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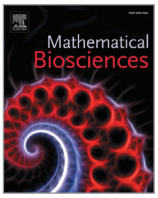

The diffusive Lotka–Volterra predator–prey system with delay

K.S. Al Noufaey[a], T.R. Marchant[b,*], M.P. Edwards[b]

[a] Mathematics and Statistics Department, Faculty of Science, University of Taif, Taif, Saudi Arabia
[b] School of Mathematics and Applied Statistics, The University of Wollongong, Wollongong, N.S.W. 2522, Australia

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ABSTRACT

Semi-analytical solutions for the diffusive Lotka–Volterra predator–prey system with delay are considered in one and two-dimensional domains. The Galerkin method is applied, which approximates the spatial structure of both the predator and prey populations. This approach is used to obtain a lower-order, ordinary differential delay equation model for the system of governing delay partial differential equations. Steady-state and transient solutions and the region of parameter space, in which Hopf bifurcations occur, are all found. In some cases simple linear expressions are found as approximations, to describe steady-state solutions and the Hopf parameter regions. An asymptotic analysis for the periodic solution near the Hopf bifurcation point is performed for the one-dimensional domain. An excellent agreement is shown in comparisons between semi-analytical and numerical solutions of the governing equations.

1. Introduction

Population models, which are used in a variety of biological and ecological applications, have been studied extensively for many decades. It is often important that these models include both time-delay and spatial diffusion to reflect the dynamic behaviour of the models, based on past history, and the trend of a species to migrate to the least densely populated areas. Delay reaction–diffusion models, which display oscillatory solutions, can describe the lagged response to past behaviour and the spatial structure of certain chemical, biological and ecological systems. Some examples include the delayed logistic diffusion equation which represents the general framework of the growth dynamics of a single species and the delayed diffusive Lotka–Volterra predator–prey systems for multiple population models [4,9,21].

Lotka and Volterra [15] proposed a model for predator–prey systems to describe the population of sharks and fish in the Adriatic Sea during World War I. This model can also be used to describe chemical reactions and physical systems such as resonantly coupled lasers [11,15]. Many theoretical and experimental studies have considered the stability of the Lotka–Volterra predator–prey model. For example, Faria [8] considered the system with one and two delays. They studied the effect of diffusion and obtained the stability of the positive equilibrium and the location of Hopf bifurcation points. Yan and Chu [22] analysed the stability for a delayed Lotka–Volterra predator–prey system and found conditions for oscillatory solutions to occur. They also examined the stability of the oscillatory solutions.

Chen et al. [5] considered the diffusive Lotka–Volterra predator–prey system with two delays. By analyzing the characteristic equations, the authors investigated the stability of Hopf bifurcations and the coexistence equilibrium. They found that the positive equilibrium point of the system could be destabilized through a Hopf bifurcation as the delay increases in magnitude. Shenghu [20] studied the dynamics of the diffusive Lotka–Volterra predator–prey model with prey-stage structure. They showed the effect of large diffusion rates on the existence of the positive steady states. A large diffusion rate for the prey species can lead to the destruction of spatial patterns while a large diffusion rate for the predator species preserves spatial patterns. Galiano et al. [10] examined the Lotka–Volterra predator–prey model with cross-diffusion terms numerically and analytically. The authors proved the existence of a global weak solution in any number of space dimensions. Also, the numerical results for the 1-D domain were shown, underlining the effects of segregation of the species. Zhang and Zhao [23] considered a delayed diffusive three species Lotka–Volterra system and analysed the Hopf bifurcations of the system. These also presented numerical solutions of stable and oscillatory solutions to illustrate the effects of both delay and diffusion.

Usually, a system of ordinary differential equations (ODEs) can be analysed by standard techniques. However reaction–diffusion equations are also important in many physically relevant modelling scenarios and are not so easily analysed. Marchant [16] considered semi-analytical solutions for the Gray & Scott cubic autocatalytic model in a reaction–diffusion cell. The governing partial differential equation

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[*] Corresponding author. Tel.: +61 2 4221 3845; fax: +61 2 4221 4845.
E-mail address: tim_marchant@uow.edu.au, tim@uow.edu.au (T.R. Marchant).

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(PDE) model was approximated by a lower-order ODE model, using the Galerkin method of averaging. The ODE model was analysed using various techniques from combustion theory which allowed bifurcation diagrams and Hopf bifurcation parameter maps to be found. An excellent comparison between the results of the semi-analytical method and the numerical solutions of the governing PDEs was found. The Galerkin averaging method has been applied to various other problems including a class of generalized diffusive logistic delay equations [2], the reversible Selkov model with feedback delay [3] and extensions to the Gray–Scott model such as Michaelis–Menten decay [17].

Fagan et al. [7] explored the importance of habitat edge effects, or boundary conditions, on species interactions and illustrated a number of scenarios using diffusive Lotka–Volterra equations. They gave physical examples of the different types of boundary conditions and related them to mathematical definitions. Scenarios considered included edge induced changes to migration patterns and mortality, cross-boundary subsidies and new types of interactions.

In this paper, the Lotka–Volterra predator–prey model with two delays is examined in both 1-D and 2-D domains where the Galerkin method is used to develop semi-analytical solutions. In Section 2, governing equations are presented and the Galerkin method is used to obtain the delay differential equations (DDEs) which represent the semi-analytical model. In Section 3, the steady-state concentration profiles and response diagrams are presented and described in detail. In Section 4, a local stability analysis of the semi-analytical model is performed. The Hopf points are found and the parameter region in which Hopf bifurcations occur is identified. In Section 5, the periodic solution near the Hopf bifurcation is developed for the semi-analytical DDE model for the 1-D domain. Comparisons are made throughout the paper between the semi-analytical results and numerical solutions of the governing PDEs.

2. The semi-analytical model

2.1. The governing equations

The Lotka–Volterra predator–prey model with two delays is considered in 1-D and 2-D domains. The governing PDEs and boundary conditions in 2-D are

$$\begin{aligned} u_t &= D_1(u_{xx}+u_{yy}) + u(\alpha - \gamma_1 u - \delta_1 v(t-\tau_1)),\\ v_t &= D_2(v_{xx}+v_{yy}) + v(-\beta + \gamma_2 u(t-\tau_2) - \delta_2 v), \end{aligned} \tag{1}$$

$$\begin{aligned} &u_x = v_x = 0,\ \text{at}\ x=0,\ u_y = v_y = 0,\ \text{at}\ y=0,\ u = v = 0,\\ &\text{at}\ x = y = 1, u = u_\phi,\ \text{at}\ -\tau_2 < t \le 0\ \text{and}\ v = v_\phi\ \text{at}\ -\tau_1 < t \le 0. \end{aligned} \tag{2}$$

The system (1) is in non-dimensional form with the scaled concentrations of the prey population density, u, and the predator population density, v. The 1-D system is the natural simplification of (1), where there are no y-variations. The boundary conditions at $x = y = 0$ are zero-flux Neumann boundary conditions while at $x = y = 1$ fixed population, Dirichlet boundary conditions are applied. Hence, it is an open system which allows the existence of steady-state solutions and sustained periodic oscillations. At $x = y = 0$ the zero-flux boundary conditions can either be interpreted as an impermeable boundary, which the species cannot cross or a simple symmetry condition. Fagan et al. [7] refers to this type of boundary condition as a “fence effect” and gives an example of the edges between old growth forests and clear-cuts as a boundary red-backed voles will not cross. As a fixed zero population boundary condition is applied at $x = y = 1$ the region beyond can be interpreted as lethal to the species. Fagan et al. [7] gives examples of the applicability of Dirichlet boundary condition such as Bison crossing national park boundaries (outside of which they are shot) and beetles crossing into cleared land (where they die of desiccation).

The system has ten other parameters; α and β represent the growth rate of the prey species and the death rate of the predator species, respectively. The parameters γ_1 and δ_2 are the carrying capacity of the prey u and the predator v populations. δ_1 is the decrease in the population of the prey due to the predator presence, while γ_2 denotes the growth in the population of predator, due to the existence of the prey. The parameters τ_1 and τ_2 represent the hunting and predator maturation delays. The parameters D_1 and D_2 are the diffusion coefficients of the two species u and v. Note that all parameters are positive for physically realistic population models.

Numerical solutions of (1) and (2) are found using a Crank–Nicholson finite-difference scheme with accuracy of $O(\Delta t,\ \Delta x^2)$, while a fourth-order Runge–Kutta method is used to solve the DDE models.

2.2. The Galerkin method

The Galerkin method is used to obtain the semi-analytical model for the Lotka–Volterra predator–prey model (1) in 1-D and 2-D domains. This method assumes a spatial structure of the population density profiles, allowing the governing PDEs (1) and boundary conditions (2) to be approximated by a set of lower-order ODEs. The expansion

$$\begin{aligned} u(x,t) &= u_1(t)\cos\left(\frac{1}{2}\pi x\right) + u_2(t)\cos\left(\frac{3}{2}\pi x\right),\\ v(x,t) &= v_1(t)\cos\left(\frac{1}{2}\pi x\right) + v_2(t)\cos\left(\frac{3}{2}\pi x\right), \end{aligned} \tag{3}$$

is used which represents a two-term method in the 1-D spatial domain. Expansion (3) satisfies the boundary conditions (2), but not the governing PDEs. The form of basis functions (3) also has the property that the concentrations at the impermeable boundary $x = 0$ are $u = u_1 + u_2$ and $v = v_1 + v_2$. The free parameters in (3) are found by evaluating averaged versions of the governing equations, weighted by the basis functions. This process gives the following DDEs

$$\begin{aligned} \frac{du_1}{dt} &= -\frac{\pi^2 D_1 u_1}{4} - \frac{8\gamma_1 u_1^2}{3\pi} - \frac{16\gamma_1 u_1 u_2}{15\pi} + \alpha u_1 - \frac{8\delta_1 u_1 v_{1d}}{3\pi}\\ &\quad - \frac{8\delta_1 u_1 v_{2d}}{15\pi} - \frac{8\delta_1 u_2 v_{1d}}{15\pi} - \frac{72\delta_1 u_2 v_{2d}}{35\pi} - \frac{72\gamma_1 u_2^2}{35\pi},\\ \frac{dv_1}{dt} &= -\frac{\pi^2 D_2 v_1}{4} - \frac{8\delta_2 v_1^2}{3\pi} - \frac{16\delta_2 v_1 v_2}{15\pi} - \beta v_1 + \frac{8\gamma_2 v_1 u_{1d}}{3\pi}\\ &\quad + \frac{8\gamma_2 v_1 u_{2d}}{15\pi} + \frac{8\gamma_2 v_2 u_{1d}}{15\pi} + \frac{72\gamma_2 v_2 u_{2d}}{35\pi} - \frac{72\delta_2 v_2^2}{35\pi},\\ \frac{du_2}{dt} &= -\frac{9\pi^2 D_1 u_2}{4} - \frac{8\gamma_1 u_1^2}{15\pi} - \frac{144\gamma_1 u_1 u_2}{35\pi} + \alpha u_2 - \frac{8\delta_1 u_1 v_{1d}}{15\pi}\\ &\quad + \frac{8\gamma_1 u_2^2}{9\pi} - \frac{72\delta_1 u_2 v_{1d}}{35\pi} - \frac{72\delta_1 u_1 v_{2d}}{35\pi} + \frac{8\delta_1 u_2 v_{2d}}{9\pi},\\ \frac{dv_2}{dt} &= -\frac{9\pi^2 D_2 v_2}{4} + \frac{8\delta_2 v_2^2}{9\pi} - \frac{144\delta_2 v_1 v_2}{35\pi} - \beta v_2 + \frac{72\gamma_2 v_2 u_{1d}}{35\pi}\\ &\quad - \frac{8\delta_2 v_1^2}{15\pi} + \frac{8\gamma_2 v_1 u_{1d}}{15\pi} + \frac{72\gamma_2 v_1 u_{2d}}{35\pi} - \frac{8\gamma_2 v_2 u_{2d}}{9\pi}, \end{aligned} \tag{4}$$

where $u_{id} = u_i(t-\tau_2)$ and $v_{id} = v_i(t-\tau_1),\ i = 1, 2$. The DDEs (4) are obtained by truncating the series (3) after two terms. It is found that a two-term method produces superior accuracy without excessive expression swell. The one-term solution (when $u_2 = v_2 = 0$) is also calculated for comparison purposes. The accuracy of the one and two-term series solutions can be estimated using Richardson extrapolation, see Nelson et al. [19] for an example of error estimation for a reaction–diffusion equation governing self-heating in compost piles. For the 2-D spatial domain, the expansion