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

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

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 delays 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

$$\frac{du_1}{dt} = u_1 \left[ k_1 - a_{11} u_1 - a_{12} \int_{-T}^{0} \gamma_1(s) u_2(t + s) ds \right]$$

and

$$\frac{du_2}{dt} = u_2 \left[ k_2 - a_{21} \int_{-T}^{0} \gamma_2(s) u_1(t + s) ds - a_{22} u_2 \right], \text{ for } t > 0,$$

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

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

where

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

(1.4)

whenever the following conditions hold:

$$\frac{a_{11}}{a_{21}} > \frac{k_1}{k_2} > \frac{a_{12}}{a_{22}},$$

and

$$\int_{-T}^{0} \gamma_1(s) ds = 1 = \int_{-T}^{0} \gamma_2(s) ds, \quad \gamma_1(s) > 0, \quad \gamma_2(s) > 0 \quad \text{for } s \in [-T, 0].$$

(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 analyzed 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:

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

and

\[
\begin{align*}
\frac{du_3}{dt} &= \alpha(u_1 - u_3), \quad \text{for } t > 0.
\end{align*}
\]

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

\[
k(s) = \alpha \exp[-\alpha s], \quad s > 0,
\]

\( \alpha \) 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

\[
u_1^* = (k_1 a_{22} - k_2 a_{12})/(a_{11} a_{22} - a_{12} a_{21})
\]and

\[
u_2^* = (k_2 a_{11} - k_1 a_{21})/(a_{11} a_{22} - a_{12} a_{21}).
\]

We assume throughout that

\[
a_{11}/a_{21} > k_1/k_2 > a_{12}/a_{22}.
\]

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:

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

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

\[
\begin{align*}
\frac{du_1}{dt} &= u_1(k_1 - a_{11} u_3 - a_{12} u_2), \\
\frac{du_2}{dt} &= u_2(k_2 - a_{21} u_1 - a_{22} u_2), \\
\frac{du_3}{dt} &= \alpha(u_1 - u_3), \quad \text{for } t > 0.
\end{align*}
\]
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

\[ u_i(t) = u^*_i + U_i(t), \quad i = 1, 2, 3, \tag{2.7} \]

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

\[
\begin{aligned}
M_1 &= \alpha + a_{22} u^*_2, \\
M_2 &= \alpha(a_{22} u^*_2 + a_{11} u^*_1) - a_{12} a_{21} u^*_1 u^*_2 \\
M_3 &= \alpha u^*_1 u^*_2 (a_{11} a_{22} - a_{12} a_{21}).
\end{aligned} \tag{2.10} \]

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

\[
M_2 > 0 \quad \text{and} \quad \alpha^2 \{a_{11} u^*_1 + a_{22} u^*_2\} + \alpha(a_{22} u^*_2)^2 - a_{22} a_{12} a_{21} u^*_1 u^*_2 > 0. \tag{2.12} \]

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

\[
(\alpha - \alpha^*_\star)(\alpha - \alpha^*_\star) > 0, \tag{2.13} \]

where

\[
\alpha^*_\star = \frac{-a_{22}^2 u^*_2 \pm [a_{22}^2 u^*_2^4 + 4\{a_{11} u^*_1 + a_{22} u^*_2\} \{a_{22} a_{12} a_{21} u^*_1 u^*_2^2\}]^\frac{1}{2}}{2(a_{22} u^*_2 + a_{11} u^*_1)}. \tag{2.14} \]

It follows that, if the positive delay parameter \(\alpha\) is such that \(\alpha < \alpha^*_\star\), 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
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 \( \alpha \) in a neighbourhood of \( \alpha^* \).

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 \( \alpha^* \), say \((\alpha^* - \eta, \alpha^* + \eta)\) 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 \( \lambda_1, \lambda_2 \) and \( \lambda_3 \) where

\[
\lambda_1 = i\omega, \quad \lambda_2 = -i\omega \quad \text{and} \quad \lambda_3 = -\mu = -(\alpha + a_{22} u_2^*),
\]

with

\[
w^2 = M_2 \quad \text{at} \quad \alpha = \alpha^*.
\]

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

\[
\begin{align*}
\lambda_1(\alpha) &= \sigma(\alpha) + i\gamma(\alpha), \\
\lambda_2(\alpha) &= \sigma(\alpha) - i\gamma(\alpha), \\
\lambda_3(\alpha) &= -\mu = -(\alpha + a_{22} u_2^*) - 2\sigma(\alpha),
\end{align*}
\]

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

\[
\text{Re} \left( \frac{d\lambda}{d\alpha} \right)_{\alpha = \alpha^*} \neq 0.
\]

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

\[
\text{Re} \left( \frac{d\lambda}{d\alpha} \right)_{\alpha = \alpha^*} = - \left[ \frac{\{2(a_{11} u_1^* + a_{22} u_2^*) + a_{22}^2 u_2^{*2}\}}{2(w^2 + M_2^2)} \right]_{\alpha = \alpha^*} \neq 0.
\]
It will now follow from Hopf’s bifurcation theorem (Marsden and McCracken [18]) that a periodic solution say \( \{ \hat{u}_1(t), \hat{u}_2(t), \hat{u}_3(t) \} \) of the system (2.6) bifurcates from the steady state \((u^*_1, u^*_2, u^*_3)\) for \( \alpha \) near \( \alpha^* \). The nonnegativity of \((\hat{u}_1(t), \hat{u}_2(t), \hat{u}_3(t))\) 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 \((\hat{u}_1(t), \hat{u}_2(t))\) 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

\[
\begin{align*}
    u_1 &= u^* + \varepsilon U_1(t), \quad u_2 = u^*_2 + \varepsilon U_2(t) \quad \text{and} \quad u_3 = u^*_3 + \varepsilon U_3(t), \\
    \alpha &= \alpha^* - \varepsilon^2
\end{align*}
\]

so that

\[
\begin{bmatrix}
    U_1 \\
    U_2 \\
    U_3
\end{bmatrix}
= \begin{bmatrix}
    0 & -a_{12} u^*_1 & -a_{11} u^*_1 \\
    -a_{21} u^*_2 & -a_{22} u^*_2 & 0 \\
    \alpha & 0 & -\alpha
\end{bmatrix}
\begin{bmatrix}
    U_1 \\
    U_2 \\
    U_3
\end{bmatrix}
+ (-\varepsilon^2)
\begin{bmatrix}
    0 & 0 & 0 \\
    0 & 0 & 0 \\
    1 & 0 & -1
\end{bmatrix}
\begin{bmatrix}
    U_1 \\
    U_2 \\
    U_3
\end{bmatrix}
+ \varepsilon
\begin{bmatrix}
    -a_{11} U_1 U_3 - a_{12} U_1 U_2 \\
    -a_{21} U_1 U_2 - a_{22} U_2^2 \\
    0
\end{bmatrix}. 
\]
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
\[
\begin{bmatrix}
0 & -a_{12} u_1^* & -a_{11} u_1^* \\
a_{21} u_2^* & -a_{22} u_2^* & 0 \\
\alpha^* & 0 & -\alpha^*
\end{bmatrix}
\begin{bmatrix}
0 & w & 0 \\
-w & 0 & 0 \\
0 & 0 & -\mu
\end{bmatrix}.
\tag{3.4}
\]
For such a choice of \(P_{ij}\), the new variables \((x, y, z)\) are determined by
\[
\frac{d}{dt}
\begin{bmatrix}
x \\
y \\
z
\end{bmatrix} =
\begin{bmatrix}
0 & w & 0 \\
-w & 0 & 0 \\
0 & 0 & -\mu
\end{bmatrix}
\begin{bmatrix}
x \\
y \\
z
\end{bmatrix} - \epsilon^2
\begin{bmatrix}
M_{11} & M_{12} & M_{13} \\
M_{21} & M_{22} & M_{23} \\
M_{31} & M_{32} & M_{33}
\end{bmatrix}
\begin{bmatrix}
x \\
y \\
z
\end{bmatrix}
+ \epsilon
\begin{bmatrix}
f_1(x, y, z) \\
f_2(x, y, z) \\
f_3(x, y, z)
\end{bmatrix},
\tag{3.5}
\]
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
\[
\begin{align*}
\frac{dx}{dt} &=wy - \epsilon^2(M_{11}x + M_{12}y) + \epsilon(b_1 x^2 + b_2 y^2 + b_{12} xy) \\
&+ \epsilon \{a \text{ quadratic polynomial in } z\}, \\
\frac{dy}{dt} &= -wx - \epsilon^2(M_{21}x + M_{22}y) + \epsilon(c_1 x^2 + c_2 y^2 + c_{12} xy) \\
&+ \epsilon \{a \text{ quadratic polynomial in } z\}, \\
\frac{dz}{dt} &= -\mu z + \epsilon \{a \text{ polynomial in } x, y \text{ and } z\},
\end{align*}
\tag{3.7}
\]
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
\[ \frac{d^2 x}{dt^2} + w^2 x = -\varepsilon^2(M_{21} x + M_{22} \dot{x}/w) - \varepsilon^2(M_{11} \dot{x} - M_{12} w x) + \varepsilon^2 b_1 x \dot{x} + \varepsilon^2 c_2 \{ \dot{x}^2 - 2\varepsilon \dot{x}(b_1 x^2 + b_2 y^2 + b_{12} xy)/w^2 \} + \varepsilon^2 c_2 \{ \dot{x} \varepsilon (c_1 x^2 + c_2 y^2 + c_{12} xy) \} + \varepsilon (b_2/w) \{ -wx \dot{x} + \varepsilon x(c_1 x^2 + c_2 y^2 + c_{12} xy) \} + \varepsilon b_{12} \{ -wx^2 + \varepsilon x(c_1 x^2 + c_2 y^2 + c_{12} xy) \} \]

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

\[ \frac{d^2 x}{dt^2} + w^2 x = \varepsilon F(x, \varepsilon) \]  

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

\[ \frac{dz}{dt} = -\mu z + \varepsilon \] (a quadratic polynomial in \( x, y \) and \( z). \)  

If we now let

\[ x(t) = a(t) \sin \phi(t), \quad y(t) = a(t) w \cos \phi(t) \]  

and

\[ \frac{d\phi}{dt} = w + \text{terms of the order of } \varepsilon, \]  

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

\[ \frac{da}{dt} = \frac{\varepsilon^2 a}{\Delta} \left[ \frac{P_{22} w^2}{\alpha^2(\alpha^2 + w^2)} + \frac{w}{\alpha(\alpha^2 + w^2)} \left\{ \frac{a_{21} u_2^*}{\alpha^2} + \frac{a_{11} \alpha^*}{(\alpha^2 + w^2) a_{12}} \right\} \right] \]

\[ \left\{ -a^2 \left[ \frac{a_{22} p_{22}}{2\alpha^*} \left( \frac{1}{a_{22} u_2^*} + \frac{\alpha^*}{\alpha^2 + w^2} \right) \right] \right\}, \]  

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

\[ P_{11} = 1/\alpha^*, \quad P_{12} = 0, \quad P_{13} = 1/\alpha^*, \quad P_{21} = -a_{11} \alpha^* / (\alpha^2 + w^2) a_{12}, \]

\[ P_{22} = a_{11} \alpha^* w / (\alpha^2 + w^2) a_{12} a_{22} u_2^*, \quad P_{23} = a_{21} u_2^* / \alpha^2, \]

\[ P_{31} = \alpha^* / (\alpha^2 + w^2), \quad P_{32} = -w / (\alpha^2 + w^2), \quad P_{33} = -1/a_{22} u_2^* \] (3.13)
and 
\[ \Delta = \frac{w a_21 \ u_2^* (a_{22} u_2^* - \alpha^*) \left( w^2 + (a_{22} u_2^* + \alpha^*)^2 \right)}{(a_{22}^2 u_2^* + w^2) (\alpha^*^2 + w^2) a_{22} u_2^* \alpha^*^3}. \]  
(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, independent of initial values, as \( t \to \infty \).

From this it follows that, for suitable \( \alpha \), 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

\[ u_1(t) = u_1^* + \varepsilon P_{11} \alpha^* \sin \omega t \]

and

\[ u_2(t) = u_2^* + \beta (P_{21} \alpha^* \sin \omega t + P_{22} \alpha^* \cos \omega t), \]

where \( \alpha^* \) 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:

\[ \frac{du_1}{dt} = u_1 \left[ 10 - 3 \int_{-\infty}^{t} \alpha \exp \left( -\alpha(t-s) \right) u_1(s) ds - u_2 \right] \]
Fig. 1. Equilibrium co-existence, \( a = 6.0, a^* = 1.88 \).

Fig. 2. Oscillatory co-existence, \( a = 1.65, a^* = 1.88 \).
**Fig. 3.** Oscillatory co-existence, $\alpha = 1.65$, $\alpha^* = 1.88$.

**Fig. 4.** Oscillations of species 1, $\alpha = 1.65$. 
In this example, $\alpha^* = 1.88$. 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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