Original articles

# Stability analysis and finite volume element discretization for delay-driven spatio-temporal patterns in a predator–prey model

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## Abstract

Time delay is an essential ingredient of spatio-temporal predator–prey models since the reproduction of the predator population after predating the prey will not be instantaneous, but is mediated by a constant time lag accounting for the gestation of predators. In this paper we study a predator–prey reaction–diffusion system with time delay, where a stability analysis involving Hopf bifurcations with respect to the delay parameter and simulations produced by a new numerical method reveal how this delay affects the formation of spatial patterns in the distribution of the species. In particular, it turns out that when the carrying capacity of the prey is large and whenever the delay exceeds a critical value, the reaction–diffusion system admits a limit cycle due to the Hopf bifurcation. This limit cycle induces the spatio-temporal pattern. The proposed discretization consists of a finite volume element (FVE) method combined with a Runge–Kutta scheme.

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## 1. Introduction

### 1.1. Scope

The effect of time delay is fundamental in continuous models of populations of single or multiple species whenever the growth rate of a population does not respond instantaneously to changes in population size. One of the first models with delay was proposed by Volterra [55], who took into account the delay in response of a population's death rate to changes in population density caused by an accumulation of pollutants in the past. Further causes of response delays include differences in resource consumption with respect to age structure, migration and diffusion of populations, gestation and maturation periods, delays in behavioral response to environmental changes, and dependence of a population on a food supply that requires time to recover from grazing [7]. Within epidemic models, time delays

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describe the incubation periods of infectious diseases, the infection periods of infective members, and the periods of recovered individuals with immunity [57]. More generally, the main expected consequence of including time delay is oscillatory solution behavior [41].

In this work we are interested in criteria for the formation, and numerical methods for the efficient simulation, of spatio-temporal patterns described by a predator–prey model with time delay and diffusion. The model is given by the following initial–boundary value problem for a pair of reaction–diffusion equations, the second of them with a delay term:

$$\partial_t u_1 - d_1 \Delta u_1 = u_1(a_1 - b_{11}u_1 - b_{12}u_2), \quad (\boldsymbol{x}, t) \in \Omega \times \mathcal{T}, \tag{1.1a}$$

$$\partial_t u_2 - d_2 \Delta u_2 = u_2(-a_2 + b_{21}(u_1)_\tau - b_{22}u_2), \quad (\boldsymbol{x}, t) \in \Omega \times \mathcal{T}, \tag{1.1b}$$

$$\partial_{\boldsymbol{n}} u_1 = \partial_{\boldsymbol{n}} u_2 = 0, \quad (\boldsymbol{x}, t) \in \Sigma_{\mathcal{T}}, \tag{1.1c}$$

$$u_1(\boldsymbol{x}, t) = \psi_1(\boldsymbol{x}, t), \quad u_2(\boldsymbol{x}, t) = \psi_2(\boldsymbol{x}, t), \quad (\boldsymbol{x}, t) \in \Omega_\tau. \tag{1.1d}$$

The model is posed on a finite time interval $\mathcal{T} := (0, T)$ for a fixed final time $T > 0$, and where $\Sigma_{\mathcal{T}} := (\partial \Omega) \times \mathcal{T}$, $\Omega_\tau := \Omega \times [-\tau, 0]$, and $\partial_{\boldsymbol{n}}$ denotes the directional derivative with respect to the outer normal vector $\boldsymbol{n}$ of the boundary $\partial \Omega$ of $\Omega$. Here $u_1 = u_1(\boldsymbol{x}, t)$ and $u_2 = u_2(\boldsymbol{x}, t)$ are the sought densities of the prey and the predator, respectively. The right-hand side of (1.1b) includes the delay term $(u_1)_\tau := u_1(\boldsymbol{x}, t - \tau)$, where the constant $\tau > 0$ is the delay. The delay in (1.1b) can be regarded as a gestation period (roughly speaking, abundance of prey at time $t$ will influence the growth of the predator population at time $t + \tau$) or reaction time of the predators [48]. The homogeneous Neumann boundary condition (1.1c) indicates zero population flux across $\partial \Omega$. Moreover, the parameters $a_1$ and $a_2$ are, respectively, the growth rate of the prey and the death rate of the predator. Both are assumed strictly positive for sake of the subsequent analysis. In addition $b_{ii}$ ($i = 1, 2$) are the rates of intra-specific competition (assumed nonzero), and $b_{12}$ and $b_{21}$ denote the rates of consumption by predator on prey and mass conversion from prey to predator, respectively. The ratios $a_i/b_{ii}$ ($i = 1, 2$) are environmental carrying capacities, and $d_1$ and $d_2$ are diffusion coefficients of each species.

The first purpose of this paper is to study the spatio-temporal patterns produced by solutions of (1.1) and to examine the onset of oscillatory solution behavior through a Hopf bifurcation with respect to the delay $\tau$ as a bifurcation parameter. The second purpose is to introduce a new numerical method for the solution of (1.1). Our objective here is to explore how delay determines the stability threshold of the steady state of (1.1a), (1.1b). The present analysis reveals that spatio-temporal patterns can be induced by a series of Hopf bifurcation critical points. Specifically, spatio-temporal patterns become possible for supercritical values of delay when the limit cycle appears due to the Hopf bifurcation. To the authors' knowledge, the formation of spatio-temporal patterns as a consequence of delay has not yet been reported in the literature related to spatial patterns. Nevertheless, there is a body of work in investigating pattern formation in reaction–diffusion systems due to the existence of a limit cycle; see, for instance, [36,39].

## 1.2. Related work

Introductions to delay differential equations are given by Kuang [33] and Smith [52]; see also Chapter 8 of McKibben [38]. For general introductions to bifurcation theory we mention [13,27], as well as [28] for Hopf bifurcations. In predator–prey systems, delay effects were first considered by Volterra [56]. He showed that under certain conditions, all solutions possess an oscillatory behavior. In fact, there are many plausible ways to introduce delays into a predator–prey model, see [48] (and the references cited therein) for a survey in the non-spatial setting. For the delayed non-spatial predator–prey model, the asymptotic stability of the equilibrium and the periodicity of the solution were investigated (see [6,16,37], and the references therein). Analyses of non-spatial variants of (1.1) also include [19,31,49,58,62], and references to spatio-temporal pattern formation include, besides [36,39] and the vast list of references in both works, [15,24]. Numerical methods tailored for these kinds of problems can be found in e.g. [2,26]. We here decide to use stable Runge–Kutta (RK) schemes proposed by Koto [32] (see also [29,30]).

For predator–prey models with diffusion, the existence of traveling wave solutions was shown in [40] and [22] for discrete and continuous delays, respectively, although the models differ from (1.1). For (1.1) and related spatio-temporal models, Gourley et al. [25] present a survey of mechanisms where diffusion and time delays may coexist in a system involving nonlocal terms, in such a way that the ability of individuals to be at different points in space, at past times, can be explained. On the other hand, Sen et al. [50] show that the *time* delay may induce *spatial* patterns in the