax(t - \tau_1) - by(t)], \\ y'(t) = y(t)[-r_2 + cx(t) - dy(t - \tau_2)]. \end{cases} \quad (E)$$

In the case $\tau_2 = 0$, system (E) was considered by May [18] and Song and Wei [27]. Some existing results show that a positive equilibrium of (E) is globally attractive for sufficiently small delays (see [10] for example). On the other hand, in [27], the existence of a local Hopf bifurcation for the positive equilibrium and the global existence of periodic solutions on (E) are shown. It is expected that the dynamics of system (E) possesses various interesting properties.

In this paper, we investigate the effect of time delays on the global dynamics of system (1.1) and (E). The global asymptotic stability and local stability of (x^*, y^*)

for system (1.1) are discussed in sections 2 and 3, respectively. In section 4, some numerical simulations are given for the global dynamics of system (E). One of the simulations demonstrates that chaotic behavior occurs.

2. Global asymptotic stability. In this section, we discuss a global asymptotic stability for the positive equilibrium of system (1.1). It is shown that the positive equilibrium is globally asymptotically stable for sufficiently small delays.

By using the transformation

$$\bar{x} = x - x^*, \bar{y} = y - y^*, \bar{\phi} = \phi - x^*, \bar{\psi} = \psi - y^*,$$

system (1.1) is reduced to

$$\begin{cases} x'(t) = (x(t) + x^*) \left[-a \int_{-\tau_1}^0 x(t+s) d\mu_1(s) - by(t) \right], \\ y'(t) = (y(t) + y^*) \left[cx(t) - d \int_{-\tau_2}^0 y(t+s) d\mu_2(s) \right] \end{cases} \quad (2.1)$$

with the initial condition

$$x(s) = \phi(s) > -x^* \text{ and } y(s) = \psi(s) > -y^* \text{ for } -\max_{i=1,2} \tau_i \leq s \leq 0. \quad (2.2)$$

Here we used $x(t)$, $y(t)$, $\phi(t)$ and $\psi(t)$ again, instead of $\bar{x}(t)$, $\bar{y}(t)$, $\bar{\phi}(t)$ and $\bar{\psi}(t)$, respectively. Inequality (1.3) ensures that system (2.1) has the zero solution. For our main theorem, we exploit a basic result for the upper-boundedness of solutions of system (2.1). Note that we can apply a similar method developed in [7] and [30] to Lemma 2.1 so that we omit the proof.

LEMMA 2.1. *Suppose that (1.3) holds. Let $(x(t), y(t))$ be an arbitrary solution of system (2.1) with (2.2). Then there exists a positive value T such that for $(t \geq T)$*

$$x(t) + x^* \leq M_1 := \frac{r_1}{a} e^{r_1 \tau_1}, \quad y(t) + y^* \leq M_2 := \frac{-r_2 + cM_1}{d} e^{(-r_2 + cM_1)\tau_2}. \quad (2.3)$$

Let us define c_1 and c_2 by

$$c_1 = a^2 M_1 h_1 + \frac{b}{2}(aM_1 h_1 + dM_2 h_2), \quad c_2 = d^2 M_2 h_2 + \frac{c}{2}(aM_1 h_1 + dM_2 h_2).$$

where M_1 and M_2 are defined in (2.3). Also, h_i s are defined by $h_i := \int_{-\tau_i}^0 (-s) d\mu_i(s)$ ($i = 1, 2$), respectively.

THEOREM 2.1. *Assume that (1.3) holds. Then the zero solution of (2.1) is globally asymptotically stable if $a > c_1$ and $d > c_2$.*

Proof. Let us construct the following Liapunov functional:

$$V_1(x_t, y_t) = c \left\{ x(t) - x^* \log \left[\frac{x(t) + x^*}{x^*} \right] \right\} + b \left\{ y(t) - y^* \log \left[\frac{y(t) + y^*}{y^*} \right] \right\}. \quad (2.4)$$

Then the derivative of $V_1(x_t, y_t)$ through $(x(t), y(t))$ is given by

$$\begin{aligned} \dot{V}_1(x_t, y_t) = & cx(t) \left[-a \int_{-\tau_1}^0 x(t+s) d\mu_1(s) - by(t) \right] \\ & + by(t) \left[cx(t) - d \int_{-\tau_2}^0 y(t+s) d\mu_2(s) \right]. \end{aligned} \quad (2.5)$$

We can calculate the first and the fourth terms in (2.5) as $\int_{-\tau_1}^0 x(t+s) d\mu_1(s) = x(t) - \int_{-\tau_1}^0 \int_{t+s}^t \dot{x}(u) du d\mu_1(s)$ and $\int_{-\tau_2}^0 y(t+s) d\mu_2(s) = y(t) - \int_{-\tau_2}^0 \int_{t+s}^t \dot{y}(u) du d\mu_2(s)$. Hence, we have

$$\begin{aligned} \dot{V}_1(x_t, y_t) &= -acx^2(t) + ac \int_{-\tau_1}^0 \int_{t+s}^t x(t)\dot{x}(u) du d\mu_1(s) \\ &\quad - bdy^2(t) + bd \int_{-\tau_2}^0 \int_{t+s}^t y(t)\dot{y}(u) du d\mu_2(s). \end{aligned}$$

Let us denote I_1 and I_2 by

$$I_1 = ac \int_{-\tau_1}^0 \int_{t+s}^t x(t)\dot{x}(u) du d\mu_1(s), \quad I_2 = bd \int_{-\tau_2}^0 \int_{t+s}^t y(t)\dot{y}(u) du d\mu_2(s).$$

Taking the absolute value of I_1 gives

$$|I_1| \leq ac \int_{-\tau_1}^0 \int_{t+s}^t |x(t)| (x(u) + x^*) \left| -a \int_{-\tau_1}^0 x(u+v) d\mu_1(v) - by(u) \right| du d\mu_1(s). \quad (2.6)$$

By Lemma 2.1, there exist $M_1 > 0$ and $T > 0$ such that $x(t) + x^* \leq M_1$ for all $t \geq T$. Then for $t \geq T_1 := T + 2 \max\{\tau_1, \tau_2\}$, we have

$$\begin{aligned} |I_1| &\leq acM_1 \int_{-\tau_1}^0 \int_{t+s}^t |x(t)| \left\{ a \left| \int_{-\tau_1}^0 x(u+v) d\mu_1(v) \right| + b|y(u)| \right\} du d\mu_1(s) \\ &\leq \frac{1}{2} acM_1 \left[(a+b)h_1x^2(t) + \int_{-\tau_1}^0 \int_{t+s}^t \{aR_1(u) + by^2(u)\} du d\mu_1(s) \right], \end{aligned}$$

where $R_1(u) = \left| \int_{-\tau_1}^0 x(u+v) d\mu_1(v) \right|^2$. We used the relation $2\alpha\beta \leq \alpha^2 + \beta^2$ in evaluating the first inequality.

In the same way, we can estimate the absolute value of I_2 as follows:

$$|I_2| \leq \frac{1}{2} bdM_2 \left[(c+d)h_2y^2(t) + \int_{-\tau_2}^0 \int_{t+s}^t \{dR_2(u) + cx^2(u)\} du d\mu_2(s) \right],$$

where $R_2(u) = \left| \int_{-\tau_2}^0 y(u+v) d\mu_2(v) \right|^2$.

Additional Liapunov functionals V_2 and V_3 are defined by:

$$\begin{aligned} V_2(x_t, y_t) &= \frac{1}{2} acM_1 \int_{-\tau_1}^0 \int_{t+s}^t \left[ah_1x^2(\sigma) + \int_{\sigma}^t \{aR_1(u) + by^2(u)\} du \right] d\sigma d\mu_1(s), \\ V_3(x_t, y_t) &= \frac{1}{2} bdM_2 \int_{-\tau_2}^0 \int_{t+s}^t \left[dh_2y^2(\sigma) + \int_{\sigma}^t \{dR_2(u) + cx^2(u)\} du \right] d\sigma d\mu_2(s). \end{aligned}$$

Then the derivative of $V_2(x_t, y_t)$ through the solution $(x(t), y(t))$ is given by

$$\begin{aligned} \dot{V}_2(x_t, y_t) &= \frac{1}{2} acM_1 \left[ah_1x^2(t) + bh_1y^2(t) - \int_{-\tau_1}^0 \int_{t+s}^t \{aR_1(u) + by^2(u)\} dud\mu_1(s) \right. \\ &\quad \left. + ah_1 \left\{ R_1(t) - \int_{-\tau_1}^0 x^2(t+s) d\mu_1(s) \right\} \right]. \end{aligned}$$

Note that $R_1(t) - \int_{-\tau_1}^0 x^2(t+s) d\mu_1(s) = \left[\int_{-\tau_1}^0 x(t+s) d\mu_1(s) \right]^2 - \int_{-\tau_1}^0 x^2(t+s) d\mu_1(s) \leq 0$. Hence, we have

$$\dot{V}_2(x_t, y_t) \leq \frac{1}{2}acM_1 \left[ah_1x^2(t) + bh_1y^2(t) - \int_{-\tau_1}^0 \int_{t+s}^t \{aR_1(u) + by^2(u)\} dud\mu_1(s) \right].$$

In the same way,

$$\dot{V}_3(x_t, y_t) \leq \frac{1}{2}bdM_2 \left[ch_2x^2 + dh_2y^2(t) - \int_{-\tau_2}^0 \int_{t+s}^t \{dR_2(u) + cx^2(u)\} dud\mu_2(s) \right].$$

Consequently, an estimate of the derivative of $V := V_1 + V_2 + V_3$ is

$$\begin{aligned} \frac{d}{dt}V(x_t, y_t) &\leq -c \left[a - \frac{1}{2}a(2a+b)M_1h_1 - \frac{1}{2}bdM_2h_2 \right] x^2(t) \\ &\quad - b \left[d - \frac{1}{2}d(2d+c)M_2h_2 - \frac{1}{2}acM_1h_1 \right] y^2(t) \\ &= -c(a-c_1)x^2(t) - b(d-c_2)y^2(t). \end{aligned}$$

If $a > c_1$ and $d > c_2$, the second method of Liapunov functional implies that the zero solution of (2.1) is globally asymptotically stable for $t \geq T_1$ [5, p. 132, Theorem 2.1]. This completes the proof. \square

Finally let us compare Theorem 2.1 with the result obtained by X.-Z. He [10] on system (E):

COROLLARY 2.1. [10, Corollary 2] *Assume that (1.3) holds. Then the zero solution of (E) is globally asymptotically stable if $a > c_1$ and $d > c_2$, where c_1 and c_2 are*

$$c_1 = a^2M_1\tau_1 + \frac{b}{2}(aM_1\tau_1 + dM_2\tau_2), \quad c_2 = d^2M_2\tau_2 + \frac{c}{2}(aM_1\tau_1 + dM_2\tau_2).$$

X.-Z. He [10] showed a sufficient condition for the positive equilibrium to be globally attractive as a corollary of his main theorem:

COROLLARY 2.2. [10, Corollary 2]. *Assume that (1.3) holds. Then the zero solution of (E) is globally attractive if $a > d_1$ and $d > d_2$, where d_1 and d_2 are*

$$d_1 = a^2M_1\tau_1 + \frac{by^*}{2x^*}(aM_1\tau_1 + dM_2\tau_2), \quad d_2 = d^2M_2\tau_2 + \frac{cx^*}{2y^*}(aM_1\tau_1 + dM_2\tau_2).$$

It is easy to see that $c_1 > d_1$ and $c_2 < d_2$ if $x^* > y^*$. While $c_1 < d_1$ and $c_2 > d_2$ if $x^* < y^*$. Conditions of global attractivity of system (E) are improved as $a > \min\{c_1, d_1\}$ and $d > \min\{c_2, d_2\}$ by combining Corollary 2.1 and 2.2.

3. Instability. The characteristic equation of the linearized system of (E) is given by

$$P(\lambda, \tau_1, \tau_2) = \lambda^2 + (pe^{-\lambda\tau_1} + qe^{-\lambda\tau_2})\lambda + pqe^{-\lambda(\tau_1+\tau_2)} + r = 0, \quad (3.1)$$

where $p = ax^*$, $q = dy^*$ and $r = bcx^*y^*$. Note that $\lambda = 0$ is not a solution of (3.1).

Substituting $\lambda = i\omega$ ($\omega > 0$) into (3.1) gives

$$q\omega \sin \omega\tau_2 + pq \cos \omega(\tau_1 + \tau_2) = \omega^2 - r - p\omega \sin \omega\tau_1, \quad (3.2)$$

$$q\omega \cos \omega\tau_2 - pq \sin \omega(\tau_1 + \tau_2) = -p\omega \cos \omega\tau_1. \quad (3.3)$$

Squaring and adding equations (3.2) and (3.3) gives

$$2p\omega(\omega^2 - r - q^2) \sin \omega\tau_1 = (\omega^2 - r)^2 + p^2\omega^2 - q^2\omega^2 - p^2q^2. \quad (3.4)$$

In the same manner, we have

$$2q\omega(\omega^2 - r - p^2) \sin \omega\tau_2 = (\omega^2 - r)^2 + q^2\omega^2 - p^2\omega^2 - p^2q^2. \quad (3.5)$$

Note that $p = q$ if $\omega^2 - r - q^2 = 0$. In fact, the right hand side of (3.4) is calculated as $(\omega^2 - r)^2 + p^2\omega^2 - q^2\omega^2 - p^2q^2 = (p^2 - q^2)r = 0$. In the same way, $p = q$ if $\omega^2 - r - p^2 = 0$. By taking contraposition, we obtain that $\omega^2 - r - p^2 \neq 0$ and $\omega^2 - r - q^2 \neq 0$ if $p \neq q$. Note that the characteristic equation (3.1) does not change its form by exchanging (p, τ_1) and (q, τ_2) . Hence, throughout the remainder of this section, we can assume that $p < q$ without loss of generality. The particular case $p = q$ is out of consideration in this paper. Then we have

$$\sin \omega\tau_1 = \frac{\omega^4 + (p^2 - q^2 - 2r)\omega^2 + r^2 - p^2q^2}{2p\omega(\omega^2 - r - q^2)}, \quad (3.6)$$

$$\sin \omega\tau_2 = \frac{\omega^4 + (q^2 - p^2 - 2r)\omega^2 + r^2 - p^2q^2}{2q\omega(\omega^2 - r - p^2)}. \quad (3.7)$$

Let us substitute (3.6) and (3.7) into (3.2). Direct calculation gives

$$\cos \omega(\tau_1 + \tau_2) = -\frac{p^2 + q^2}{2pq} + \frac{(p^2 - q^2)^2 r}{2pq(\omega^2 - r - p^2)(\omega^2 - r - q^2)}. \quad (3.8)$$

Let us define $f_1 : (0, r + q^2) \cup (r + q^2, \infty) \rightarrow \mathbb{R}$, $f_2 : (0, r + p^2) \cup (r + p^2, \infty) \rightarrow \mathbb{R}$ and $f_3 : [0, r + p^2) \cup (r + p^2, r + q^2) \cup (r + q^2, \infty) \rightarrow \mathbb{R}$ as

$$f_1(u) = \frac{u^2 + (p^2 - q^2 - 2r)u + r^2 - p^2q^2}{2p\sqrt{u}(u - r - q^2)}, \quad (3.9)$$

$$f_2(u) = \frac{u^2 + (q^2 - p^2 - 2r)u + r^2 - p^2q^2}{2q\sqrt{u}(u - r - p^2)}, \quad (3.10)$$

$$f_3(u) = -\frac{p^2 + q^2}{2pq} + \frac{(p^2 - q^2)^2 r}{2pq(u - r - p^2)(u - r - q^2)}. \quad (3.11)$$

Intervals I_1 , I_2 and I_3 are defined by

$$I_1 = \{u \in (0, r + q^2) \cup (r + q^2, \infty) : -1 \leq f_1(u) \leq 1\},$$

$$I_2 = \{u \in (0, r + p^2) \cup (r + p^2, \infty) : -1 \leq f_2(u) \leq 1\},$$

$$I_3 = \{u \in [0, r + p^2) \cup (r + q^2, \infty) : -1 \leq f_3(u) \leq 1\}.$$

Note that it suffices to consider the interval I_3 without $(r + p^2, r + q^2)$, since for $u \in (r + p^2, r + q^2)$,

$$\begin{aligned} f_3(u) &= -\frac{p^2 + q^2}{2pq} + \frac{(p^2 - q^2)^2 r}{2pq(u - r - p^2)(u - r - q^2)} \\ &< -1 + \frac{(p^2 - q^2)^2 r}{2pq(u - r - p^2)(u - r - q^2)} < -1. \end{aligned}$$

On $I := I_1 \cap I_2 \cap I_3$, inverse functions of $\sin \omega\tau_1$ and $\sin \omega\tau_2$ are well defined, and hence we obtain the following relations:

$$\begin{cases} \tau_1^k := \frac{\theta_1 + 2k\pi}{\omega}, & \frac{\pi - \theta_1 + 2k\pi}{\omega}, & (k = 0, 1, 2, \dots), \\ \tau_2^l := \frac{\theta_2 + 2l\pi}{\omega}, & \frac{\pi - \theta_2 + 2l\pi}{\omega}, & (l = 0, 1, 2, \dots). \end{cases} \quad (3.12)$$

Here, $\theta_1 = \sin^{-1} f_1(u)$ and $\theta_2 = \sin^{-1} f_2(u)$.

PROPOSITION 3.1. (3.2) and (3.3) are equivalent to (3.6)–(3.8).

Proof. In the procedure of deriving (3.6)–(3.8) from (3.2) and (3.3), it is clear that (3.2) and (3.3) imply (3.6)–(3.8). Conversely, suppose that (3.6)–(3.8) hold. Then it is easy to see that (3.6)–(3.8) imply (3.2).

Let us check (3.3) by evaluating $(p\omega \cos \omega\tau_1 + q\omega \cos \omega\tau_2)^2 - \{pq \sin \omega(\tau_1 + \tau_2)\}^2$ as follows:

$$\begin{aligned} & (p\omega \cos \omega\tau_1 + q\omega \cos \omega\tau_2)^2 - \{pq \sin \omega(\tau_1 + \tau_2)\}^2 \\ &= p^2\omega^2(1 - \sin^2 \omega\tau_1) + q^2\omega^2(1 - \sin^2 \omega\tau_2) \\ &\quad + 2pq\omega^2\{\cos \omega(\tau_1 + \tau_2) + \sin \omega\tau_1 \sin \omega\tau_2\} - p^2q^2\{1 - \cos^2 \omega(\tau_1 + \tau_2)\} \\ &= -\omega^4 + (p^2 + q^2)\omega^2 - p^2q^2 + \{pq \cos \omega(\tau_1 + \tau_2) + \omega^2 + p\omega \sin \omega\tau_1 - q\omega \sin \omega\tau_2\} \times \\ &\quad \{pq \cos \omega(\tau_1 + \tau_2) + \omega^2 - p\omega \sin \omega\tau_1 + q\omega \sin \omega\tau_2\} \\ &= -\omega^4 + (p^2 + q^2)\omega^2 - p^2q^2 + (2\omega^2 - r - 2q\omega \sin \omega\tau_2)(2\omega^2 - r - 2p\omega \sin \omega\tau_1). \end{aligned}$$

Here we used (3.2) in evaluating the last equality. By (3.6) and (3.7), $2p\omega \sin \omega\tau_1 = \omega^2 - r + p^2 + \frac{(p^2 - q^2)r}{\omega^2 - r - q^2}$ and $2q\omega \sin \omega\tau_2 = \omega^2 - r + q^2 + \frac{(q^2 - p^2)r}{\omega^2 - r - p^2}$. Direct calculation gives $(p\omega \cos \omega\tau_1 + q\omega \cos \omega\tau_2)^2 - \{pq \sin \omega(\tau_1 + \tau_2)\}^2 = 0$. Hence, either (3.3) or $p\omega \cos \omega\tau_1 + q\omega \cos \omega\tau_2 + pq \sin \omega(\tau_1 + \tau_2) = 0$ holds. If $p\omega \cos \omega\tau_1 + q\omega \cos \omega\tau_2 + pq \sin \omega(\tau_1 + \tau_2) = 0$, the same manner of deriving (3.4) and (3.5) gives $\sin \omega(\tau_1 + 2\tau_2) = \sin \omega\tau_1$ and $\sin \omega(2\tau_1 + \tau_2) = \sin \omega\tau_2$. Consequently, $\sin \omega\tau_1 = \sin \omega\tau_2 = 0$. Then it follows from (3.6) and (3.7) that $p = q$. This is a contradiction and hence the proof is completed. \square

PROPOSITION 3.2. *Assume that $r \neq pq$. Then I_1, I_2, I_3 are not empty and $I_1 = I_2 = I_3$. Moreover, there exists a set of critical values $(\omega, \tau_1^k, \tau_2^l)$ such that $(\omega, \tau_1^k, \tau_2^l)$ satisfies (3.6)–(3.8).*

Proof. First, let us show I_3 is not an empty set. Direct calculation gives

$$f_3(0) + 1 = \frac{-(p - q)^2(r - pq)^2}{2pq(r + p^2)(r + q^2)} < 0.$$

Hence $f_3(0) < -1$. The derivative of $f_3(u)$ on $[0, r + p^2) \cup (r + q^2, \infty)$ is

$$-\frac{(p^2 - q^2)^2 r \{(u - r - p^2) + (u - r - q^2)\}}{2pq(u - r - p^2)^2(u - r - q^2)^2}.$$

This implies that $f_3'(u)$ is positive on $[0, r + p^2)$ and negative on $(r + q^2, \infty)$. Hence, $f_3(u)$ is strictly monotonically increasing on $[0, r + p^2)$, and strictly monotonically decreasing on $(r + q^2, \infty)$. It is easy to see that $f_3(u) \rightarrow +\infty$ as $u \rightarrow r + p^2 - 0$ and $f_3(u) \rightarrow +\infty$ as $u \rightarrow r + q^2 + 0$. Moreover, $f_3(u) \rightarrow -\frac{p^2 + q^2}{2pq} < -1$ as $u \rightarrow +\infty$. Therefore, $I_3 = [\bar{u}_{-L}, \bar{u}_{+L}] \cup [\bar{u}_{-R}, \bar{u}_{+R}]$, where \bar{u}_{-L} and \bar{u}_{+L} are roots of equations $f_3(u) = -1$ and $f_3(u) = 1$ on $[0, r + p^2)$, respectively, while \bar{u}_{-R} and \bar{u}_{+R} are respective roots of equations $f_3(u) = 1$ and $f_3(u) = -1$ on $(r + q^2, \infty)$ (see Fig. 3). It follows that

$$f_3(u) = 1 \iff u^2 - (p^2 + q^2 + 2r)u + (r + pq)^2 = 0, \tag{3.13}$$

$$f_3(u) = -1 \iff u^2 - (p^2 + q^2 + 2r)u + (r - pq)^2 = 0. \tag{3.14}$$

Hence, explicit values of $\bar{u}_{-L}, \bar{u}_{+L}, \bar{u}_{-R}$ and \bar{u}_{+R} can be obtained by solving (3.13) and (3.14).

Second, let us show the following statement:

$$f_1(u) = -1 \text{ or } 1 \iff f_2(u) = -1 \text{ or } 1 \iff f_3(u) = -1 \text{ or } 1. \tag{3.15}$$

Suppose that $f_1(u) = 1$. By (3.6), $\sin \omega \tau_1 = f_1(u) = 1$. Hence, $\cos \omega \tau_1 = 0$. Then in (3.3), $q(\omega - p) \cos \omega \tau_2 = 0$. Assume that $\omega = p$. Then $r = 0$ in (3.2). This is a contradiction. Hence, $\cos \omega \tau_2 = 0$ and $f_2(u) = -1$ or 1 . In the same manner, we can show that $f_1(u) = -1 \iff f_2(u) = -1$ or 1 . Next, suppose that $f_3(u) = 1$. By (3.8), $\cos \omega(\tau_1 + \tau_2) = f_3(u) = 1$. Hence, $\sin \omega(\tau_1 + \tau_2) = 0$, or equivalently, $\sin \omega \tau_1 \cos \omega \tau_2 + \cos \omega \tau_1 \sin \omega \tau_2 = 0$. It follows from (3.3) that $p \cos \omega \tau_1 + q \cos \omega \tau_2 = 0$. Hence $\cos \omega \tau_2(p \sin \omega \tau_1 - q \sin \omega \tau_2) = 0$. If $p \sin \omega \tau_1 - q \sin \omega \tau_2 = 0$, it follows that

$$\begin{aligned} & (p \cos \omega \tau_1 + q \cos \omega \tau_2)^2 + (p \sin \omega \tau_1 - q \sin \omega \tau_2)^2 \\ &= p^2 + q^2 + 2pq \cos \omega(\tau_1 + \tau_2) = (p + q)^2 = 0. \end{aligned}$$

This is a contradiction, and hence $\cos \omega \tau_2 = \cos \omega \tau_1 = 0$. The other cases can be proved similarly.

Third, let us show I_1 and I_2 are not an empty set and $I_1 = I_2 = I_3$. Here, $g_1(u)$ denotes the numerator of $f_1(u)$. Then $g_1(0) = r^2 - p^2 q^2$ and $g_1(r + q^2) = -(q^2 - p^2)r$. If $r > pq$, $g_1(0) > 0$ and $g_1(r + q^2) < 0$, because $p < q$. Hence, for $u \in (0, r + q^2)$, we have $f_1(u) \rightarrow -\infty$ as $u \rightarrow 0+$, and $f_1(u) \rightarrow +\infty$ as $u \rightarrow r + q^2 - 0$. For $u \in (r + q^2, \infty)$, $f_1(u) \rightarrow -\infty$ as $u \rightarrow r + q^2 + 0$ and $f_1(u) \rightarrow +\infty$ as $u \rightarrow +\infty$. By (3.15), I_1 exists. Moreover, $f_1(\bar{u}_{-L}) = -1$, $f_1(\bar{u}_{+L}) = 1$, $f_1(\bar{u}_{-R}) = -1$ and $f_1(\bar{u}_{+R}) = 1$. Hence, $I_1 = I_3$ (see Fig. 1). Now, $g_2(u)$ denotes the numerator of $f_2(u)$. Then $g_2(0) = r^2 - p^2 q^2$ and $g_2(r + p^2) = (q^2 - p^2)r$. Since $r > pq$ and $p < q$, $g_2(0) > 0$ and $g_2(r + p^2) > 0$. Hence, for $u \in (0, r + p^2)$, we have $f_2(u) \rightarrow -\infty$ as $u \rightarrow 0+$, and $f_2(u) \rightarrow -\infty$ as $u \rightarrow r + p^2 - 0$. For $u \in (r + p^2, \infty)$, $f_2(u) \rightarrow +\infty$ as $u \rightarrow r + p^2 + 0$ and $f_2(u) \rightarrow +\infty$ as $u \rightarrow +\infty$. Since $f_2(u)$ is continuous on $(0, r + p^2) \cup (r + p^2, \infty)$, I_2 exists. Moreover, $f_2(\bar{u}_{-L}) = -1$, $f_2(\bar{u}_{+L}) = -1$, $f_2(\bar{u}_{-R}) = 1$, and $f_2(\bar{u}_{+R}) = 1$. Hence, $I_2 = I_3$ (see Fig. 2). In $r < pq$, the same approach can be used, and hence it is shown that I_1, I_2 are not empty and $I_1 = I_2 = I_3$.

By substituting (3.12) into (3.8), we have the following equations with respect to u :

$$\begin{cases} \cos [\sin^{-1} f_1(u) + \sin^{-1} f_2(u)] = f_3(u), \\ \cos [\sin^{-1} f_1(u) - \sin^{-1} f_2(u)] = -f_3(u). \end{cases} \quad (3.16)$$

Note that $f_3(u)$ is a monotone function on I and $f_3(I) = [-1, 1]$. Hence, the intermediate theorem implies that there exists at least one root of (3.16) on I . This completes the proof. \square

Hereafter, let us suppose that there exists at least one positive root ω of (3.2) and (3.3). Let τ_2 be arbitrary fixed. Derivatives of $P(\lambda, \tau_1, \tau_2)$ with respect to λ and τ_1 at $\lambda = i\omega$, $\tau_1 = \tau_1^k$ and $\tau_2 = \tau_2^l$ are

$$\begin{aligned} \frac{\partial P(i\omega, \tau_1^k, \tau_2^l)}{\partial \lambda} &= 2\lambda + pe^{-\lambda \tau_1} + qe^{-\lambda \tau_2} - (p\tau_1 e^{-\lambda \tau_1} + q\tau_2 e^{-\lambda \tau_2})\lambda \\ &\quad - pq(\tau_1 + \tau_2)e^{-\lambda(\tau_1 + \tau_2)} \Big|_{\substack{\lambda=i\omega \\ \tau_1=\tau_1^k, \tau_2=\tau_2^l}}, \\ \frac{\partial P(i\omega, \tau_1^k, \tau_2^l)}{\partial \tau_1} &= -pe^{-\lambda \tau_1}(\lambda + qe^{-\lambda \tau_2})\lambda \Big|_{\substack{\lambda=i\omega \\ \tau_1=\tau_1^k, \tau_2=\tau_2^l}}, \end{aligned}$$

respectively. If $\lambda + pe^{-\lambda \tau_1} = 0$, then it follows from (3.1) that $r = 0$, since (3.1) is written as $(\lambda + pe^{-\lambda \tau_1})(\lambda + qe^{-\lambda \tau_2}) + r = 0$. Consequently, $\lambda + pe^{-\lambda \tau_1} \neq 0$. In the

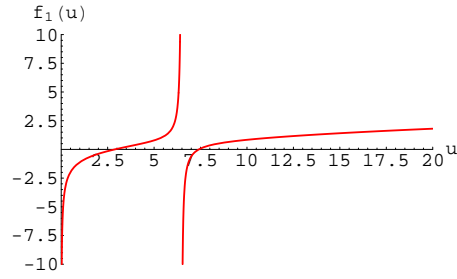


FIGURE 1. $f_1(u)$

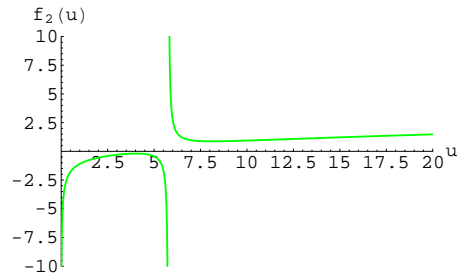


FIGURE 2. $f_2(u)$

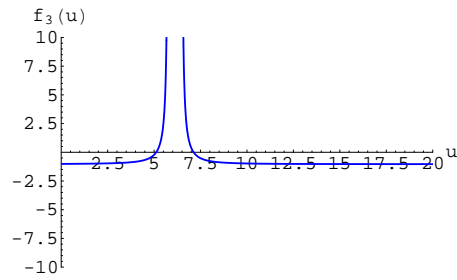


FIGURE 3. $f_3(u)$

same way, $\lambda + qe^{-\lambda\tau_2} \neq 0$. Hence, the implicit function theorem gives

$$\begin{aligned} \frac{\partial\tau_1}{\partial\lambda} &= -\frac{\tau_1 + \tau_2}{\lambda} + \frac{\lambda^2 - r - pqe^{-\lambda(\tau_1+\tau_2)} + \tau_2(pe^{-\lambda\tau_1} - qe^{-\lambda\tau_2})\lambda^2}{pe^{-\lambda\tau_1}(\lambda + qe^{-\lambda\tau_2})\lambda^2} \\ &:= -\frac{\tau_1 + \tau_2}{\lambda} + \frac{F_1(\lambda, \tau_1, \tau_2)}{G_1(\lambda, \tau_1, \tau_2)}. \end{aligned}$$

Define δ_1 as

$$\begin{aligned} \delta_1 &:= (\omega^2 - r)\{\omega^2 + r + pq \cos \omega(\tau_1^k + \tau_2^l)\} - q\omega\{(\omega^2 + r) \sin \omega\tau_2^l - pq \sin \omega\tau_1^k\} \\ &\quad + \omega^2\tau_2^l [pq\omega \sin \omega(\tau_1^k - \tau_2^l) + (\omega^2 - r)(p \cos \omega\tau_1^k - q \cos \omega\tau_2^l)]. \end{aligned}$$

Let us show

$$\operatorname{sgnRe} \left[-\frac{\frac{\partial P(\lambda, \tau_1, \tau_2)}{\partial \lambda}}{\frac{\partial P(\lambda, \tau_1, \tau_2)}{\partial \tau_1}} \Bigg|_{\substack{\lambda=i\omega \\ \tau_1=\tau_1^k, \tau_2=\tau_2^l}} \right] = \operatorname{sgn}\delta_1. \quad (3.17)$$

In fact,

$$\operatorname{sgnRe} \left[\frac{\partial \tau_1}{\partial \lambda} \Big|_{\substack{\lambda=i\omega \\ \tau_1=\tau_1^k, \tau_2=\tau_2^l}} \right] = \operatorname{sgn} [F_{1R}G_{1R} + F_{1I}G_{1I}],$$

where $F_{1R} = \operatorname{Re}[F_1(i\omega, \tau_1^k, \tau_2^l)]$, $F_{1I} = \operatorname{Im}[F_1(i\omega, \tau_1^k, \tau_2^l)]$, $G_{1R} = \operatorname{Re}[G_1(i\omega, \tau_1^k, \tau_2^l)]$ and $G_{1I} = \operatorname{Im}[G_1(i\omega, \tau_1^k, \tau_2^l)]$. By (3.2), we have

$$\begin{aligned} G_{1R} &= -\omega^2(\omega^2 - r - q\omega \sin \omega \tau_2^l), \\ G_{1I} &= q\omega^3 \cos \omega \tau_2^l. \end{aligned}$$

Direct calculation gives

$$\begin{aligned} (F_{1R}G_{1R} + F_{1I}G_{1I})/\omega^2 &= \\ (\omega^2 - r - q\omega \sin \omega \tau_2^l) \{ \omega^2 + r + pq \cos \omega(\tau_1^k + \tau_2^l) + \tau_2^l \omega^2 (p \cos \omega \tau_1^k - q \cos \omega \tau_2^l) \} \\ - q\omega \cos \omega \tau_2^l \{ -pq \sin \omega(\tau_1^k + \tau_2^l) + \tau_2^l \omega^2 (-p \sin \omega \tau_1^k + q \sin \omega \tau_2^l) \} &= \delta_1. \end{aligned}$$

Hence, (3.17) holds. By (3.17), $\partial P(i\omega, \tau_1^k, \tau_2^l)/\partial \lambda \neq 0$ if and only if $\delta_1 \neq 0$. If $\delta_1 \neq 0$, again using the implicit function theorem gives

$$\operatorname{sgnRe} \left[\frac{\partial \lambda}{\partial \tau_1} \Big|_{\substack{\lambda=i\omega \\ \tau_1=\tau_1^k, \tau_2=\tau_2^l}} \right] = \operatorname{sgnRe} \left[\left(-\frac{\frac{\partial P(\lambda, \tau_1^k, \tau_2^l)}{\partial \lambda}}{\frac{\partial P(\lambda, \tau_1^k, \tau_2^l)}{\partial \tau_1}} \right)^{-1} \right] = \operatorname{sgn} \delta_1.$$

Define δ_2 as

$$\begin{aligned} \delta_2 &:= (\omega^2 - r) \{ \omega^2 + r + pq \cos \omega(\tau_1^k + \tau_2^l) \} - p\omega \{ (\omega^2 + r) \sin \omega \tau_1^k - pq \sin \omega \tau_2^l \} \\ &\quad + \omega^2 \tau_1^k [pq\omega \sin \omega(\tau_2^l - \tau_1^k) + (\omega^2 - r)(q \cos \omega \tau_2^l - p \cos \omega \tau_1^k)]. \end{aligned}$$

In the same way, we can show that $\operatorname{sgnRe} \left[\frac{\partial \lambda}{\partial \tau_2} \Big|_{\substack{\lambda=i\omega \\ \tau_1=\tau_1^k, \tau_2=\tau_2^l}} \right] = \operatorname{sgn} \delta_2$. Hence, we obtain the following result:

THEOREM 3.1. *Assume that ω^* is a positive real root of (3.2) and (3.3). Then a pair of simple conjugate pure imaginary roots $\lambda_+ = i\omega^*$ and $\lambda_- = -i\omega^*$ of (3.1) exists at $\tau_1 = \tau_1^k$ and $\tau_2 = \tau_2^l$, which crosses the imaginary axis as τ_1 (τ_2) increases for fixed τ_2 (τ_1) from left to right if $\delta_1 > 0$ ($\delta_2 > 0$) and right to left if $\delta_1 < 0$ ($\delta_2 < 0$).*

If $\tau_2 = 0$, the same result obtained by Song and Wei [27] is obtained.

COROLLARY 3.1. [27, Theorem 2.1.] *Assume that $\tau_2 = 0$. Let*

- (H1) *either $r > pq$ and $q^2 - p^2 - 2r > 0$ or $(q^2 - p^2 - 2r)^2 - 4(r^2 - p^2q^2) < 0$,*
- (H2) *either $r < pq$ or $q^2 - p^2 - 2r < 0$ and $(q^2 - p^2 - 2r)^2 - 4(r^2 - p^2q^2) = 0$,*
- (H3) *$r > pq$, $q^2 - p^2 - 2r < 0$ and $(q^2 - p^2 - 2r)^2 - 4(r^2 - p^2q^2) > 0$.*

- i. If (H1) holds, then the positive equilibrium of (E) is (locally) asymptotically stable for all $\tau_1 \geq 0$.*
- ii. If (H2) holds, then the positive equilibrium of (E) is (locally) asymptotically stable for $\tau_1 \in [0, \tau_{10}^+)$ and unstable for $\tau_1 > \tau_{10}^+$. System (E) undergoes a Hopf bifurcation at the positive equilibrium for $\tau_1 = \tau_{10}^+$.*
- iii. If (H3) holds, a finite number of stability switches occurs. Finally system (E) becomes unstable.*

Here $\omega = \omega_{\pm}$ are real roots of the polynomial equation

$$\omega^4 + (q^2 - p^2 - 2r)\omega^2 + r^2 - p^2q^2 = 0 \tag{3.18}$$

satisfying $\omega_- < \omega_+$; τ_{10}^{\pm} is defined by $\frac{1}{\omega_{\pm}} \cos^{-1} \left[\frac{-qr}{p(\omega_{\pm} + q^2)} \right]$.

Proof. Note that (3.18) is derived from (3.7). If (H1) holds, (3.18) has no real roots. Since all roots of the characteristic equation (3.1) have negative real parts when $\tau_1 = \tau_2 = 0$, (i) holds. It follows that (3.18) has at least one positive root if and only if either (H2) or (H3) holds. Then, δ_1 is calculated as follows:

$$\begin{aligned} \delta_1 &= (\omega^2 - r)(2\omega^2 - p\omega \sin \omega\tau_1) + pq^2\omega \sin \omega\tau_1 \\ &= \omega^4 - (r^2 - p^2q^2). \end{aligned} \tag{3.19}$$

Here we used (3.2) with $\tau_2 = 0$ and (3.6). If (H2) holds, then it immediately follows from (3.19) that $\delta_1 > 0$. If (H3) holds, then $\omega_-^2 < -(q^2 - p^2 - 2r)/2 < \omega_+^2$. Moreover, $\delta_1 > 0$ for $\omega = \omega_+^2$ and $\delta_1 < 0$ for $\omega = \omega_-^2$. The remainder of the proof proceeds as the same manner used by Cooke and van den Driessche [3]. This completes the proof. \square

Finally let us show the existence of a Hopf bifurcation. By Proposition 3.2, there exists at least one set of critical values $(\omega, \tau_1^k, \tau_2^l)$ which satisfies (3.6)–(3.8) if $r \neq pq$. Since a number of ω which satisfies (3.6)–(3.8) is finite, there exists a set of minimum values (τ_1^*, τ_2^*) . Since all roots of the characteristic equation (3.1) have negative real parts when $\tau_1 = \tau_2 = 0$, The Hopf bifurcation theorem [5, p. 332, Theorem 1.1.] is applicable to system (E).

COROLLARY 3.2. *Assume that $ax^* \neq dy^*$ and $ad - bc \neq 0$. Let ω^* be a positive real root of (3.2) and (3.3). If either $\delta_1 > 0$ or $\delta_2 > 0$, a family of periodic solutions of (E) bifurcates from the positive equilibrium for τ_1 near τ_1^* or τ_2 near τ_2^* . Furthermore, the period of periodic solution is approximately $2\pi/\omega^*$.*

4. Numerical simulations. In this section, let us apply the results obtained in section 3 and give some numerical simulation results. Hereafter, parameters are fixed at the following values:

$$r_1 = 2.4, r_2 = 2.1, a = 1.4, b = 2.2, c = 5.5, d = 3.3. \tag{P}$$

Then $p = 1.05$, $q = 2.025$ and $r = 5.56875$. Note that if $\tau_2 = 0$, Corollary 3.1-(i) holds. Hence the positive equilibrium is locally asymptotically stable for all $\tau_1 \geq 0$ with $\tau_2 = 0$. Since $r \neq pq$, Proposition 3.2 implies that I_1, I_2, I_3 are not empty and $I = I_1 = I_2 = I_3$. The interval I becomes $[0.760643, 5.42423] \cup [10.9164, 15.58]$. By (3.12) and (3.16), $(\omega^*, \tau_1^*, \tau_2^*)$ is approximately calculated as $\omega^* = 3.63978$, $\tau_1^* = 0.706884$ and $\tau_2^* = 0.365617$.

In the remainder of this section, some numerical simulation results of (E) are given. The positive equilibrium is numerically calculated as $(x^*, y^*) = (0.75, 0.6136)$. First, let us fix τ_1 and τ_2 as $\tau_1 = 0.7$ and $\tau_2 = 0.35$. Hence all roots of (3.1) have negative real parts. Figures 4 and 5 illustrate the time series and the projection into xy plane of the trajectory of the solution of (E) with initial functions $\phi = 0.75$ and $\psi = 0.1$, respectively. It is observed that the solution tends to the positive equilibrium (see Figs. 4 and 5). Next, let us show figures on which only the initial function ψ is changed from 0.1 to 0.05. Then it is observed in Figures 6 and 7 that the solution evolves to some periodic solution; δ_1 and δ_2 are numerically calculated as $\delta_1(\tau_2^*) = -0.673553 < 0$ and $\delta_2(\tau_1^*) = 20.2818 > 0$. Corollary 3.2

implies that a family of periodic solution bifurcates from the positive equilibrium for τ_2 near τ_2^* . Figures 8 and 9 illustrate the trajectory of the solution with (P), $\tau_1 = 0.71$ and $\tau_2 = 0.37$. The initial functions are taken near the equilibrium point, $(\phi, \psi) = (0.75, 0.6)$. Then it is observed that the solution evolves to some periodic solution (see Figs. 8 and 9). In Figures 4–9, it seems that an unstable closed curve appears around the positive equilibrium. Further, the solution starting at the inside of the closed curve tends to the positive equilibrium (Figs. 4 and 5), while the solution starting at the outside of the curve evolves to some robust periodic solution (Figures 6 and 7). Since the positive equilibrium is locally asymptotically stable and system (E) undergoes a Hopf bifurcation by Corollary 3.2, existence of a subcritical Hopf bifurcation is suggested from these figures. Finally, let us change the values of τ_2 from 0.37 to 1.73. Then, a complicated dynamics is observed in Figure 10. The trajectory of the solution of (E) with $\phi = 0.75$ and $\psi = 0.6$ is attracted in a shark-head shaped region. In other words, shark-head chaos occurs on system (E) as the time delay in an intraspecific competition of predator becomes large. We observe that shark-head chaos is formed by repeating the following three steps:

- Step 1. The low density of the predator makes the density of the prey increase.
- Step 2. The growth of the predator follows the growth of the prey with delay.
- Step 3. The exhaustion of the prey results in the decrease of the predator.

Chaotic behavior occurs markedly in Step 2 : it seems that the trajectory forms the upper lip of the *shark* with the high growth of predator y , while the trajectory forms the lower lip of the *shark* with the relatively low growth of predator y . The predator repeats such high and low growth alternatively. The solution never moves on the same path and finally the shark-head region is filled densely.

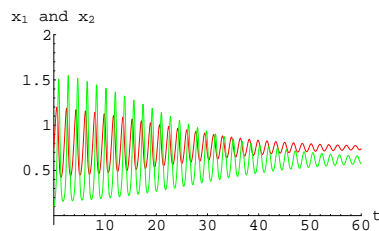


FIGURE 4. $\tau_1 = 0.7$, $\tau_2 = 0.35$

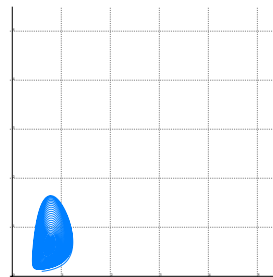


FIGURE 5. $\phi = 0.75$, $\psi = 0.1$

5. Conclusions. In section 2, we obtained Theorem 2.1 for global asymptotic stability of the positive equilibrium of (1.1). The theorem for global attractivity of system (E) is improved by combining with the result obtained by He [10]. It was also shown that Liapunov functionals used in the proof of global attractivity are also applicable to prove the uniform stability for the zero solution of linearized system. In section 3, critical values of time delay through which system (E) undergoes a Hopf bifurcation were analytically determined. Furthermore, for the existence of local Hopf bifurcation, the result by Song and Wei [27] is obtained as a special case. In section 4, some numerical simulations were carried out and it was suggested that subcritical Hopf bifurcation occurs on system (E). Moreover chaotic behavior was

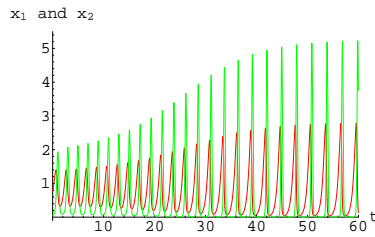


FIGURE 6. $\tau_1 = 0.7, \tau_2 = 0.35$

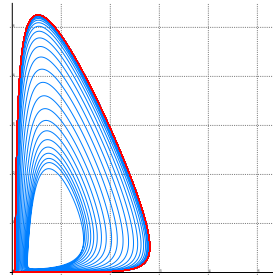


FIGURE 7. $\phi = 0.75, \psi = 0.05$

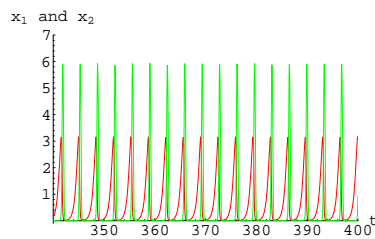


FIGURE 8. $\tau_1 = 0.71, \tau_2 = 0.37$

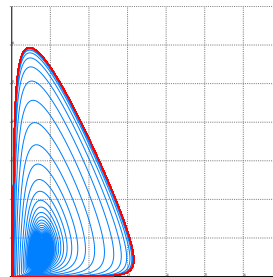


FIGURE 9. $\phi = 0.75, \psi = 0.6$

observed when the time delay in an intraspecific competition of predator τ_2 becomes large. The chaotic behavior was not discussed in He [10]. We believe this is the first time such chaotic behavior has been observed. Compared to results of May [18] and Song and Wei [27], our model brings new aspects of the effect of time delay, since $\tau_2 = 0$ in their model. Other values of τ_2 may generate other type of chaotic behavior, which is an interesting problem. Further analyses and considerations for the global dynamics of (E) are left for future work.

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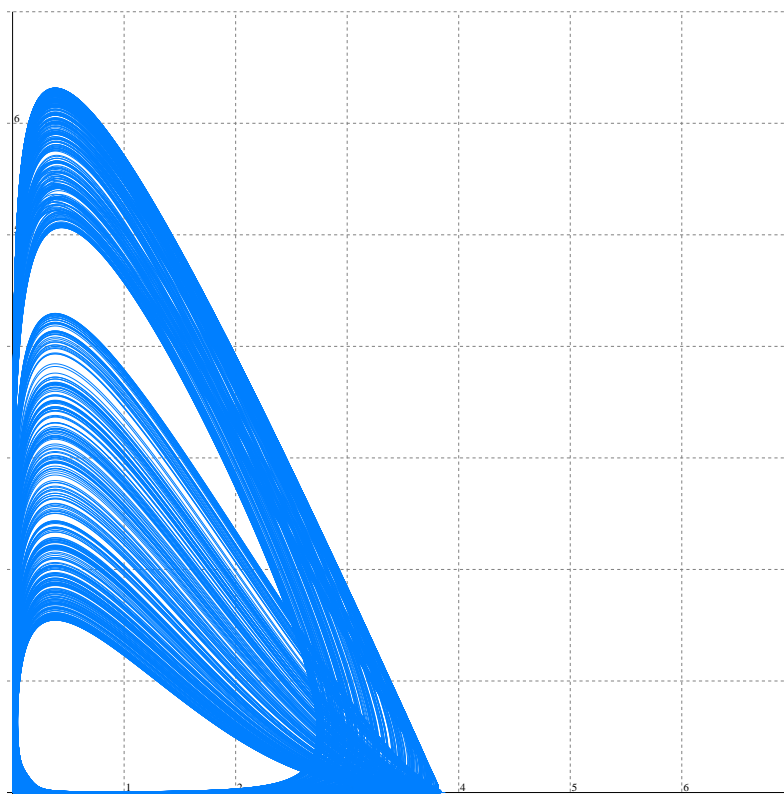


FIGURE 10. $\tau_1 = 0.71$, $\tau_2 = 1.73$, $\phi = 0.75$, $\psi = 0.6$: shark-head chaos

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E-mail address: r5445020@ipc.shizuoka.ac.jp

E-mail address: y-saito@sys.eng.shizuoka.ac.jp

E-mail address: takeuchi@sys.eng.shizuoka.ac.jp