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Stable spatio-temporal oscillations of diffusive Lotka-Volterra system with three or more species

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Abstract. A stability condition for Hopf-bifurcating solutions from the uniform equilibrium of clasical Lotka-Volterra interaction–diffusion equations is presented. Using this condition, it is shown that stable spatio-temporal oscillations exist in the framework of such equations.

Key words: Diffusive Lotka–Volterra system — Hopf-bifurcation — Spatio-temporal oscillation — Stability

1. Introduction

The population dynamics of J interacting species which disperse by diffusion are modelled by Lotka–Volterra interaction-diffusion equations in a bounded domain $\Omega \subset R^N$.

$$\frac{\partial u_i}{\partial t} = \sigma_i \Delta u_i + f_i(u_1, \dots, u_J) u_i, \qquad i = 1, 2, \dots, J,$$
$$\mathbf{x} \in \Omega, \qquad t > 0. \tag{1.1}$$

(Skellam, 1951; Segel and Jackson, 1972; Levin, 1974; Steele, 1974; Okubo, 1980; and others). Here, $u_i = u_i(\mathbf{x}, t)$ is the density of the i-th species at position $\mathbf{x} = (x_1, x_2, \dots, x_N)'$ and at time t, which is assumed to satisfy Neumann boundary conditions:

$$\partial u_i / \partial \mathbf{n} = 0, \qquad i = 1, 2, \dots, J. \tag{1.2}$$

In the case of $J = 1$, the non-existence of stable spatially non-constant equilibrium solutions for these equations has been settled in convex domains (Casten and Holland, 1978; Matano, 1979) as well as in one dimensional domains (Chafee,

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1975). In the case of $J=2$, non-existence of such solutions has also been settled both for

1) predator-prey dynamics with intra-specific competition in arbitrary domains (Rothe, 1976; Leung, 1978; Mimura and Nishida, 1978; Williams and Chow, 1978; Mimura, 1979;

and for

2) competitive dynamics in any convex domains (Kishimoto and Weinberger, submitted for publication) as well as in one dimensional domains (Kishimoto, 1981).

Thus in the framework of (1.1) and (1.2) with two or less species, stable non-constant solutions are realizable only in suitable non-convex domains (Matano, 1979), or under more special assumptions of intraspecific cooperation (Segel and Levin, 1976; Mimura et al., 1978). Even for $J\geq 3$, until recently, only sufficient conditions for the global convergence to a constant equilibrium were known (Murray, 1975; Jorne and Carmi, 1977; Hastings, 1978; Conway et al. 1978; and others). These results gave a basis for introducing a more complicated framework of cross diffusion (Shigesada, et al., 1979; Mimura, 1981) or of a spatially non-constant environment (Fleming, 1975; Fife, 1982) to explain the spatially non-constant distribution of species.

However, it was found recently, that for $J\geq 3$ the simplest system of (1.1) with (1.2) can have stable non-constant equilibrium solutions: the diffusive instability takes place not only for systems with intraspecific cooperations in one or more species (Evans, 1980), but also for systems with intraspecific competition for all species. In fact, Kishimoto (1982) gave such examples, and showed that the equilibrium bifurcating solution is stable.

Thus, an interesting problem is whether the system can also have more complicated solutions. The purpose of this paper is partially answer this problem positively by showing that (1.1) and (1.2), in fact, has solutions with stable spatio-temporal oscillations. Since the bifurcation technique is employed, we first give stability conditions for the Hopf-bifurcating solutions from a uniform equilibrium, assuming that the nonlinear term f_i in (1.1) have the form of clasical Lotka–Volterra dynamics:

$$f_i(u_1,\ldots,u_J)=p_i+\sum_{j=1}^{J}a_{ij}u_j.$$

We then give three examples of the system with this nonlinear term which have stable bifurcating solutions: one has a one predator-two prey interaction, another a two predator-one prey interaction, and the third competitive interactions among four species.

These results, together with the recent discoveries of regular and irregular oscillations of the ordinary Lotka–Volterra system (May and Leonard, 1975; Nakajima, 1978; Arneodo et al., 1982; and others) suggest the possible importance of the further investigation of the system of clasical Lotka–Volterra dynamics.

We are concerned only with the mathematical analysis. For the observational aspect of these phenomena in the field, we only recommend references such as Schoener (1974).

2. The equations and its stability criterion

In this section, a stability criterion for the solution bifurcating from a spatially constant equilibrium solution of the diffusive Lotka–Volterra system is given by following the well known method of integral averaging (see Chow and Mallet-Paret, 1977). Consider the diffusive Lotka–Volterra system parametrized by μ in a one-dimensional interval:

$$\partial u_i(x, t)/\partial t = (\sigma_i + \mu\gamma_i)\Delta u_i(x, t) + \left(r_i + \sum_{j=1}^{J} a_{ij}u_j(x, t)\right)u_i(x, t),$$
$$0<x<\pi,\ t>0, \qquad i = 1, 2, \ldots, J. \tag{2.1}$$

Here, $u_i(x, t)$ is the density of the ith species at time t and at position x. The diffusion coefficients σ_i and γ_i ($i = 1, 2, \ldots, J$) are positive constants. The diagonal coefficients a_{ii} ($i = 1, 2, \ldots, J$) are non-positive constants, which reflect intra-specific competition, while the off-diagonal coefficients $a_{ij}(i \neq j)$ are any real valued constants. This means that the interspecific relatons may be competitive, cooperative, predator-prey type or combinations. The solution $\mathbf{u} = (u_1, u_2, \ldots, u_J)'$ is always assumed to satisfy Neumann boundary conditions:

$$\partial \mathbf{u}(x, t)/\partial x = 0, \qquad x = 0, \pi; \qquad t>0. \tag{2.2}$$

where $'$ means the transposition of a vector.

Assume that (2.1) has a spatially constant equilibrium solution $\mathbf{u}_0 = (u_{01}, u_{02}, \ldots, u_{0J})'$ ($u_{0i}>0$, $i = 1, 2, \ldots, J$) which is independent of μ, so that (2.2) can be written as

$$\partial u_i/\partial t = (\sigma_i + \mu\gamma_i)\Delta u_i + \sum_{j=1}^{J} a_{ij}(u_j - u_{0j})u_i, \qquad i = 1, 2, \ldots, J.$$

By using $J \times J$ matrices $\mathbf{A} = (a_{ij})$ together with $J \times J$ diagonal matrices $\mathbf{D}$, $\mathbf{G}$ and $\mathbf{U}$ whose (i, i)-components are, respectively, σ_i γ_i, and $u_i(x, t)$, the system (2.2) is rewritten into a more compact form:

$$\partial \mathbf{u}/\partial t = (\mathbf{D} + \mu\mathbf{G})\Delta\mathbf{u} + \mathbf{U}\mathbf{A}(\mathbf{u} - \mathbf{u}_0). \tag{2.3}$$

The perturbation system of (2.3) around $\mathbf{u}_0$ and its associated eigenvalue problem are, respectively, written as follows:

$$\partial \mathbf{v}(x, t)/\partial t = (\mathbf{D} + \mu\mathbf{G})\Delta\mathbf{v} + \mathbf{U}_0\mathbf{A}\mathbf{v}, \tag{2.4}$$

$$\lambda(\mu)\mathbf{p}(\mu) = -n^2(\mathbf{D} + \mu\mathbf{G}) + \mathbf{U}_0\mathbf{A}\mathbf{p}(\mu), \qquad n = 0, 1, \ldots, \tag{2.5}$$

where $\mathbf{v} = (v_1, v_2, \ldots, v_J)'$, $\mathbf{p} = (p_1, p_2, \ldots, p_J)'$ and $\mathbf{U}_0$ is the diagonal matrix whose (i, i)-components are u_{0i}.

Assume that

A1) for some $n = N>0$, there is a real number $\delta>0$ such that, for any μ with $-\delta<\mu<\delta$, the eigenvalue problem (2.5) has a unique pair of complex conjugate eigenvalues $\lambda_0(\mu)$ and $\overline{\lambda_0(\mu)}$ such that $\lambda_0(\mu) = \alpha_0(\mu) + i\omega_0(\mu)$, where $\omega_0(0) = \omega_0>0$, $\alpha_0(0) = 0$, $d\alpha(\mu)/d\mu|_{\mu=0}>0$.

A2) all the eigenvalues except for λ_0 and $\overline{\lambda_0}$ have strictly negative real parts for any n.

Then, a periodic bifurcating solution exists in the neighborhood of $\mu = 0$; the first approximation is given by $\mathbf{u} = \varepsilon(\boldsymbol{\phi} \cos(\omega_0 t - t_0) + \boldsymbol{\psi} \sin(\omega_0 t - t_0))$, where $\boldsymbol{\phi} + i\boldsymbol{\psi} = (\phi_1, \phi_2, \ldots, \phi_J)' + i(\psi_1, \psi_2, \ldots, \psi_J)'$ is the eigenvector corresponding to the eigenvalue λ_0.

The calculation of the stability criterion for the bifurcating solution by the method of averaging (Chow and Mallet-Paret, 1977) is routine, but is rather long. We only give the final result.

Let P be a $J \times J$ matrix such that its first column is $\boldsymbol{\phi}$, the second column is $\boldsymbol{\psi}$, and the other jth columns $(j = 3, 4, \ldots, J)$ are $\boldsymbol{\zeta}_j$, where $\boldsymbol{\zeta}_j$ is taken so that $\mathbf{P}^{-1}(-N^2\mathbf{D} + \mathbf{U}_0\mathbf{A})\mathbf{P} = \boldsymbol{\Lambda}$. Here,

$$\boldsymbol{\Lambda} = \begin{pmatrix} 0 & -\omega_0 & 0 \\ \omega_0 & 0 & \\ & 0 & \Lambda_3 \end{pmatrix},$$

where Λ_3 is $(J-2)\times(J-2)$ matrix. Let c_{ij} be the (i, j)-components of $\mathbf{P}^{-1}$. We define a square symmetric matrices $\mathbf{B}_k = (b_{kij})(k = 1, 2)$ by $b_{kij} = (c_{ki}a_{ij} + a_{ji}c_{kj})/2$. Denoting by $\boldsymbol{\Phi}$ and $\boldsymbol{\Psi}$, respectively, the diagonal matrices whose (i, i)-components are ϕ_i and ψ_i, we have a quantity K as

$$\begin{aligned} K = &-(\boldsymbol{\phi}'\mathbf{B}_1 + \boldsymbol{\psi}'\mathbf{B}_2)\{(\mathbf{U}_0\mathbf{A})^{-1} + (1/2)(-4N^2\mathbf{D} + \mathbf{U}_0\mathbf{A})^{-1}\}(1/4)(\boldsymbol{\Phi}\mathbf{A}\boldsymbol{\phi} + \boldsymbol{\Psi}\mathbf{A}\boldsymbol{\psi}) \\ &- \mathrm{Re}[\{(\boldsymbol{\phi}'\mathbf{B}_1 - \boldsymbol{\psi}'\mathbf{B}_2) + i(\boldsymbol{\psi}'\mathbf{B}_1 + \boldsymbol{\phi}'\mathbf{B}_2)\} \\ &\cdot \{(-2i\omega_0 + \mathbf{U}_0\mathbf{A})^{-1} + (1/2)(-2i\omega_0 - 4N^2\mathbf{D} + \mathbf{U}_0\mathbf{A})^{-1}\} \\ &+ (1/8)(\boldsymbol{\Phi} - i\boldsymbol{\Psi})\mathbf{A}(\boldsymbol{\phi} - i\boldsymbol{\psi}). \end{aligned} \tag{2.6}$$

If $K < 0$, the bifurcating solution is stable, while if $K > 0$, it is unstable.

3. Examples

In this section we show, by giving examples, that the system (2.2) and (2.3) with intra-specific competition can really have a stable spatio-temporal oscillation Hopf-bifurcating from the spatially constant equilibrium $\mathbf{u}_0$, under the ecologically plausible assumptions on its interspecific interactions. We also give some considerations on the behavior of the solutions.

Example 1 (1 predator–2 prey case)

Consider the case:

$$\mathbf{D} = \begin{pmatrix} 316 & & \\ & 316 & \\ & & 2844 \end{pmatrix}, \quad \mathbf{G} = \begin{pmatrix} 0 & & \\ & 0 & \\ & & 1 \end{pmatrix},$$

$$\mathbf{u}_0 = \begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix}, \quad \mathbf{A} = \begin{pmatrix} -632 & 10\,112 & 2212 \\ -15\,800 & -948 & -9401 \\ -2528 & -12\,008 & -8532 \end{pmatrix}.$$

The first species $\mathbf{S}_1$ is predator while the second $\mathbf{S}_2$ and the third $\mathbf{S}_3$ are preys. The two preys are competing. In this competition, $\mathbf{S}_3$ always goes to extinction in the absence of the predator. Since the existence of the predator relaxes this competition, the system has unique stable constant coexisting equilibrium $\mathbf{u}_0$ for $\mu < 0$. We also remark that the parameters are set so that each prey can thrive by itself, while the predator cannot survive in the absence of its prey.

The characteristic equation (2.5) obtained from $\mathbf{u}_0$ is

$$\begin{aligned}\det(\lambda\mathbf{I}+N^2(\mathbf{D}+\mu\mathbf{G})-\mathbf{U}_0\mathbf{A}) = {} & \lambda^3+\{(3476+\mu)N^2+10\,112\}\lambda^2 \\ & +316\{(6004+2\mu)N^4 \\ & +(32\,864+5\mu)N^2+210\,614\}\lambda \\ & +99\,856\{(2844+\mu)N^6+(22\,752+5\mu)N^4 \\ & +(4\,270\,582+1606\mu)N^2+6\,431\,548\}=0.\end{aligned}$$

The bifurcating solution is given by

$$\begin{aligned}\mathbf{u} = {} & \mathbf{u}_0+\varepsilon^2\{(-83\,424, -39\,685, 74\,260)'\cos(158\sqrt{3158}t-t_0) \\ & +\sqrt{3158}(-316, 1343, -316)'\sin(158\sqrt{3158}t-t_0)\}\cos x+O(\varepsilon^3). \end{aligned} \tag{3.1}$$

Using these values, the K in (2.6) is given by $K=-1.03314596\cdots\times 10^{12}$, and the $\mathbf{u}$ is stable.

Let us rewrite (3.1) into the following from:

$$\begin{aligned}\mathbf{u} = \mathbf{u}_0+\varepsilon^2(& 85\,293.0\ldots\cos(158\sqrt{3158}t+2.931\,85\ldots-t_0), \\ & 85\,256.5\ldots\cos(158\sqrt{3158}t-2.054\,61\ldots-t_0), \\ & 76\,353.7\ldots\cos(158\sqrt{3158}t+0.234\,724\ldots-t_0))'\cos x \\ +O(\varepsilon^3). & \end{aligned} \tag{3.2}$$

From (3.2) one sees that the species pass the peaks of their prosperity in the order of $\mathrm{S}_3, \mathrm{S}_2, \mathrm{S}_1, \mathrm{S}_3, \ldots$. This ordering is the only one which satisfies the plausible condition that S_2 supersedes S_3. Numerical computations show that stable large amplitude oscillations exist for larger values of μ. We give the portrait of the $\mathbf{u}$ for $\mu=6$ in Fig. 1. One can check that the ordering $\mathrm{S}_3, \mathrm{S}_2, \mathrm{S}_1$ is also valid in this case.

Example 2 (2 predator–1 prey case)

$$\mathbf{D}=\begin{pmatrix}180 & & \\ & 90 & \\ & & 1440\end{pmatrix}, \quad \mathbf{D}=\begin{pmatrix}0 & & \\ & 0 & \\ & & 1\end{pmatrix},$$

$$\mathbf{u}_0=\begin{pmatrix}1\\1\\1\end{pmatrix}, \quad \mathbf{A}=\begin{pmatrix}-90 & -450 & -180\\ 17\,280 & -270 & -5940\\ 3780 & -1337 & -2160\end{pmatrix}.$$

The first species is prey while the other two species are predators. The system has unique stable constant equilibrium solution $\mathbf{u}_0$. The characteristic equation

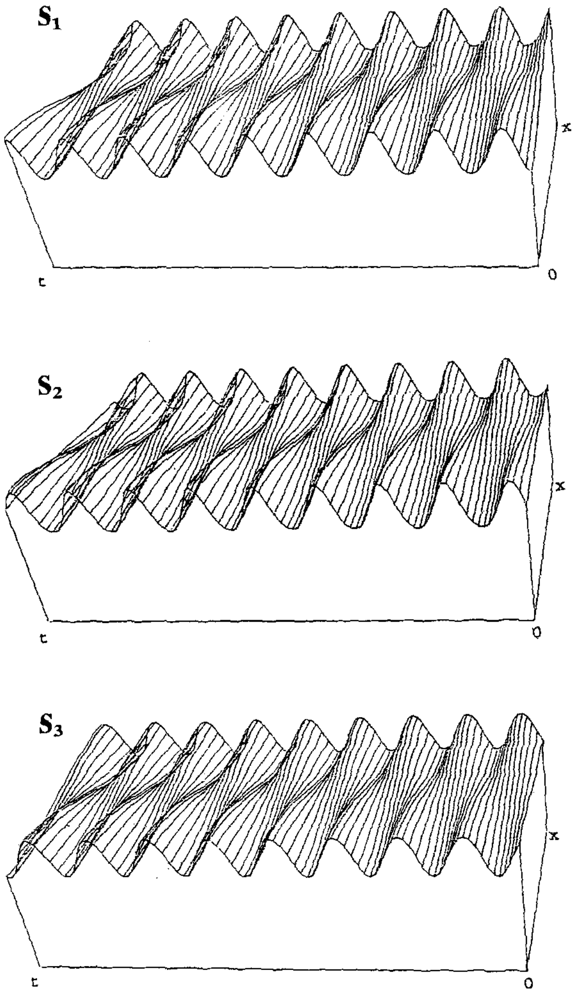

Fig. 1. Portrait of the Hopf-bifurcating solution of Example 1 when $\mu = 6$.

(2.5) obtained from $\mathbf{u}_0$ is

$$\det(\lambda \mathbf{I} + N^2(\mathbf{D} + \mu \mathbf{G}) - \mathbf{U}_0\mathbf{A}) = \lambda^3 + \{(1710 + \mu)N^2 + 2520\}\lambda^2 + 90\{(4500 + 3\mu)N^4 + (12\,870 + 4\mu)N^2 + 14\,628\}\lambda + 8100\{(2800 + 2\mu)N^6 + (14\,400 + 7\mu)N^4 + (1\,232\,916 + 963\mu)N^2 + 253\,710\} = 0.$$

The bifurcating solution is given by

$$\mathbf{u} = \mathbf{u}_0 + \varepsilon^2((24\,150, -43\,650, 46\,235)' \cos(6\sqrt{79\,995}t - t_0) + \sqrt{79\,995}(10, 330, -35)' \sin(6\sqrt{79\,995}t - t_0)) + O(\varepsilon^3).$$

$$
\begin{aligned}
&= \mathbf{u}_0 + \varepsilon^2(24\,315.0\ldots\cos(6\sqrt{79\,995}t - 0.116\,58\ldots - t_0),\\
&\qquad 103\,037.7\ldots\cos(6\sqrt{79\,995}t - 2.0082\ldots - t_0),\\
&\qquad 47\,282.8\ldots\cos(6\sqrt{79\,995}t + 0.210\,92\ldots - t_0))'\cos x\\
&\quad + O(\varepsilon^3).
\end{aligned}
$$

Using these values, one sees that the value of $K = -2.668\,883\,094\ldots\times 10^{10}$ assures the stability of $\mathbf{u}$, and that the species pass the peaks of their prosperity in the order of $\mathbf{S}_1$, $\mathbf{S}_2$, $\mathbf{S}_3$, $\mathbf{S}_1, \ldots$.

Example 3 (4 species case)

Elementary calculations show that Hopf bifurcation never takes place in the 3 species competitive system. However, it takes place in the 4 species system. Consider the case:

$$
\mathbf{D} = \begin{pmatrix} 1 & & & \\ & 1 & & \\ & & 2 & \\ & & & 12 \end{pmatrix}, \quad \mathbf{G} = \begin{pmatrix} 0 & & & \\ & 0 & & \\ & & 0 & \\ & & & 1 \end{pmatrix},
$$

$$
\mathbf{u}_0 = \begin{pmatrix} 1 \\ 1 \\ 1 \\ 1 \end{pmatrix}, \quad \mathbf{A} = \begin{pmatrix} -15-\beta & -13 & -30 & -21 \\ -42 & -29-\beta & -36 & -18 \\ -18 & -34 & -32-\beta & -28 \\ -5 & -17 & -27 & -26-\beta \end{pmatrix},
$$

where $\beta = 0.722\,875\,71\ldots$. In this system all the species are competing. In particular, the third species $\mathbf{S}_3$ expels the fourth species $\mathbf{S}_4$ in the absence of the other species. Similarly, the second species $\mathbf{S}_2$ expels $\mathbf{S}_3$, and the first $\mathbf{S}_1$ expels $\mathbf{S}_2$, while $\mathbf{S}_1$ and $\mathbf{S}_4$ coexist in the absence of the other species. The total system has unique stable constant equilibrium $\mathbf{u}_0$ for $\mu<0$. The characteristic equation (2.5) obtained from $\mathbf{u}_0$ is

$$
\begin{aligned}
\det(\lambda\mathbf{I} + N^2(\mathbf{D}+\mu\mathbf{G}) - \mathbf{U}_0\mathbf{A}) &= \lambda^4 + \{(16+\mu)N^2 + 104.891\}\lambda^3\\
&\quad + \{(53+4\mu)N^4 + (1246.69 + 78.1686\mu)N^2\\
&\quad + 566.335\}\lambda^2\\
&\quad + \{(62+5\mu)N^6 + (2678.62 + 201.783\mu)N^4\\
&\quad + (-2053.66 - 355.555\mu)N^2 + 12\,384.8\}\\
&\quad + \{(24+2\mu)N^8 + (1536.81 + 123.614\mu)N^6\\
&\quad + (-3458.38 - 434.226\mu)N^4\\
&\quad + (165\,854.04 + 13\,394.5\mu)N^2 + 26\,150.6\} = 0.
\end{aligned}
$$

The bifurcating solution is

$$\begin{aligned}\mathbf{u} &= \mathbf{u}_0 + \varepsilon^2((-0.326\,786, 1, -0.334\,960, -0.274\,405)' \cos(10.3984t - t_0) \\ &\quad + (0.795\,896, 0, -0.846\,634, 0.413\,870)' \sin(10.3984t - t_0)) \\ &\quad + O(\varepsilon^3) \\ &= \mathbf{u}_0 + \varepsilon^2(0.860\,371 \cos(10.3984t - 1.960\,39 - t_0), \cos(10.3984t - t_0), \\ &\qquad 0.910\,487 \cos(10.3984t + 1.947\,53 - t_0), \\ &\qquad 0.496\,574 \cos(10.3984t - 2.156\,27 - t_0))' \\ &\quad + O(\varepsilon^3).\end{aligned}$$

Using these values, one sees that the value of $K = -1.089\,352\,7\ldots$ assures the stability of $\mathbf{u}$, and that the species pass the peaks of their prosperity in the order of $S_4, S_3, S_2, S_1, S_4, \ldots$. We remark that this order is compatible with the interspecific relations which we mentioned above. We also remark that the phase shift between the coexisting pair S_4 and S_1 is rather small, which is also plausible.

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