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LIMIT CYCLES IN TWO SPECIES COMPETITION WITH TIME DELAYS

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Abstract

The existence of stable periodic oscillatory solutions in a two species competition model with time delays is established using a combination of Hopf-bifurcation theory and the asymptotic method of Krylov, Bogoliuboff and Mitropolsky.

1. Introduction

The classical Volterra–Lotka equations used to describe the dynamic behaviour of a competitive association between two species are

$$\frac{du_1(t)}{dt} = u_1[k_1 - a_{11} u_1 - a_{12} u_2]$$

and (1.1)

$$\frac{du_2(t)}{dt} = u_2[k_2 - a_{21} u_1 - a_{22} u_2], \quad \text{for } t > 0,$$

where $u_1(t)$ and $u_2(t)$ denote the population sizes (or biomasses) of two species at time t sharing a common pool of resources and k_i, a_{ij}, $i, j = 1, 2$, are positive constants. It is generally considered that the conventional model (1.1) is rather uninteresting in the sense that its asymptotic behaviour is convergence to any of the four possible constant equilibrium states. Perhaps this may be the reason why, apart from certain discussions dealing with the "principle of competitive exclusion", the model (1.1) has not been "studied to that extent as its counterpart 'the prey–predator system' has been studied". One of the realistic modifications of (1.1) is to incorporate continuous time dealys in (1.1) and examine the asymptotic behaviour for various time delays. Beginning with the seminal work of Volterra [21], a number of authors have considered continuous time delays in population dynamic models. Most of the analysis has been restricted to single population models (Miller [19], Cushing [8, 9], May [16, 17]) or to prey–predator models (Bownds and Cushing [1], Cushing [5, 6], MacDonald [15]). Time lags in competition models have not been fully investigated although there are some indications of possible results in the works of Caswell [2], Gomatam and MacDonald [11] and Cushing [7]. It has been the belief of many that oscillatory (non-stationary) coexistence in the classical Volterra–Lotka two species competition model is unlikely although such a possibility is indicated in Cushing [7] where sufficient conditions are given which guarantee the existence of non-constant periodic solutions. If such periodic solutions are stable then we have non-stationary coexistence.

Recently it has been proved by one of the authors [12] that if (1.1) is modified to include time delays so that

$$\left.\begin{aligned} \frac{du_1}{dt} &= u_1\left[k_1 - a_{11}u_1 - a_{12}\int_{-T}^{0}\gamma_1(s)\,u_2(t+s)\,ds\right] \\ \text{and}\qquad & \\ \frac{du_2}{dt} &= u_2\left[k_2 - a_{21}\int_{-T}^{0}\gamma_2(s)\,u_1(t+s)\,ds - a_{22}u_2\right], \quad \text{for } t>0, \end{aligned}\right\} \tag{1.2}$$

then, for any arbitrary fixed T, the system (1.2) is globally asymptotically stable in the sense that, for (1.2),

$$(u_1(t), u_2(t)) \to (u_1^*, u_2^*) \quad \text{as } t \to \infty, \tag{1.3}$$

where

$$a_{11}u_1^* + a_{12}u_2^* = k_1 \quad \text{and} \quad a_{21}u_1^* + a_{22}u_2^* = k_2, \tag{1.4}$$

whenever the following conditions hold:

$$\left.\begin{aligned} & \frac{a_{11}}{a_{21}} > \frac{k_1}{k_2} > \frac{a_{12}}{a_{22}} \\ & \text{and} \\ & \int_{-T}^{0}\gamma_1(s)\,ds = 1 = \int_{-T}^{0}\gamma_2(s)\,ds, \quad \gamma_1(s)>0, \quad \gamma_2(s)>0 \quad \text{for } s\in[-T,0]. \end{aligned}\right\} \tag{1.5}$$

The purpose of the present paper is to show that, if there are continuous time delays in the intraspecific reaction rates in (1.1), then it is possible to have stable "limit cycle" type oscillatory coexistence of the two competing species. This aspect has an interesting further extension to a diffusive competition system in which case there can arise competition wave trains. A similar case has been analysed in a prey-predator system and the existence of "pursuit evasion wave trains" has been shown in [13].

2. Hopf bifurcation to oscillations

We will consider a modified form of (1.1) as follows:

$$\left.\begin{aligned} \frac{du_1}{dt} &= u_1\left[k_1 - a_{11}\int_{-\infty}^{t} u_1(s)\,k(t-s)\,ds - a_{12}\,u\right] \\ \text{and}\qquad & \\ \frac{du_2}{dt} &= u_2[k_2 - a_{21}\,u_1 - a_{22}\,u_2], \quad \text{for } t>0, \end{aligned}\right\} \tag{2.1}$$

where k_i, a_{ij}, $i,j = 1,2$, are positive constants and we choose

$$k(s) = \alpha\exp[-\alpha s], \quad s>0, \tag{2.2}$$

α being a positive constant parameter. It is easy to see that the system (2.1) and (2.2) has four equilibrium states given by

$$(0,0), \quad (k_1/a_{11}, 0), \quad (0, k_2/a_{22}) \quad \text{and} \quad (u_1^*, u_2^*),$$

where

$$\left.\begin{aligned} u_1^* &= (k_1\,a_{22} - k_2\,a_{12})/(a_{11}\,a_{22} - a_{12}\,a_{21}) \\ \text{and}\qquad & \\ u_2^* &= (k_2\,a_{11} - k_1\,a_{21})/(a_{11}\,a_{22} - a_{12}\,a_{21}). \end{aligned}\right\} \tag{2.3}$$

We assume throughout that

$$a_{11}/a_{21} > k_1/k_2 > a_{12}/a_{22}. \tag{2.4}$$

It is known that, when (2.4) holds, all solutions $(u_1(t), u_2(t))$ of (1.1) with positive initial values converge to (u_1^*, u_2^*) as $t \to \infty$. This can be shown using either phase plane methods or by means of a Lyapunov function.

To investigate the asymptotic behaviour of (2.1) let us introduce a third recovery variable $u_3(t)$ as follows:

$$u_3(t) \equiv \int_{-\infty}^{t} u_1(s)\,\alpha\exp[-\alpha(t-s)]\,ds. \tag{2.5}$$

In terms of u_3, we can rewrite the integro-differential system (2.1) in the form of an equivalent automonous differential system

$$\left.\begin{aligned} \frac{du_1}{dt} &= u_1(k_1 - a_{11}\,u_3 - a_{12}\,u_2), \\ \frac{du_2}{dt} &= u_2(k_2 - a_{21}\,u_1 - a_{22}\,u_2), \\ \text{and}\qquad & \\ \frac{du_3}{dt} &= \alpha(u_1 - u_3), \quad \text{for } t>0. \end{aligned}\right\} \tag{2.6}$$

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The differential system (2.6) has a constant nontrivial equilibrium at (u_1^*, u_2^*, u_3^*), where $u_3^* = u_1^*$. If we let

$$u_1(t) \equiv u_i^* + U_i(t), \quad i = 1, 2, 3, \tag{2.7}$$

then the variational system corresponding to (2.6) about (u_1^*, u_2^*, u_3^*) is

$$\frac{d}{dt}\begin{bmatrix} U_1 \\ U_2 \\ U_3 \end{bmatrix} = \begin{bmatrix} 0 & -a_{12}u_1^* & -a_{11}u_1^* \\ -a_{21}u_2^* & -a_{22}u_2^* & 0 \\ \alpha & 0 & -\alpha \end{bmatrix}\begin{bmatrix} U_1 \\ U_2 \\ U_3 \end{bmatrix}. \tag{2.8}$$

The steady state (u_1^*, u_2^*, u_3^*) of (2.6) is locally stable if and only if all the eigenvalues of the coefficient matrix in (2.8) have negative real parts. The eigenvalues of the coefficient matrix in (2.8) are the roots of the cubic equation

$$\lambda^3 + \lambda^2 M_1 + \lambda M_2 + M_3 = 0, \tag{2.9}$$

where

$$\left.\begin{aligned} M_1 &= \alpha + a_{22}u_2^*, \\ M_2 &= \alpha(a_{22}u_2^* + a_{11}u_1^*) - a_{12}a_{21}u_1^*u_2^* \\ M_3 &= \alpha u_1^* u_2^*(a_{11}a_{22} - a_{12}a_{21}). \end{aligned}\right\} \tag{2.10}$$

and

A set of necessary and sufficient conditions for all the roots of the cubic in (2.8) to have negative real parts is, by the Routh–Hurwitz criterion,

$$M_1 > 0, \quad M_3 > 0 \quad \text{and} \quad M_1 M_2 > M_3. \tag{2.11}$$

By virtue of (2.4), the first two of (2.11) always hold while the third will hold if and only if

$$M_2 > 0 \quad \text{and} \quad \alpha^2\{a_{11}u_1^* + a_{22}u_2^*\} + \alpha(a_{22}u_2^*)^2 - a_{22}a_{12}a_{21}u_1^*u_2^{*2} > 0. \tag{2.12}$$

The second part of (2.12) will hold if and only if

$$(\alpha - \alpha_*)(\alpha - \alpha^*) > 0, \tag{2.13}$$

where

$$\left.\begin{matrix} \alpha^* \\ \alpha_* \end{matrix}\right\} = \frac{-\alpha_{22}^2 u_2^{*2} \pm [a_{22}^4 u_2^{*4} + 4\{a_{11}u_1^* + a_{22}u_2^*\}\{a_{22}a_{12}a_{21}u_1^*u_2^{*2}\}]^{\frac{1}{2}}}{2(a_{22}u_2^* + a_{11}u_1^*)}. \tag{2.14}$$

It follows that, if the positive delay parameter α is such that $\alpha < \alpha^*$, then the constant equilibrium (u_1^*, u_2^*, u_3^*) of (2.6) is locally unstable and hence (u_1^*, u_2^*) of (2.1) and (2.2) is locally unstable; for, otherwise, $(u_1(t), u_2(t) \to (u_1^*, u_2^*)$ as $t \to \infty$ will imply $(u_1(t), u_2(t), u_3(t)) \to (u_1^*, u_2^*, u_3^*)$ as $t \to \infty$ by (2.5). We can now formulate the following:

THEOREM. *In the two-dimensional system* (2.1) *and* (2.2), *suppose* (2.4) *holds. Then a periodic solution of* (2.1) *and* (2.1) *in the region* $u_1 > 0, u_2 > 0$ *bifurcates from the steady state* (u_1^*, u_2^*) *for suitable values of* α *in a neighbourhood of* α^*.

The stability of the bifurcating periodic solution is investigated in the next section where we examine whether the bifurcation is supercritical, critical or subcritical.

PROOF. When $\alpha = \alpha^*$ it follows from (2.9) and (2.12) that $M_1 M_2 = M_3$. Since M_1 and M_3 are positive we have $M_2 > 0$ for $\alpha = \alpha^*$. Hence there exists an interval containing α^*, say $(\alpha^* - \eta, a^* + \eta)$ for some $\eta > 0$, $\alpha^* - \eta > 0$, such that $M_2 > 0$ for $\alpha \in (\alpha^* - \eta, \alpha^* + \eta)$. Thus, for $\alpha \in (\alpha^* - \eta, \alpha^* + \eta)$, the characteristic equation (2.9) cannot have purely positive roots. For $\alpha = \alpha^*$, the roots of (2.9) are λ_1, λ_2 and λ_3 where

$$\lambda_1 = iw, \quad \lambda_2 = -iw \quad \text{and} \quad \lambda_3 = -\mu = -(\alpha + a_{22} u_2^*), \tag{2.15}$$

with

$$w^2 = M_2 \quad \text{at } \alpha = \alpha^*. \tag{2.16}$$

For $\alpha \in (\alpha^* - \eta, \alpha^* + \eta)$, the roots of (2.9) are in general of the form

$$\left.\begin{aligned} \lambda_1(\alpha) &= \sigma(\alpha) + i\gamma(\alpha), \\ \lambda_2(\alpha) &= \sigma(\alpha) - i\gamma(\alpha), \\ \text{and} \qquad \lambda_3(\alpha) &= -\mu = -(\alpha + a_{22} u_2^*) - 2\sigma(\alpha), \end{aligned}\right\} \tag{2.17}$$

where, for $\alpha \in (\alpha^* - \eta, \alpha^*)$, $\sigma(\alpha) > 0$ and, for $\alpha \in (\alpha^*, \alpha^* + \eta)$, $\sigma(\alpha) < 0$; this is verified from the Routh–Hurwitz criterion resulting in (2.13) in which $\alpha_* < 0$. In order to apply Hopf's bifurcation theorem to ascertain the existence of periodic solutions for (2.6), we need to verify the transversality condition

$$\operatorname{Re}\left(\frac{d\lambda}{d\alpha}\right)_{\alpha=\alpha^*} \neq 0. \tag{2.18}$$

A direct calculation of $d\lambda/d\alpha$ from (2.9) leads to

$$\operatorname{Re}\left(\frac{d\lambda}{d\alpha}\right)_{\alpha=\alpha^*} = -[\{2(a_{11} u_1^* + a_{22} u_2^*) + a_{22}^2 u_2^{*2}\}/2(w^2 + M_1^2)]_{\alpha=\alpha^*} \neq 0. \tag{2.19}$$

It will now follow from Hopf's bifurcation theorem (Marsden and McCracken [18]) that a periodic solution say $\{\tilde{u}_1(t), \tilde{u}_2(t), \tilde{u}_3(t)\}$ of the system (2.6) bifurcates from the steady state (u_1^*, u_2^*, u_3^*) for α near α^*. The nonnegativity of $(\tilde{u}_1(t), \tilde{u}_2(t), \tilde{u}_3(t))$ will follow from the vector field of (2.6) since the vector field does not point to the outside of the positive octant. This completes the proof of the existence of a periodic solution $(\tilde{u}_1(t), \tilde{u}_2(t))$ of (2.1) and (2.2). We show below that the bifurcation is supercritical, that is, there exists a constant $\varepsilon^* > 0$ such that $0 < \alpha^* - \eta < \alpha^* - \varepsilon^* < \alpha < \alpha^*$.

3. Stability of the periodic solution via the KBM asymptotic method

In the literature on Hopf bifurcation theory there are certain algorithms developed by Poore [20] and Hsü and Kazarinoff [14] to investigate the stability of the bifurcating periodic solutions. Another alternative to investigate such a stability is to use a multi-time perturbational approach which has the added benefit of approximately determining the bifurcating solution. (See Cohen and Keener [4], Cohen, Coutsias and Neu [3].) The author's attempts to use these established procedures for investigating the stability of the periodic solution bifurcating in (2.6) have not been successful. The calculations needed to verify stability or instability of the periodic solution are too numerous to carry out. However, there is another relatively easy way to determine the stability of periodic solutions arising from Hopf's bifurcation.

This method is based on perturbation theory of invariant manifolds, especially invariant tori. We will essentially use theorem 2 of Golets [10]; this method results in a smaller number of computations than in the other methods. In order to apply Golets' theorem we proceed as follows:

Let $\alpha = \alpha^* - \varepsilon^2$ in (2.6), where $0 < \alpha^* - \eta < \alpha^* - \varepsilon^2 < \alpha$, and let

$$u_1 = u^* + \varepsilon U_1(t), u_2 = u_2^* + \varepsilon U_2(t) \quad \text{and} \quad u_3 = u_3^* + \varepsilon U_3(t), \tag{3.1}$$

so that

$$\begin{aligned} \frac{d}{dt}\begin{bmatrix} U_1 \\ U_2 \\ U_3 \end{bmatrix} &= \begin{bmatrix} 0 & -a_{12}u_1^* & -a_{11}u_1^* \\ -a_{21}u_2^* & -a_{22}u_2^* & 0 \\ \alpha^* & 0 & -\alpha^* \end{bmatrix}\begin{bmatrix} U_1 \\ U_2 \\ U_3 \end{bmatrix} \\ &+(-\varepsilon^2)\begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 1 & 0 & -1 \end{bmatrix}\begin{bmatrix} U_1 \\ U_2 \\ U_3 \end{bmatrix} + \varepsilon\begin{bmatrix} -a_{11}U_1U_3 - a_{12}U_1U_2 \\ -a_{21}U_1U_2 - a_{22}U_2^2 \\ 0 \end{bmatrix}. \end{aligned} \tag{3.2}$$

Introduce a new set of variables (x, y, z) by the linear transformation

$$\begin{bmatrix} U_1 \\ U_2 \\ U_3 \end{bmatrix} = \begin{bmatrix} P_{11} & P_{12} & P_{13} \\ P_{21} & P_{22} & P_{23} \\ P_{31} & P_{32} & P_{33} \end{bmatrix} \begin{bmatrix} x \\ y \\ z \end{bmatrix}, \tag{3.3}$$

and choose P_{ij}, $i, j = 1, 2, 3$, so that

$$P^{-1} \begin{bmatrix} 0 & -a_{12} u_1^* & -a_{11} u_1^* \\ a_{21} u_2^* & -a_{22} u_2^* & 0 \\ \alpha^* & 0 & -\alpha^* \end{bmatrix} P = \begin{bmatrix} 0 & w & 0 \\ -w & 0 & 0 \\ 0 & 0 & -\mu \end{bmatrix}. \tag{3.4}$$

For such a choice of P_{ij}, the new variables (x, y, z) are determined by

$$\frac{d}{dt}\begin{bmatrix} x \\ y \\ z \end{bmatrix} = \begin{bmatrix} 0 & w & 0 \\ -w & 0 & 0 \\ 0 & 0 & -\mu \end{bmatrix} \begin{bmatrix} x \\ y \\ z \end{bmatrix} - \varepsilon^2 \begin{bmatrix} M_{11} & M_{12} & M_{13} \\ M_{21} & M_{22} & M_{23} \\ M_{31} & M_{32} & M_{33} \end{bmatrix} \begin{bmatrix} x \\ y \\ z \end{bmatrix} + \varepsilon \begin{bmatrix} f_1(x, y, z) \\ f_2(x, y, z) \\ f_3(x, y, z) \end{bmatrix}, \tag{3.5}$$

where

$$(M_{ij}) = p^{-1} \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 1 & 0 & -1 \end{bmatrix} P, \tag{3.6}$$

and f_1, f_2 and f_3 are quadratic polynomials in x, y and z. A direct calculation in (3.5) leads to

$$\left.\begin{aligned} \frac{dx}{dt} &= wy - \varepsilon^2(M_{11} x + M_{12} y) + \varepsilon(b_1 x^2 + b_2 y^2 + b_{12} xy) \\ &\qquad + \varepsilon \,\{\text{a quadratic polynomial in } z\}, \\ \frac{dy}{dt} &= -wx - \varepsilon^2(M_{21} x + M_{22} y) + \varepsilon(c_1 x^2 + c_2 y^2 + c_{12} xy). \\ &\qquad + \varepsilon \,\{\text{a quadratic polynomial in } z\}, \\ \frac{dz}{dt} &= -\mu z + \varepsilon \text{ (a polynomial in } x, y \text{ and } z), \end{aligned}\right\} \tag{3.7}$$

in which M_{ij}, b_i, b_{ij}, c_i, c_{ij} are constants which can be calculated from (3.2) to (3.6). Eliminating dy/dt in the first two equations of (3.7) and retaining terms up to order of

ε^2, we get

$$\left.\begin{aligned}\frac{d^2x}{dt^2}+w^2x = &-w\varepsilon^2(M_{21}x+M_{22}\dot{x}/w)-\varepsilon^2(M_{11}\dot{x}-M_{12}wx)\\ &+w\varepsilon c_1x^2+\varepsilon 2b_1x\dot{x}+w\varepsilon c_2\{\dot{x}^2-2\dot{x}\varepsilon(b_1x^2+b_2y^2+b_{12}xy)/w^2\}\\ &+w\varepsilon c_{12}x\{\dot{x}-\varepsilon(b_1x^2+b_2y^2+b_{12}xy)\}/w\\ &+(\varepsilon b_2/w)\{-wx\dot{x}+\dot{x}\varepsilon(c_1x^2+c_2y^2+c_{12}xy)\\ &+w\varepsilon x(b_1x^2+b_2y^2+b_{12}xy)\}\\ &+\varepsilon b_{12}\{-wx^2+\varepsilon x(c_1x^2+c_2y^2+c_{12}xy)\}\\ &+\varepsilon b_{12}\dot{x}\{\dot{x}-\varepsilon(b_1x^2+b_2y^2+b_{12}xy)\}/w,\end{aligned}\right\}\tag{3.8}$$

where $\dot{x} = dx/dt$; in (3.8), if we replace y by $\dot{x}/w$, we get an equation of the form

$$\frac{d^2x}{dt^2}+w^2x = \varepsilon F(x,\varepsilon)\tag{3.9}$$

for a polynomial F in x and ε. In addition to (3.8) we have

$$\frac{dz}{dt} = -\mu z+\varepsilon\text{ (a quadratic polynomial in } x,\ y \text{ and } z).\tag{3.10}$$

If we now let

$$\left.\begin{aligned}&x(t) = a(t)\sin\phi(t),\quad y(t) = a(t)\,w\cos\phi(t)\\ \text{and}\quad &\frac{d\phi}{dt} = w+\text{terms of the order of }\varepsilon,\end{aligned}\right\}\tag{3.11}$$

then, by a combination of the Krylov Bogoliubov Mitropolsky (KBM) asymptotic method and Theorem 2 of Golets [10], we find, after a lengthy calculation and simplification, that

$$\begin{aligned}\frac{da}{dt} = \frac{\varepsilon^2a}{\Delta}\Bigg[&\frac{P_{22}w^2}{\alpha^{*2}(\alpha^{*2}+w^2)}+\frac{w}{\alpha^*(\alpha^{*2}+w^2)}\left\{\frac{a_{21}u_2^*}{\alpha^{*2}}+\frac{a_{11}\alpha^*}{(\alpha^{*2}+w^2)a_{12}}\right\}\\ &-a^2\left\{\frac{a_{22}p_{22}^2}{2\alpha^*}\left(\frac{1}{a_{22}u_2^*}+\frac{\alpha^*}{\alpha^{*2}+w^2}\right)\right\}\Bigg],\end{aligned}\tag{3.12}$$

in which $\Delta = \det(P_{ij})$ and

$$\begin{aligned}&P_{11} = 1/\alpha^*,\quad P_{12} = 0,\quad P_{13} = 1/\alpha^*,\quad P_{21} = -a_{11}\alpha^*/(\alpha^{*2}+w^2)\,a_{12},\\ &P_{22} = a_{11}\alpha^*w/(\alpha^{*2}+w^2)a_{12}a_{22}u_2^*,\quad P_{23} = a_{21}u_2^*/\alpha^{*2},\\ &P_{31} = \alpha^*/(\alpha^{*2}+w^2),\quad P_{32} = -w/(\alpha^{*2}+w^2),\quad P_{33} = -1/a_{22}u_2^*\end{aligned}\tag{3.13}$$

and

$$\Delta = \frac{wa_{21}\, u_2^*(a_{22}\, u_2^* - \alpha^*)\,\{w^2 + (a_{22}\, u_2^* + \alpha^*)^2\}}{(a_{22}^2\, u_2^{*2} + w^2)(\alpha^{*2} + w^2)\, a_{22}\, u_2^*\, \alpha^{*3}}. \tag{3.13 contd}$$

Since

$$\alpha^*(w^2 + a_{22}^2\, u_2^{*2}) = a_{12}\, a_{21}\, u_1^*\, u_2^*(a_{22}\, u_2^* - \alpha^*),$$

It follows that $\Delta > 0$ and hence we can conclude from (3.12) that the amplitude of the oscillations in (3.11) approaches a constant, idependent of initial values, as $t \to \infty$. From this it follows that, for suitable α, arbitrary solutions of (2.1) and (2.2) approach in the limit as $t \to \infty$ the limit cycle type oscillatory solutions of the form

$$u_1(t) = u_1^* + \varepsilon P_{11}\, a^* \sin wt$$

and

$$u_2(t) = u_2^* + \varepsilon(P_{21}\, a^* \sin wt + P_{22}\, a^*\, w(\cos wt)),$$

where a^* is the positive stationary solution in (3.12).

4. Some comments

If there are time delays in the interspecific interaction terms as in (1.2) and if the intraspecific interactions are strong (that is, $a_{11}\, a_{22} > a_{12}\, a_{21}$), then oscillatory coexistence is not possible; this is established in [12]. In his monograph Cushing [7] shows that, when there are delays in the interspecific interactions, oscillations are possible in two species competition provided the interspecific interactions are strong (see Cushing [7, pages 171–175]). However, Cushing [7] remarks that the periodic solutions found by him are unlikely to be stable since his numerical integrations do not support the possibility of stable periodic solutions. By considering a simpler model, we have demonstrated stable oscillations in a two species competition model system when the intraspecific interactions are stronger. The authors are unable to comment on the absence of oscillations when there are delays in the interspecific interactions and the presence of oscillations when there are delays in the intraspecific interactions.

5. An example

The following example has been numerically simulated in a digital computer and the oscillations are graphically illustrated:

$$\frac{du_1}{dt} = u_1\left[10 - 3\int_{-\infty}^{t} \alpha \exp[-\alpha(t-s)]\, u_1(s)\, ds - u_2\right]$$

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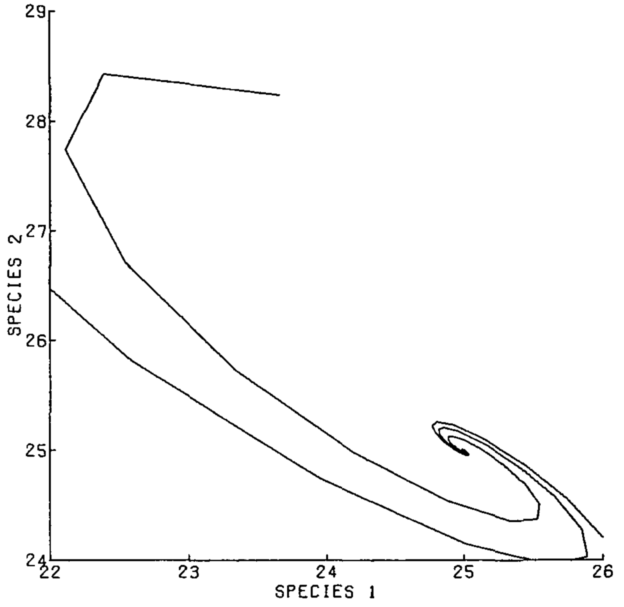

Fig. 1. Equilibrium co-existence, $\alpha = 6.0$, $\alpha^* = 1.88$.

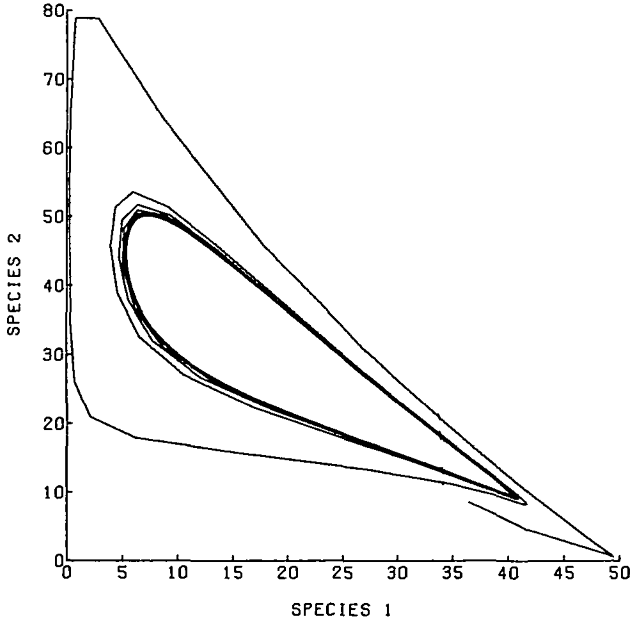

Fig. 2. Oscillatory co-existence, $\alpha = 1.65$, $\alpha^* = 1.88$.

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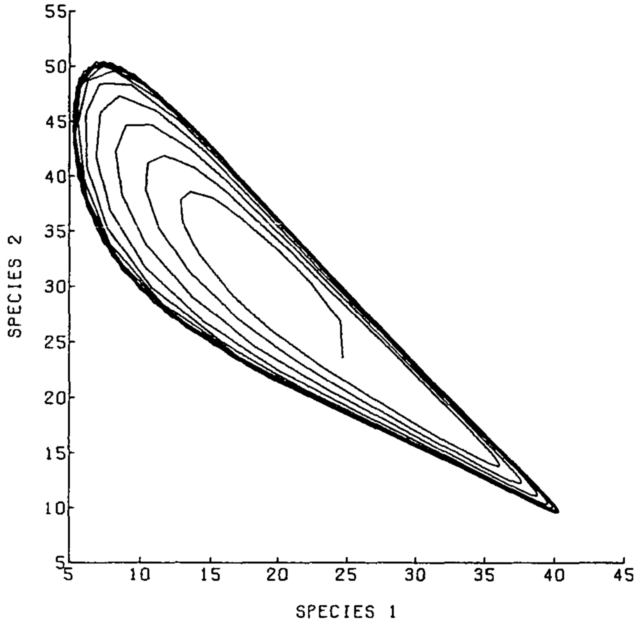

Fig. 3. Oscillatory co-existence, $\alpha = 1.65$, $\alpha^* = 1.88$.

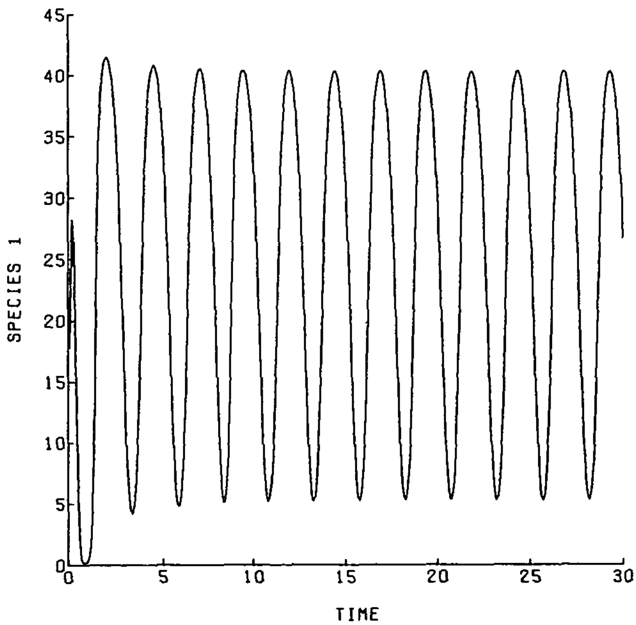

Fig. 4. Oscillations of species 1, $\alpha = 1.65$.

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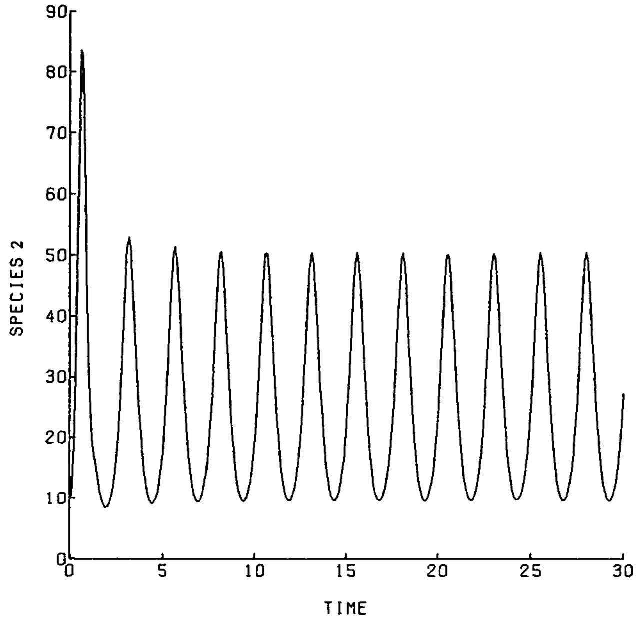

Fig. 5. Oscillations of species 2, $\alpha = 1.65$.

and

$$\frac{du_2}{dt} = u_2[20-4u_1-4u_2].$$

In this example, $\alpha^* = 1{\cdot}88$. We have chosen $\alpha = 1.65$. To show rapid convergence to a stationary steady state, we have also chosen $\alpha = 6.0$.

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