



## Original Research Article

## Existence and non-existence of spatial patterns in a ratio-dependent predator–prey model

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## ABSTRACT

In this paper, first we consider the global dynamics of a ratio-dependent predator–prey model with density dependent death rate for the predator species. Analytical conditions for local bifurcation and numerical investigations to identify the global bifurcations help us to prepare a complete bifurcation diagram for the concerned model. All possible phase portraits related to the stability and instability of the coexisting equilibria are also presented which are helpful to understand the global behaviour of the system around the coexisting steady-states. Next we extend the temporal model to a spatiotemporal model by incorporating diffusion terms in order to investigate the varieties of stationary and non-stationary spatial patterns generated to understand the effect of random movement of both the species within their two-dimensional habitat. We present the analytical results for the existence of globally stable homogeneous steady-state and non-existence of non-constant stationary states. Turing bifurcation diagram is prepared in two dimensional parametric space along with the identification of various spatial patterns produced by the model for parameter values inside the Turing domain. Extensive numerical simulations are performed for better understanding of the spatiotemporal dynamics. This work is an attempt to make a bridge between the theoretical results for the spatiotemporal model of interacting population and the spatial patterns obtained through numerical simulations for parameters within Turing and Turing–Hopf domain.

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## 1. Introduction

Spatial pattern formation by spatiotemporal models of predator–prey interaction has received significant attention from several researchers during last three decades. Intense research works have been initiated based upon the classical works of Segel and his coworkers (Levin and Segel, 1976; Segel and Jackson, 1972), who had first explained the plankton patchiness based upon the mathematical result, namely, diffusive instability. The concept of diffusive instability was introduced by A. Turing in his seminal work (Turing, 1952) to explain the chemical basis of morphogenesis. Turing explained how small amplitude heterogeneous perturbation from the stable homogeneous steady-state of a reaction–diffusion system can lead to instability, known as diffusive instability, and results in Turing patterns. This concept is utilized to explain the formation of stationary and non-stationary patchy patterns, known as spatial pattern, by the individuals of prey and predator species when we

incorporate their random movement into our modeling approach. The reaction–diffusion models of population interaction are built up to incorporate random mobility of the individuals of species into the modeling approach of interacting populations. Reaction part takes care of intra- and inter-species interactions whereas the random movement of the individuals within their habitat is modeled with the diffusion term. The formation of such models is based upon the Fick's law (Grindrod, 1996). The reaction–diffusion models of population interaction with appropriate initial and boundary conditions are capable to produce spatial patterns due to Turing instability (Murray, 2002; Malchow et al., 2008; Okubo and Levin, 2001). Apart from the stationary Turing pattern formation, the non-stationary and spatiotemporal chaotic patterns are also capable to explain the patchy distribution of the species (Banerjee and Banerjee, 2012; Banerjee and Petrovskii, 2011; Baurmann et al., 2004, 2007; Camara, 2011; Morozov et al., 2004; Petrovskii et al., 2004; Petrovskii and Malchow, 1999; Sherratt et al., 1997, 1995; Tian, 2010; Tian and Zhang, 2013, 2013; Upadhyay et al., 2012).

Initial research on the reaction–diffusion models of predator–prey interaction were focused towards the derivation of Turing instability condition and determination of the resulting stationary

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patterns by perturbing the stable homogeneous steady-state with small heterogeneous perturbations. Most of the time one can find stationary spot pattern (hot spot or cold spot) as a resulting pattern for parameters within the Turing domain (Alonso et al., 2002; Banerjee, 2010; Fasani and Rinaldi, 2011; Sun et al., 2009; Wang et al., 2007; Volpert and Petrovskii, 2009). It is interesting to note that the instability of steady-state for temporal models of predator–prey interaction leads to either oscillatory coexistence state or extinction of one or both the species. However the instability of the homogeneous distribution of the species, due to the movement of the individuals, leads to stationary as well as non-stationary distribution over the space depending upon the intrinsic rate constants and the rates of diffusion. Non-stationary distribution of the species is characterized by periodic, quasi-periodic or chaotic change in the population distribution with the advancement of time. Stationary and non-stationary patterns can be classified as hot spot pattern, cold spot pattern, labyrinthine pattern, stripe pattern, target pattern, spiral pattern, tip-splitting pattern, interacting spiral pattern and chaotic pattern (Banerjee and Banerjee, 2012; Cantrell and Cosner, 2003; Malchow et al., 2008; Shoji et al., 2003; Shoji and Iwasa, 2005; Upadhyay et al., 2010). These wide varieties of patterns are already reported by several researchers based upon their works on reaction–diffusion models of predator–prey interactions (Alonso et al., 2002; Banerjee and Banerjee, 2012; Banerjee and Petrovskii, 2011; Baurmann et al., 2004, 2007; Camara, 2011; Fasani and Rinaldi, 2011; Petrovskii et al., 2004; Petrovskii and Malchow, 1999; Sherratt et al., 1997; Wang et al., 2007). Interestingly one can find only spot pattern for parameter values lying within the Turing domain only and rest of the patterns appears for parameter values within the Turing–Hopf domain, outside the Turing domain and also as a result of specific choices of initial condition (Malchow et al., 2008; Medvinsky et al., 2002). It is well-known fact that Turing instability is not the only mechanism for spatial patterns rather biological invasion, turbulence, travelling wave, periodic travelling wave are also responsible mechanisms (Malchow et al., 2008; Sherratt and Smith, 2008; Shigesada and Kawasaki, 1997; Volpert et al., 1994). In reality the distribution of population over their habitat is far away from the homogeneous steady-state and hence investigation of spatial patterns due to the arbitrary choice of initial condition (which includes large magnitude perturbation from the homogeneous steady-state (Banerjee, 2011; Riaz et al., 2007)) is not coming under the heading of Turing pattern formation (Banerjee, 2011). As a result the investigations of non-Turing patterns are more realistic from theoretical point of view as well as relevant in the context of ecology.

The conditions for the Turing bifurcation and Turing–Hopf bifurcations can be obtained through local stability analysis around the specific homogeneous steady-state (Wang et al., 2007). These analytical results are unable to predict the generation of spatial patterns due to large spatiotemporal perturbation from the homogeneous steady-state. There exist some analytical techniques to derive mathematical criteria for the stability of homogeneous steady-state and derivation of appropriate conditions for the existence and/or non-existence of non-constant stationary states (Pang and Wang, 2003; Peng and Shi, 2009; Peng et al., 2008; Shi, 2002; Shi et al., 2010; Smoller, 1994; Wang et al., 2011). These techniques are already utilized by the researchers to obtain analytical results for some spatiotemporal models of interacting populations but those results are not cross verified with the scenario of spatial pattern formation for specific choices of the parameters involved with the targeted models. Most of the researchers overlooked this important as well as interesting aspect only due to the complicated nature of the desired analytical results. Another notable issue is that the analytical results involved with the parametric restrictions to be satisfied for the stability of

homogeneous steady-state and the existence of non-constant steady-state are sufficient conditions. These conditions only helpful to understand the long time survival of the species at some positive steady-state.

Based upon the above mentioned facts, in this paper we have considered a spatiotemporal model of predator–prey interaction with ratio-dependent functional response and density dependent death rate for the predator. In Sections 2 and 3, we have described the basic dynamical features of the temporal counterpart to understand the stable and oscillatory coexistence for both the species. Special attention have been paid to study all possible dynamic behaviors those can be exhibited by the solution trajectories of the temporal model with the help of complete global bifurcation analysis. The spatiotemporal model is introduced in Section 4 and we have provided analytical results for the global stability of homogeneous steady-state and obtained the conditions required for the non-existence of non-constant steady-state. Detailed proofs of the analytical results are presented at Appendix. The preliminary results for Turing instability are also discussed in brief. Exhaustive numerical simulations are carried out to obtain the spatiotemporal patterns for parameter values lying within the Turing and Turing–Hopf domain and outcomes are reported in Section 5. Detailed discussions about various results obtained throughout this paper are presented at the discussion section and some future directions are also mentioned.

## 2. Temporal model

The temporal model for predator–prey interaction with ratio-dependent functional response (Akçakaya et al., 1995; Arditi and Ginzburg, 1989; Bandyopadhyay and Chattopadhyay, 2005; Berezovskaya et al., 2001; Hsu et al., 2001; Sen et al., 2012; Xiao and Ruan, 2001) and density dependent death rate for the predator (Bazykin, 1998; Freedman, 1979; Pal et al., 2012) is governed by the following system of nonlinear ordinary differential equations

$$\frac{du}{dt} = u(1 - u) - \frac{\alpha uv}{u + v}, \quad (1a)$$

$$\frac{dv}{dt} = \frac{\beta uv}{u + v} - \gamma v - \delta v^2, \quad (1b)$$

subjected to the positive initial condition  $u(0), v(0) > 0$ . Here  $\alpha, \beta, \gamma$  and  $\delta$  are all dimensionless and positive parameters. Here  $u, v$  are dimensionless variables representing the population densities of the prey and predator and  $t$  stands for dimensionless time. The dimensionless parameters can be interpreted as:  $\alpha$  is the rate of predation,  $\beta$  is growth rate of the predators,  $\gamma$  is linear intrinsic death rate of predator and  $\delta$  is the intra-specific competition rate for the predators. Hence ' $\gamma + \delta v$ ' is the density dependent death rate for the predator.

The above mentioned model (with  $\gamma = 0$ ) is studied in the context of spatiotemporal pattern formation by Baurmann et al. (2007) and then studied by Haque (2009) with a different parametrization. The ratio-dependent functional response is relevant in the situation when the predators have to search for prey and hence have to compete among themselves to search for their food. Hence in this context it is quite relevant to study a ratio-dependent prey–predator model with density dependent death rate for the predator as such kind of death rate is known to regulate or restrict the unlimited growth of the predators (Freedman, 1979; Peet et al., 2005). In some literature (see McGehee and Peacock-Lopez, 2005; McGehee et al., 2008) the quadratic mortality term ( $\delta v^2$ ) is called as mutual interference of predators and higher-order terms are not biologically realistic (Neubert et al., 2004). Various

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