Oscillations and Pattern Formation in a Slow–Fast Prey–Predator System

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Abstract
We consider the properties of a slow–fast prey–predator system in time and space. We first argue that the simplicity of the prey–predator system is apparent rather than real and there are still many of its hidden properties that have been poorly studied or overlooked altogether. We further focus on the case where, in the slow–fast system, the prey growth is affected by a weak Allee effect. We first consider this system in the non-spatial case and make its comprehensive study using a variety of mathematical techniques. In particular, we show that the interplay between the Allee effect and the existence of multiple timescales may lead to a regime shift where small-amplitude oscillations in the population abundances abruptly change to large-amplitude oscillations. We then consider the spatially explicit slow–fast prey–predator system and reveal the effect of different timescales on the pattern formation. We show that a decrease in the timescale ratio may lead to another regime shift where the spatiotemporal pattern becomes spatially correlated, leading to large-amplitude oscillations in spatially average population densities and potential species extinction.

Keywords Slow–fast timescale · Relaxation oscillation · Canard cycle · Spatial pattern · Regime shift

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1 Introduction

In the natural environment, interactions in a population community are usually quite complex (Brown 1994; Kareiva 1990; Turchin 2003). This ubiquitous complexity has several different sources such as the complexity of the wood web, nonlinearity of species feedbacks, and multiplicity of temporal and spatial scales. It is extremely difficult, in fact hardly possible at all to capture the entire complexity of ecological interactions in a single mathematical model or framework. Instead, the usual means of analysis tend to focus on a particular aspect or feature of the ecological system. For instance, while the food web theory endeavors to link the properties of a realistic population community to the complexity of the corresponding food web, in particular by analyzing the web connectivity and revealing the bottlenecks (Allesina and Bodini 2004; Polis and Strong 1996), a lot of attention focuses on the properties of simpler ‘building blocks’ from which the web is made (Jordan et al. 2002). A variety of blocks of intermediate complexity have been considered, a few examples are given by the three-species competition system (Hofbauer and Sigmund 1998), intraguild predation (Holt and Polis 1997) and a three-species resource–consumer–predator food chain (Hastings and Powell 1991).

Arguably, the most basic block is the prey–predator system. It has been a focus of research for almost a century (Rosenzweig and MacArthur 1963; Volterra 1926) and there is a tendency to think about it as a fully studied, textbook material (M. Gyllenberg). However, this is far from true. The apparent mathematical simplicity of the prey–predator system (usually associated with the classical Rosenzweig–MacArthur model as a paradigm (Rosenzweig and MacArthur 1963; Turchin 2003)) is superficial rather than real, and there has recently been a surge of interest and an increase in mathematical modeling literature dealing with its ‘hidden,’ overlooked properties, with more than a hundred of papers published in the first quarter of 2021 alone.1 New properties readily arise as soon as one introduces relatively small (i.e., preserving the defining structure of the model), biologically motivated changes into the paradigmatic system, e.g., adding explicit heterogeneous space (Zou and Guo 2020), changing the specialist predator to a generalist one (Rodrigues et al. 2020; Sen et al. 2020), changing the properties of predator’s functional response (Arditi and Ginzburg 1989; Huang et al. 2014), considering different types of density dependence in the population growth or mortality (Edwards and Brindley 1999; Jiang et al. 2021), or taking into account the fact that the intraspecific dynamics of prey and predator often occur on a very different timescale (Kooi and Poggiale 2018; Poggiale et al. 2020).

While one of the generic properties of a prey–predator system is its intrinsic capability to produce sustained population cycles (due to the emergence of a stable limit cycle in a certain parameter range (May 1972)), with many fundamental implications for the population dynamics, another equally important property is its capacity to exhibit pattern formation, in particular due to the Turing instability (Segel and Jackson 1972; Turing 1952). The latter has been a focus of many groundbreaking studies that linked the patterns observed in various biological and ecological systems to the dissipative instability in a prey–predator (or, more generically, activator–inhibitor) system,

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1 Data are taken from the Web of Science.
e.g., see (Gurney et al. 1998; Hastings et al. 1997; Jansen 1995; McCauley and Murdoch 1990; Mimura and Murray 1978; Murray 1968, 1975, 1976, 1981, 1982, 1988; Rosenzweig 1971), also (Murray 1989) for an exhaustive review of earlier research. Other studies also discovered and considered in detail a possibility of non-Turing pattern formation, in particular due to the interplay between the Hopf bifurcation and diffusion (Pascual 1993; Petrovskii et al. 2001, 2002; Petrovskii and Malchow 1999; Scheffer et al. 1997; Sherratt et al. 1995) as well as pattern formation resulting from the Turing–Hopf bifurcation (Baurmann et al. 2007; Rovinsky and Menzinger 1992; Song et al. 2016).

Interestingly, in spite of the large number of modeling papers concerned with the prey–predator system, there are still a number of issues poorly investigated. Two such issues are the interaction between different types of density dependence and the existence of different timescales, either in a spatial or a non-spatial system. One context where the prey–predation framework has been particularly successful to provide a new insight into the mechanisms of ecological interactions is large-magnitude nearly periodical fluctuations in population size that have been observed in many species and ecosystems. In such a case, typically, a large outbreak in population abundance is followed by a population decline, often to a small population size or density. For instance, fluctuations in populations of snowshoe hares and Canadian lynx in the Canadian Boreal forest where the lynx population explosion was observed every 9–11 years followed by a rapid decline in the hare population was modeled with a tri-trophic food web model (Stenseth et al. 1997). As another example, in a lake plankton ecosystem, a high seasonal abundance of zooplankton (particularly Daphnia) is frequently observed, which completely grazes down the algal biomass thus resulting in clear-water phases in lakes (Scheffer et al. 1997). One common trait observed in the above examples is that the bottom level of a multi-trophic system or the basal prey has much faster growth and decay rates compared to their consumers. A yet another example, the budworm population can increase by a few orders of magnitude over just a few years, whereas their main food source (leaves of adult trees) grows at a much slower rate. This resulted in the outbreak of spruce budworm that destroyed the balsam forest of eastern Northern America (Ludwig et al. 1978). To capture the existence of different timescales in the dynamics of interacting species, mathematical models with slow–fast timescale were introduced (Rinaldi and Muratori 1992).

In mathematical literature, the slow–fast systems are considered as singularly perturbed ordinary differential equation, where $\varepsilon$ is the singular perturbation parameter. A variety of mathematical techniques were developed to study this class of systems. In the late 1970s, Fenichel (1979) introduced a geometric approach based on the invariant manifold theory to study the singularly perturbed coupled systems, known as Geometric Singular Perturbation Theory (GSPT). Using this theory the dynamics of the full slow–fast system are studied by reducing it to sub-systems of lower dimension and thereby studying the complete dynamics of the subsystems. The application of Fenichel’s theory in the context of biology was well explained by Hek (2010). But this theory fails to approximate the dynamics near the non-hyperbolic equilibrium points where the system encounters a singularity. Later in 2001, Krupa and Szomolyan (2001a, b) extended Fenichel’s theory to overcome the difficulty around non-hyperbolic points using the blow-up technique. This was based on the pioneering
work of Dumortier (1978, 1993) and Dumortier and Roussarie (1996). The main idea behind this was to blow up the non-hyperbolic equilibrium points of the system by a four-dimensional unit sphere $S^3$ and the trajectories of the blow-up system are mapped on and around the sphere.

Before the development of mathematical tools to study this class of systems, a Dutch Physicist (Dumortier and Roussarie 1996; Van der Pol 1926) observed large-amplitude periodic oscillation consisting of slow and fast dynamics, which he named relaxation oscillation. These are periodic solutions consisting of slow curvilinear motion and sudden fast jumps. These types of slow–fast limit cycles were later observed in many chemical and biological systems (Kooi and Poggiale 2018; Muratori and Rinaldi 1989; Rinaldi and Muratori 1992; Wang and Zhang 2019a, b). Another type of periodic solution observed in singularly perturbed systems is canard solutions. This was first investigated by Benoit et al. (1981) while studying the Van der Pol Oscillator. Dumortier and Roussarie, in their seminal work (Dumortier and Roussarie 1996), analyzed this phenomenon through a geometric approach, using blow-up technique and with the help of invariant manifold theory. The fast transition from small stable limit cycles appearing through Hopf bifurcation to large-amplitude relaxation oscillation via a sequence of canard cycles within an exponentially small range of the parameter is known as canard explosion. In real-world ecosystems, this phenomenon can be related to sudden outbreak or decline of a particular species (Ludwig et al. 1978; Scheffer et al. 1997, 2000; Siteur et al. 2016; Stenseth et al. 1997).

Over the last few years, several works have been done on prey–predator systems with slow–fast timescale. In Muratori and Rinaldi (1989, 1992) and Rinaldi and Muratori (1992), the authors have analyzed the periodic bursting of high and low-frequency oscillations in interacting population models with two and three-trophic level with slow–fast timescale. The classical Rosenzweig–MacArthur (RM) model in the slow–fast setting is studied in Kooi and Poggiale (2018), where the authors have shown that the RM model exhibits canard explosion in the oscillatory regime of the parameter space. In Poggiale et al. (2020), the authors have used the blow-up technique to obtain an analytical expression of the bifurcation thresholds for which maximal canard solution occurs in the RM-model. The existence and uniqueness of the relaxation oscillation cycle have been studied for the Leslie–Gower model with the help of entry–exit function and GSPT in Wang and Zhang (2019b). The rich and complex slow–fast dynamics of the predator–prey model with Beddington–DeAngelis functional response is studied in Saha et al. (2021).

In spite of considerable previous work done on slow–fast prey–predator systems, to the best of our knowledge, one important issue has been almost completely overlooked—that is, how the system properties may be affected by the presence of the Allee effect. Meanwhile, in population ecology, the Allee effect is a widely observed phenomenon especially at low population density, which describes a positive relationship between species population and per capita population growth rate of species (Dennis 1989; Stephens and Sutherland 1999). The leading causes of Allee effect include difficulties in mate finding, inbreeding depression, cooperative defense mechanism, etc. Courchamp et al. (2008). Mostly, we are concerned about the demographic Allee effect which can be classified as: strong Allee and weak Allee effect. For strong Allee effect, the per capita growth rate is negative below some critical population
density (Allee threshold). Whereas, in case of weak Allee effect, the per capita growth rate is low and remains positive even at low population densities.

In this paper, we intend to bridge this gap. We have incorporated the weak Allee effect in prey’s growth in order to provide a comprehensive study of the slow–fast cycles. The main objective of this paper is to provide a detailed analysis of the slow–fast dynamics of the classical Rosenzweig–MacArthur (RM) model with multiplicative weak Allee effect in prey growth equation. For the non-spatial model, we perform rigorous mathematical analysis using GSPT and blow-up technique. For the spatial extension of the corresponding slow–fast model, the dynamics of traveling waves and corresponding scenarios of pattern formation are investigated numerically. In prey–predator models, the oscillatory dynamics of the system arises from the Hopf bifurcation but in the slow–fast setting other than Hopf bifurcating limit cycle, the system exhibit canard and relaxation oscillation. Here, we explore these solutions analytically and numerically using a variety of sophisticated analytical techniques as discussed above.

This paper is divided into two parts. In the first part, we provide a rigorous mathematical analysis of the non-spatial slow–fast model and in the second part we investigate, by means of extensive numerical simulations, the effect of multiple timescales on the dynamics of traveling waves and associated pattern formation. Specifically, in Sect. 2, we introduce the non-dimensionalized temporal model and standard stability analysis is performed. Then, in Sect. 3 we introduced the slow–fast system. In Sect. 4 we discussed GSPT and blow-up technique for a detailed mathematical analysis of slow–fast systems. The existence and uniqueness of the relaxation oscillation are studied here followed by the phenomenon of canard explosion. In Sect. 5, we consider the corresponding slow–fast spatiotemporal model to examine how the spread of invasive species is affected by timescale parameters. Finally, we draw the conclusion of our work in Sect. 6.

2 Temporal Model and Its Linear Stability Analysis

We consider the classical Rosenzweig–MacArthur prey–predator model with the multiplicative weak Allee effect in prey growth (Courchamp et al. 2008; Murray 1989; Sen et al. 2011). Let $u$ and $v$ be the prey and its specialist predator densities, respectively, at time $t$. For appropriately chosen dimensionless variables and parameters (see Morozov et al. 2006 for details), the model is given by the following equations:

\begin{align}
\frac{du}{dt} &= f(u, v) := \gamma u (1 - u)(u + \beta) - v \left( \frac{u}{1 + \alpha u} \right), \quad (1a) \\
\frac{dv}{dt} &= g(u, v) := v \left( \frac{u}{1 + \alpha u} - \delta \right). \quad (1b)
\end{align}

Here and below, the sign ‘:=’ means ‘is defined’. We focus on the case where the growth rate of the prey population is damped by the weak Allee effect, that is $0 < \beta < 1$. For $\beta < 0$, the Allee effect becomes strong (in this case, the prey population has another (unstable) equilibrium at $u = -\beta/\beta \geq 1$ (Lewis and Kareiva 1993). The
per capita growth rate \( f(u, 0)/u \) is increasing for \( 0 < u < \frac{1 - \beta}{2} \) and decreasing for \( \frac{1 - \beta}{2} < u < 1 \). The predator is a specialist predator as they do not have any alternative food source to survive apart from \( u \). The prey-dependent functional response is taken to be Holling type II (Holling 1965). The system contains four positive dimensionless parameters where \( \beta \) quantifies the weak Allee effect parameter, \( \gamma \) is the coefficient proportional to the maximum per capita growth rate of prey, called characteristic growth rate (Jankovic and Petrovskii 2014). The parameter \( \alpha \) characterizes the inverse saturation level of the functional response and \( \delta \) is the natural mortality rate of the predator. Throughout this paper we will consider \( \delta \) as the bifurcation parameter to determine the stability conditions of the coexisting steady state for the model (1).

Depending on the species traits, the prey population often grows much faster than its predator; one well known example is given by hare and lynx where hares reproduce much faster than lynx (Stenseth et al. 1997). This motivated researchers to introduce a small timescale parameter \( \varepsilon \), \( 0 < \varepsilon < 1 \) in the basic model (1). The parameter \( \varepsilon \) is interpreted as the ratio between the linear death rate of the predator and the linear growth rate of the prey (Hek 2010; Rinaldi and Muratori 1992). The assumption \( \varepsilon < 1 \) implies that one generation of predator can encounter several generations of prey (Holling 1965; Kuehn 2015). Therefore, considering the difference in the timescale, the slow–fast version of the dimensionless model (1) can be written as

\[
\frac{du}{dt} = f(u, v) = \gamma u(1 - u)(u + \beta) - \frac{uv}{1 + \alpha u}, \tag{2a}
\]
\[
\frac{dv}{dt} = \varepsilon g(u, v) = \varepsilon v\left(\frac{u}{1 + \alpha u} - \delta\right), \tag{2b}
\]

with initial conditions \( u(0) \geq 0, v(0) \geq 0 \). Since the prey population grows faster compared to the predator, \( u \) and \( v \) are referred to as fast and slow variables, respectively, and time \( t \) is called fast time. The equilibrium points for the system are independent of \( \varepsilon \), thus system (1) and (2) has same equilibrium points. The extinction equilibrium point and prey only equilibrium point of system (1) (as well as for (2)) are given by \( E_0 = (0, 0) \) and \( E_1 = (1, 0) \), respectively. The interior equilibrium point \( E_*(u_*, v_*) \) of the system is the point where the non-trivial prey nullcline intersect with non-trivial predator nullcline in the interior of the positive quadrant, and we have,

\[ u_* = \frac{\delta}{1 - \alpha \delta}, \quad v_* = \gamma (1 - u_*)(u_* + \beta)(1 + \alpha u_*). \]

\( E_* \) is feasible if the parametric restriction \( \delta(\alpha + 1) < 1 \) holds. With the help of linear stability analysis, we find \( E_0 \) is always a saddle point. \( E_1 \) is stable for \( \delta > \frac{1}{1 + \alpha} \) and saddle point for \( \delta < \frac{1}{1 + \alpha} \). \( E_* \) bifurcates from predator free equilibrium point \( E_1 \) through transcritical bifurcation at \( \delta = \delta_T \equiv \frac{1}{1 + \alpha} \).
Fig. 1 The bifurcation diagram of system (1) using $\delta$ as the bifurcation parameter shown for two different values of $\beta$ and other parameters as $\alpha = 0.5$, $\gamma = 3$. Here, the blue solid curve shows either the stable steady state (for $\delta > \delta_H$) or the size of the stable limit cycle (for $\delta < \delta_H$), the solid red line shows the semitrivial 'prey-only' state in the range where it is a saddle (hence unstable), and the dashed red line shows the unstable coexistence steady state (Color figure online).

Now evaluating the Jacobian matrix for the system (2) at the interior equilibrium point $E^*_\ast (u^*_\ast, v^*_\ast)$ we have

$$J^*_\ast = \begin{pmatrix} \gamma(u^*_\ast(2 - 3u - 2\beta) + \beta) - \frac{v^*_\ast}{(1 + u^*_\ast\alpha)^2} & -\frac{u^*_\ast}{1 + u^*_\ast\alpha} \\ \frac{v^*_\ast}{(1 + u^*_\ast\alpha)^2} & \frac{1}{1 + u^*_\ast\alpha^2} \end{pmatrix}.$$

From the feasibility condition of $E^*_\ast$, we always have $\text{Det}(J^*_\ast) > 0$. The interior equilibrium point is stable if $\text{Tr}(J^*_\ast) < 0$, and it loses its stability via super-critical Hopf bifurcation when $\text{Tr}(J^*_\ast) = 0$ and is unstable for $\text{Tr}(J^*_\ast) > 0$. The Hopf threshold $\delta = \delta_H$ can be obtained by solving $\text{Tr}(J^*_\ast) = 0$ which on simplification gives

$$\delta_H = \frac{1 + \alpha^2 \beta - \sqrt{1 + \alpha + \alpha^2 - \alpha \beta + \alpha^2 \beta + \alpha^2 \beta^2}}{\alpha(-1 - \alpha + \alpha \beta + \alpha^2 \beta)}.$$

Transversality condition for Hopf bifurcation is satisfied at $\delta = \delta_H$. The coexistence steady state $E^*_\ast (u^*_\ast, v^*_\ast)$ is stable for $\delta > \delta_H$ and it destabilizes for $\delta < \delta_H$, surrounded by a stable limit cycle. The bifurcation diagrams of the system (1) with $\delta$ as bifurcation parameter and for two different values of $\beta$ are plotted in Fig. 1. It is readily seen that, in case $\beta < 1/\alpha$, with an increase in the Allee threshold $\beta$ (hence making the Allee effect weaker) the Hopf bifurcation point shifts to the left. Correspondingly, the coexistence occurs for a broader parameter range of $\delta$ (see Fig. 1). Furthermore, with the increase in $\beta$ the size of the limit cycle is reduced. Increase in the strength of the weak Allee effect not only enhance the stable coexistence rather reduces the amplitude of stable oscillatory coexistence.

Interestingly, the linear stability results remain unaltered in the presence of slow–fast timescale as the analytical conditions are independent of $\varepsilon$. The linear stability analysis fails to capture the complete dynamics of the slow–fast system (2) for $0 <$
\( \varepsilon \ll 1 \). The system (2) exhibits catastrophic transition which cannot be captured by standard stability analysis, rather the model may sometimes overestimate ecological resilience (Siteur et al. 2016). Therefore, to study the complete dynamics of the system we take help of geometric singular perturbation theory and blow-up technique which will be discussed in next sections.

### 3 Slow–Fast System

In this section, we shall describe the dynamics of the slow–fast system (2) when \( 0 < \varepsilon \ll 1 \). To understand the dynamics of the system (2) for sufficiently small \( \varepsilon (> 0) \) we need to consider the behavior of two subsystems corresponding to (2), which can be obtained for \( \varepsilon = 0 \). The system in its singular limit, \( \varepsilon = 0 \) is obtained as follows

\[
\begin{align*}
\frac{du}{dt} &= f(u, v) = \gamma u(1 - u)(u + \beta) - \frac{uv}{1 + \alpha u}, \quad (4a) \\
\frac{dv}{dt} &= 0. \quad (4b)
\end{align*}
\]

The above system is known as fast subsystem or layer system corresponding to the slow–fast system (2). The fast flow consists with constant predator density determined by the initial condition \( v(0) = c \), and by integrating the differential equation

\[
\frac{du}{dt} = \gamma u(1 - u)(u + \beta) - \frac{uc}{1 + \alpha u},
\]

with initial condition \( u(0) > 0 \). The direction of the fast flow depends on the choice of initial conditions \( u(0), v(0) \) and other parameter values. Green horizontal lines are solution trajectories of (4) with appropriate direction as shown in Fig. 2a. Now writing system (2) in terms of the slow time \( \tau := \varepsilon t (\varepsilon > 0) \), we get the equivalent system in terms of slow time derivatives,

\[
\begin{align*}
\varepsilon \frac{du}{d\tau} &= f(u, v) = \gamma u(1 - u)(u + \beta) - \frac{uv}{1 + \alpha u}, \quad (6a) \\
\frac{dv}{d\tau} &= g(u, v) = v\left(\frac{u}{1 + \alpha u} - \delta\right). \quad (6b)
\end{align*}
\]

Substituting \( \varepsilon = 0 \) in the above system we find the following differential algebraic equation (DAE),

\[
\begin{align*}
0 &= f(u, v) = \gamma u(1 - u)(u + \beta) - \frac{uv}{1 + \alpha u}, \quad (7a) \\
\frac{dv}{d\tau} &= g(u, v) = v\left(\frac{u}{1 + \alpha u} - \delta\right). \quad (7b)
\end{align*}
\]

which is known as the slow subsystem corresponding to the slow–fast system (6). The solution of the above system is constrained to the set \( \{(u, v) \in \mathbb{R}^2_+ : f(u, v) = 0\} \)
and is known as critical manifold $C_0$. This set has one-one correspondence with the set of equilibrium of the system (5). The critical manifold consists of two different manifolds

\[
C^0_0 = \{(u, v) \in \mathbb{R}^2_+ : u = 0, v \geq 0\},
\]

\[
C^1_0 = \{(u, v) \in \mathbb{R}^2_+ : v = q(u) := \gamma(1 - u)(u + \beta)(1 + \alpha u), 0 < u < 1, v > 0\},
\]

such that $C_0 = C^0_0 \cup C^1_0$ where $C^0_0$ is the positive $v$-axis and $C^1_0$ is a portion of the cubic curve in the first quadrant shown in Fig. 2a, marked with black color. The slow flow on the critical manifold is given by

\[
\frac{du}{d\tau} = \frac{g(u, q(u))}{\dot{q}(u)},
\]

where \(\cdot\) refers to the differentiation with respect to $u$. The solution of the system (2) for sufficiently small $\varepsilon > 0$ cannot be approximated from its limiting solution at $\varepsilon = 0$. Therefore, $\varepsilon = 0$ is the singular limit of the system (2). The solution of the full system is obtained by combining the solution of the system in its singular limits. And depending on the region in the phase space we use either of the subsystems.

For $\alpha = 0.5$, $\beta = 0.22$, $\gamma = 3$ and $\delta = 0.3$, the coexistence steady state is unstable for $0 < \varepsilon \leq 1$ and is surrounded by a stable limit cycle. Interestingly the size and shape of stable limit cycle change with the variation of $\varepsilon$ which is shown in Fig. 2b. The size and shape of closed curve attractor (blue), obtained for $\varepsilon = 0.001$ is quite different from stable limit cycle (magenta) which is obtained for $\varepsilon = 1$. Keeping other parameters fixed, as we decrease $\varepsilon (\ll 1)$ there is a small change in the solution and the change in the shape of the limit cycle is not clearly distinguishable. This observation is based upon the numerical simulation and we need detailed analysis to understand the possible shape of the trajectories in singular limit $\varepsilon \to 0$. For $\varepsilon = 0.001$, the closed curve attractor (blue) consists of two horizontal segments on which flow is fast and one curvilinear and vertical segment where the flow is slow. This solution can be viewed as perturbation of the solution for $\varepsilon = 0$, which is obtained by the concatenating the solution of the layer system (4) and the slow subsystem (7). The two horizontal segments of the attractor (blue) are the perturbed trajectories corresponding to the layer system. This signifies the fast growth or decay of the prey species while predator density remains unaltered. The vertical portion close to $v$-axis and curvilinear part are close to the critical manifolds $C^0_0$ and $C^1_0$. Change in shape and size of the attractor does not solely depend upon the magnitude of $\varepsilon$ rather determined by the magnitude of the parameters involved with the reaction kinetics and timescale parameter.

Now we fix $\varepsilon = 0.01$ and other parameters as mentioned above, except $\delta$. Small variation in $\delta$ just below the $\delta_H$ results in rapid change in size and shape of the periodic attractor (see Fig. 2c). A small limit cycle (cyan) appears for $\delta = 0.3762$ known as canard cycle without head. This cycle encounters a change in curvature when $\delta = 0.376165$ and the resulting cycle is known as canard cycle with head (blue). Further decreasing $\delta$ to 0.36 the system settles down to a closed cycle known as relaxation oscillation. Further decrease in $\delta$ does not alter the size and shape of the
closed attractor and the trajectories converge to the stable relaxation oscillation cycle for $\varepsilon$ sufficiently small. In the next section, we will derive the analytical conditions for the existence of canard cycle and relaxation oscillation. The analytical results will help us to identify the domains in the parametric plane where we can find these different types of closed curve attractors.

### 4 Analysis of Slow–Fast System

The critical manifold $C_1^0$ can be divided into two parts, one part consists of the attractors of the fast sub-system and another part is repelling in nature. The attracting and repelling part of the manifold is separated by a non-degenerate fold point $P$. The fold point $P(u_f, v_f)$ is characterized by the following conditions (Krupa and Szmolyan التي لم يتم قراءتها بشكل طبيعي).
\[
\frac{\partial f}{\partial u}(u_f, v_f) = 0, \quad \frac{\partial f}{\partial v}(u_f, v_f) \neq 0, \quad \frac{\partial^2 f}{\partial u^2}(u_f, v_f) \neq 0, \quad \text{and } g(u_f, v_f) \neq 0.
\]

The components of the fold point are given by

\[
\begin{align*}
u_f &= \frac{(\alpha - \alpha\beta - 1) + (1 + \alpha + \alpha^2 - \alpha\beta + \alpha^2\beta + \alpha^2\beta^2)^{1/2}}{3\alpha}, \\
v_f &= \gamma(1 - u_f)(u_f + \beta)(1 + \alpha u_f),
\end{align*}
\]

which is the maximum of the critical manifold. The fold point divides the critical manifold into normally hyperbolic attracting \((C^{1,a}_0)\) and repelling \((C^{1,r}_0)\) submanifolds given by

\[
\begin{align*}
C^{1,a}_0 &= \left\{(u, v) \in \mathbb{R}^2_+ : v = q(u), u_f < u \leq 1\right\}, \\
C^{1,r}_0 &= \left\{(u, v) \in \mathbb{R}^2_+ : v = q(u), 0 \leq u < u_f\right\}.
\end{align*}
\]

The point of intersection of \(C^1_0\) with the \(v\)-axis is \(T_C(0, \beta\gamma)\), which is the transcritical bifurcation point for the fast subsystem. \(C^1_0\) can be written explicitly as \(v = q(u)\), and it follows from Fenichel’s theorem (Fenichel 1979; Kuehn 2015), that for \(\varepsilon\) small enough there exist locally invariant slow sub-manifolds \(C^1_{\varepsilon}\) and \(C^0_{\varepsilon}\) which are diffeomorphic to the respective critical manifolds \(C^1_0\) and \(C^0_0\), except at the non-hyperbolic points \(P\) and \(T\). Therefore, the invariant manifold \(C^1_{\varepsilon}\) can be obtained as a perturbation of \(v = q(u)\) as follows, with \(\varepsilon\) as perturbation parameter,

\[
C^1_{\varepsilon} = \left\{(u, v) \in \mathbb{R}^2_+ : v = q(u, \varepsilon), 0 < u < 1, \ v \geq 0\right\},
\]

where \(q(u, \varepsilon) = q_0(u) + \varepsilon q_1(u) + \varepsilon^2 q_2(u) + \cdots\), and \(C^0_{\varepsilon} = \{(u, v) \in \mathbb{R}^2_+ : u = 0, v \geq 0\}\). Using the invariance condition and the asymptotic expansion of \(q(u, \varepsilon)\), we can find the perturbed invariant manifold approximated up to the desired order. The approximation of \(q(u, \varepsilon)\) up to second order is provided in Appendix A with explicit expressions for \(q_0, q_1, q_2\). The approximations of invariant manifold for different values of \(\varepsilon\) are shown in Fig. 3. This approximation has two non-removable discontinuities in the vicinity of the non-hyperbolic points \(P\) and \(T\).

The critical manifold \(C^1_0\) is normally hyperbolic except at the points \(P(u_f, v_f)\) and \(T_C(0, \beta\gamma)\) and so is \(C^1_{\varepsilon}\). Thus, any trajectory starting near the attracting (repelling) submanifold \(C^{1,a}_0\) \((C^{1,r}_0)\) cannot cross the fold point \(P\) (transcritical point \(T_C\)). We can see from Fig. 2 that for sufficiently small values of \(\varepsilon\) the trajectories pass enough close to the attracting manifold \(C^{1,a}_0\) and cross the point \(P\). Fenichel’s theory is not adequate to determine the analytical expression for perturbed sub-manifolds close to \(C^1_0\) and is continuous in the vicinity of the non-hyperbolic points.

Therefore, to construct a trajectory passing through the vicinity of the point \(P\) we must remove the singularity at this point. Depending on parameter \(\delta\), the predator
nullcline intersects either $C_{1,a}^0$ or $C_{1,r}^0$ or passes through the point $P$. Thus, the coexistence equilibrium point $E_*$ of the system (2) lies either on $C_{1,a}^0$ or $C_{1,r}^0$ or coincides with $P$. When $E_*$ lie on $C_{1,a}^0$ it is globally asymptotically stable and every trajectory converges to $E_*$. When $E_*$ coincides with the fold point $P$ then $f_u(E_*) = 0$, $f_v(E_*) \neq 0$, $f_{uu}(E_*) \neq 0$ and $g(E_*) = 0$, this point is called the canard point. For the model (2), the Hopf point coincides with the canard point. The solution passing through the proximity of this point is known as the canard solution. For $\delta < \delta_H$, the coexistence equilibrium point $E_*$ lies on the repelling sub manifold $C_{0,r}^1$, it is unstable and we obtain a special kind of periodic solution consisting of two fast flow (almost horizontal) and two slow flow (passing close to $C_{0,a}^1$ and $C_0^0$) called relaxation oscillation. We will discuss the existence of such solutions in following subsections.

To remove the singularity at the fold point, we use blow-up transformation at the non-hyperbolic fold point which will extend the system over a 3-sphere in $\mathbb{R}^4$, denoted by $S^3 = \{x \in \mathbb{R}^4 : ||x|| = 1\}$. Using the blow-up technique we remove the singularity from the system and determine the canard solution passing through this point.

To apply the blow-up technique, first, we transform the slow–fast system (2) into its desired slow–fast normal form.

### 4.1 Slow–Fast Normal Form

Here, we consider a topologically equivalent form of the system (2) by re-scaling the time with the help of a transformation $dt \rightarrow (1 + \alpha u)dt$, where $(1 + \alpha u) > 0$
The transformed system is
\[\begin{align*}
\frac{du}{dt} &= \gamma u(1-u)(u+\beta)(1+\alpha u) - uv \equiv F(u, v, \delta), \\
\frac{dv}{dt} &= \varepsilon (uv - \delta v(1+\alpha u)) \equiv \varepsilon G(u, v, \delta).
\end{align*}\] (10)

The fold point \(P\) coincides with the coexistence equilibrium point at \(\delta = \delta_\ast\). As a consequence, the following conditions hold
\[\begin{align*}
F(u_\ast, v_\ast, \delta_\ast) &= 0, \\
F_u(u_\ast, v_\ast, \delta_\ast) &= 0, \\
F_v(u_\ast, v_\ast, \delta_\ast) &\neq 0, \\
F_{uu}(u_\ast, v_\ast, \delta_\ast) &\neq 0, \\
G_u(u_\ast, v_\ast, \delta_\ast) &\neq 0, \\
G_\delta(u_\ast, v_\ast, \delta_\ast) &= 0.
\end{align*}\] (11)

Using the transformation \(U = u - u_\ast, \ V = v - v_\ast, \ \lambda = \delta - \delta_\ast\), we translate the fold point to the origin, and together with the conditions (11) the system reduces to the slow–fast normal form near \((0, 0)\) as follows
\[\begin{align*}
\frac{dU}{dt} &= -Vh_1(U, V) + U^2h_2(U, V) + \varepsilon h_3(U, V), \\
\frac{dV}{dt} &= \varepsilon (Uh_4(U, V) - \lambda h_5(U, V) + Vh_6(U, V)),
\end{align*}\] (12)

where \(h_i\), \(i = 1, 2, 3 \ldots 6\) are given in ‘Appendix B.’

Here, \(\lambda\) measures the perturbation of \(\delta\) from \(\delta_\ast\) and is considered as bifurcation parameter for the system (12). The bifurcation parameter \(\lambda\) and timescale parameter \(\varepsilon\) are assumed to be independent of time. We now extend the above system to \(\mathbb{R}^4\) by augmenting the equations \(\frac{d\lambda}{dt} = 0\) and \(\frac{d\varepsilon}{dt} = 0\) to system (12) and study the dynamics of the system in the vicinity of \((0, 0, 0, 0)\).

### 4.2 Blow-Up Transformation

The fold point \(P\) of the system (2) and the equilibrium point \(E_\ast\) coincides at the Hopf bifurcation threshold. Thus, \(P\) is a Canard point. We apply a geometric transformation by which the non-hyperbolic equilibrium point is ‘blown up’ to a sphere known as blow-up space (Dumortier and Roussarie 1996; Krupa and Szmolyan 2001a). In this case we consider the blow-up space as a 3-sphere, \(S^3 = \{(\bar{U}, \bar{V}, \bar{\lambda}, \bar{\varepsilon}) \in \mathbb{R}^4 : \bar{U}^2 + \bar{V}^2 + \bar{\lambda}^2 + \bar{\varepsilon}^2 = 1\}\). Let \(I := [0, \rho]\) where \(\rho > 0\) is a small constant and let \(r \in I\). We define a manifold \(\mathcal{M} := S^3 \times I\) and the blow-up map, \(\Phi : \mathcal{M} \to \mathbb{R}^4\) where
\[\Phi(\bar{U}, \bar{V}, \bar{\lambda}, \bar{\varepsilon}, \bar{r}) = (\bar{r}\bar{U}, \bar{r}^2\bar{V}, \bar{r}\bar{\lambda}, \bar{r}^2\bar{\varepsilon}) := (U, V, \lambda, \varepsilon).\] (13)
Using the above map, we can write the transformed system as follows

\[
\frac{d\bar{U}}{dt} = \frac{1}{\bar{r}} \left( \frac{dU}{dt} - \bar{U} \frac{d\bar{r}}{dt} \right), \quad \frac{d\bar{V}}{dt} = \frac{1}{\bar{r}^2} \left( \frac{dV}{dt} - 2\bar{r} \bar{V} \frac{d\bar{r}}{dt} \right), \\
\frac{d\bar{\lambda}}{dt} = \frac{1}{\bar{r}} \left( \frac{d\lambda}{dt} - \bar{\lambda} \frac{d\bar{r}}{dt} \right), \quad \frac{d\bar{\epsilon}}{dt} = \frac{1}{\bar{r}^2} \left( \frac{d\epsilon}{dt} - 2\bar{r} \bar{\epsilon} \frac{d\bar{r}}{dt} \right),
\]

(14)

where \( \frac{dU}{dt}, \frac{dV}{dt} \) are given in (12) and \( \frac{d\bar{\lambda}}{dt} = \frac{d\bar{\epsilon}}{dt} = 0 \). To study the dynamics of the transformed system on and around the hemisphere \( S^3_{\bar{\epsilon} \geq 0} \), we will introduce the charts with direction blow-up maps (Kuehn 2015; Tu 2008). Along each direction of the coordinate axis, we define the charts \( K_1, K_2, K_3 \) and \( K_4 \) by setting \( \bar{V} = 1, \bar{\epsilon} = 1, \bar{U} = 1 \) and \( \bar{\lambda} = 1 \), respectively, in (14). The charts \( K_1 \) and \( K_3 \) describe the dynamics in the neighborhood of the equator of \( S^3 \) and \( K_2 \) describes the dynamics in a neighborhood of the positive hemisphere. Here, we mainly focus on chart \( K_2 \) to prove the existence of a periodic solution for \( 0 < \bar{\epsilon} \ll 1 \). Re-scaling the time with the transformation \( \bar{t} := \bar{r} t \), we desingularize the system (14) so that the factor \( \frac{1}{\bar{r}} \) disappears. The transformed version of the system (14) can be written in chart \( K_2 \) as follows

\[
\frac{d\bar{U}}{dt} = -\bar{V} b_1 + \bar{U}^2 b_2 + \bar{r} \left( a_1 \bar{U} - a_2 \bar{U} \bar{V} + a_3 \bar{U}^3 \right) + O(\bar{r} (\bar{\lambda} + \bar{r})), \\
\frac{d\bar{V}}{dt} = \bar{U} b_3 - \bar{\lambda} b_4 + \bar{r} \left( a_4 \bar{U}^2 + a_5 \bar{V} \right) + O(\bar{r} (\bar{\lambda} + \bar{r})), \\
\frac{d\bar{\lambda}}{dt} = 0, \\
\frac{d\bar{\epsilon}}{dt} = 0,
\]

(15)

where \( b_j \)'s are given in ‘Appendix B,’ and

\[
a_1 = a_5 = 0, \quad a_2 = 1, \quad a_3 = -(\gamma + \alpha \gamma (4u_* + \beta - 1)), \quad a_5 = u_* - (1 + u_* \alpha) \delta_*.
\]

(16)

The condition for the destabilization of the coexistence equilibrium point through singular Hopf bifurcation is summarized in the following theorem. The Hopf bifurcation of the system (12) occurs at \( \lambda = 0 \). At Hopf bifurcation, the purely imaginary eigenvalues of the corresponding Jacobian matrix are a function of \( \epsilon \), which tends to zero as \( \epsilon \to 0 \). Also, in slow-time derivative, the eigenvalues are a function of \( 1/\epsilon \). Thus, on both the timescales, the Hopf bifurcation is singular as \( \epsilon \to 0 \).

**Theorem 1** Let \((U, V) = (0, 0)\) be the canard point of the transformed system (12) at \( \lambda = 0 \) such that \((0, 0)\) is a folded singularity and \( G(0, 0, 0) = 0 \). Then, for sufficiently small \( \epsilon \) there exist a singular Hopf bifurcation curve \( \lambda = \lambda_H(\sqrt{\epsilon}) \) such that the
equilibrium point \( p \) of the system (12) is stable for \( \lambda > \lambda_H(\sqrt{\varepsilon}) \) and

\[
\lambda_H(\sqrt{\varepsilon}) = -\frac{b_3(a_1 + a_5)}{2b_2b_4}\varepsilon + O(\varepsilon^{3/2}). \tag{17}
\]

**Proof** The proof of the theorem is given in ‘Appendix B.’ □

The singular Hopf bifurcation curve for the system (10) is given by

\[
\delta_H(\sqrt{\varepsilon}) = \frac{1 + \alpha^2 \beta - \sqrt{1 + \alpha + \alpha^2 - \alpha \beta + \alpha^2 \beta + \alpha^2 \beta^2}}{\alpha(-1 - \alpha + \alpha \beta + \alpha^2 \beta)} - \frac{b_3(a_1 + a_5)}{2b_2b_4}\varepsilon + O(\varepsilon^{3/2}). \tag{18}
\]

In Fig. 4, the singular Hopf bifurcation curve (red) is plotted in \( \delta - \varepsilon \) parametric plane, it clearly explains how the singular Hopf bifurcation threshold changes with the variation in \( \varepsilon \). Once the coexistence equilibrium loses stability through Hopf bifurcation, at the Canard point, we find a closed orbit as attractor surrounding the unstable equilibrium point. From this point, small-amplitude stable canard cycle originates enclosing the point \( P \) and then forms canard cycle with head depending on the parameter values. The following theorem provides an analytical expression of the maximal canard curve in \( (\lambda - \varepsilon) \) plane.

**Theorem 2** Let \((U, V) = (0, 0)\) be the canard point of the slow–fast normal form (12) at \( \lambda = 0 \) such that \((0, 0)\) is a folded singularity and \( G(0, 0, 0) = 0 \). Then, for \( \varepsilon > 0 \) sufficiently small there exists maximal canard curve \( \lambda = \lambda_c(\sqrt{\varepsilon}) \), i.e., the parametric curve of maximal canard solution such that the slow flow on the normally hyperbolic invariant submanifolds \( M_{1,a}^1 \) connects with \( M_{1,r}^1 \) in the blow-up space. \( \lambda_c(\sqrt{\varepsilon}) \) is given by

\[
\lambda_c(\sqrt{\varepsilon}) = -\frac{1}{A_5}\left(\frac{3A_1}{4A_3^2} + \frac{A_2}{2A_4} + A_3\right)\varepsilon + O(\varepsilon^{3/2}) \tag{19}
\]

**Proof** The proof of this theorem is given in ‘Appendix C.’ □

The maximal canard curve, along which the canard cycle with head appears for the system (10) is given by

\[
\delta_c(\sqrt{\varepsilon}) = \frac{1 + \alpha^2 \beta - \sqrt{1 + \alpha + \alpha^2 - \alpha \beta + \alpha^2 \beta + \alpha^2 \beta^2}}{\alpha(-1 - \alpha + \alpha \beta + \alpha^2 \beta)} - \frac{1}{A_5}\left(\frac{3A_1}{4A_3^2} + \frac{A_2}{2A_4} + A_3\right)\varepsilon + O(\varepsilon^{3/2}). \tag{20}
\]

Keeping \( \alpha, \beta, \gamma \) and \( \varepsilon (> 0) \) fixed, \( \delta_c(\sqrt{\varepsilon}) \) gives the threshold for the existence of canard cycle with head. A schematic diagram of the threshold curves in \( \delta - \varepsilon \) plane is illustrated in Fig. 4 and it divides the \( \delta - \varepsilon \) parametric plane into four domains.

In domain I, when \( \delta > \delta_H \), the coexistence equilibrium point is stable. For a fixed \( \varepsilon > 0 \), as we decrease \( \delta \) from domain I to domain II small-amplitude canard cycles
Fig. 4 Schematic diagram showing singular Hopf bifurcation curve $\delta_H$ (red), maximal canard curve $\delta_c$ (blue) and $\delta_{ro}$ (dashed black) relaxation oscillation cycle (Color figure online)

appear after crossing the Hopf bifurcation threshold $\delta = \delta_H$. In domain II, that is when $\delta_c < \delta < \delta_H$, the system experiences a transition from canard cycle with head to canard cycle without head. The size of the canard cycle increases on decreasing $\delta$ and the shape of the cycle changes to canard with a head at $\delta = \delta_c$. The canard cycle with head persists in a narrow domain III, where $\delta_{ro} < \delta < \delta_c$. On further decreasing $\delta$, that is, when $\delta \leq \delta_{ro}$ the unstable equilibrium point is surrounded by a stable periodic attractor called relaxation oscillation. This periodic attractor consists of two concatenated slow (close to the critical manifold) and fast (almost horizontal and away from the critical manifold) flow. We can see that for sufficiently small $\epsilon$, this transition, from small canard cycle to relaxation oscillation through canard cycle with head, takes place within a narrow interval of the parameter $\delta$ and the phenomenon is known as canard explosion. This mechanism is further illustrated with the help of numerical example in Sect. 4.4.

4.3 Entry–Exit Function

The canard cycle and relaxation oscillation pass through the vicinity of $P$ for $\epsilon \ll 1$. We now prove the existence of a trajectory that jumps from the fold point to the other attracting slow manifold $C_0^0$ through fast horizontal flow and continuing there for a constant time the trajectory leaves $C_0^0$ at a certain point. This is determined by the entry–exit function and we can find the coordinates of the exit point from the slow manifold $C_0^0$. To do this, first, rewrite the system (2) as a Kolmogorov system (Freedman 1980) as follows

\[
\frac{du}{dt} = uf_1(u, v) = u(\gamma(1-u)(u+\beta) - \frac{v}{1+\alpha u}),
\]

\[
\frac{dv}{dt} = \epsilon vg_1(u, v) = \epsilon v\left(\frac{u}{1+\alpha u} - \delta\right).
\]

We can verify $f_1(0, v) = \gamma\beta - v, g_1(0, v) = -\delta < 0$, which implies that $f_1(0, v) < 0$ if $v > \gamma\beta, f_1(0, v) > 0$ if $v < \gamma\beta$. $T(0, \beta\gamma)$ on the vertical axis is the transcritical bifurcation point and we can divide the slow manifold $C_0^0$ into two parts $V^+ := \{(u, v) : u = 0, v > \gamma\beta\}$ and $V^- := \{(u, v) : u = 0, 0 \leq v < \gamma\beta\}$. Clearly $V^+$ is attracting and $V^-$ is repelling.
Let us fix \(\varepsilon > 0\) and let \(u_{\text{max}}\) be the point of maximum of the critical manifold \(C_0^1\) obtained from the extremum condition \(q_0(u) = 0\), where \(q_0(u)\) is given in ‘Appendix A.’ Solving for \(u_{\text{max}}\), we find

\[
u_{\text{max}} = \frac{(\alpha - \alpha \beta - 1) + \sqrt{1 + \alpha + \alpha^2 - \alpha \beta + \alpha^2 \beta + \alpha^2 \beta^2}}{3\alpha}\]  

(22)

and from the expression of \(C_0^1\) we have

\[v_{\text{max}} = q(u_{\text{max}}) = \gamma (1 - u_{\text{max}})(u_{\text{max}} + \beta)(1 + \alpha u_{\text{max}}).\]  

(23)

Now we consider a trajectory starting from a point, say \((u_1, v_1)\), where \(u_1 < u_{\text{max}}\) and \(v_1 = v_{\text{max}}\). The trajectory gets attracted toward the attracting manifold \(V^+\) and starts moving downward maintaining proximity to \(V^+\). It was expected that the trajectory would leave the vertical axis at the bifurcation point \(T\) where it loses its stability (Muratori and Rinaldi 1989). The trajectory crosses the point \(T\) and continues to move vertically downward remaining close to the repelling part \(V^-\), for a certain time, until a minimum predator population \(p(v_1)\) is attained such that \(0 < p(v_1) < \gamma \beta\). After leaving the slow manifold near the point \(p(v_1)\), the trajectory starts moving along a fast horizontal segment and gets attracted toward attracting slow manifold \(C_{0,a}^1\). This point of exit is determined by an implicit function \(p(v_1)\), called entry–exit function, which is defined implicitly as

\[
\int_{v_1}^{v_0} \frac{f_1(0, v)}{v g_1(0, v)} dv = 0.
\]

For simplicity, we define \(v_0 := p(v_1)\), then we have

\[
\int_{v_0}^{v_1} \frac{v - \gamma \beta}{v \delta} dv = 0 \implies (v_1 - v_0) - \gamma \beta \ln \left(\frac{v_1}{v_0}\right) = 0 \tag{24}
\]

Substituting for \(v_1 = v_{\text{max}}\) from (23) into Eq. (24), we obtain a transcendental equation in \(v_0\) which we solve numerically to obtain the exit point.

For the parameter values \(\alpha = 0.5, \beta = 0.2, \gamma = 3, \delta = 0.3\), we obtain \(u_{\text{max}} = 0.472, v_1 = 1.316\), and solving the transcendental equation (24) we get \(v_0 = p(v_1) = 0.207509\), which is the exit point from the manifold \(C_0^0\).

**Theorem 3** Let \(P\) be the fold point on the critical manifold \(C_0^1\) where the slow flow on the attracting manifold \(C_{0,a}^1\) is given by (8). Also assume that the coexistence equilibrium point lies on the normally hyperbolic repelling critical submanifold under the parametric restriction,

\[
\frac{\delta}{1 - \alpha \delta} < \frac{(\alpha - \alpha \beta - 1) + \sqrt{1 + \alpha + \alpha^2 - \alpha \beta + \alpha^2 \beta + \alpha^2 \beta^2}}{3\alpha}
\]
and let $U$ denote a small neighborhood of a singular trajectory $\gamma_0$ consisting of alternate slow and fast trajectories. Then, for sufficiently small $\varepsilon$ there exist a unique attracting limit cycle $\gamma_\varepsilon \subset U$ such that $\gamma_\varepsilon \to \gamma_0$ as $\varepsilon \to 0$.

**Proof** The proof is given in ‘Appendix D.’

These cycles are shown with the help of a numerical example in ‘Appendix D.’ When $\varepsilon \to 0$, all the trajectories asymptotically converge to this stable limit cycle consisting of alternate slow and fast transitions of prey and predator densities. This cycle can be interpreted as follows. When the predator population reaches some high density there is a rapid decline in the prey population due to excessive consumption by the specialist predator and the prey reaches a considerably low level. As a consequence, the predator population declines slowly until it reaches a low threshold density at which the prey population again starts growing. Consequently, the prey regenerates within a very short time while predator density remains more or less fixed. As the prey density approaches its carrying capacity, the predator population grows slowly due to the abundance of resources. Finally, when the predator density reaches its maximum level, the slow–fast cycle completes and this dynamics continues with time.

### 4.4 Canard Explosion

In the previous sub-sections, we have observed the periodic dynamics of the slow–fast system near the canard point, where the predator nullcline intersects the non-trivial prey nullcline at the fold point. This occurs at a certain threshold of the parameter $\delta$. At this point, the coexistence equilibrium point loses stability through singular Hopf bifurcation and a small-amplitude stable limit cycle is observed. Due to the decrease in the parameter $\delta$, the Hopf bifurcating stable cycle grows in size and settles down to relaxation oscillation. The fast transition in the size of the limit cycle from small canard cycles to relaxation oscillation occurs in an exponentially small range of the parameter $\delta$. This phenomenon is known as the canard explosion.

The family of canard cycles is already shown in Fig. 2c for fixed $\varepsilon$ and three values of $\delta$ close to the singular Hopf bifurcation threshold $\delta_H$. The coexistence equilibrium is stable for $\delta > \delta_H$ and the trajectory converges to the stable steady state for any initial condition as it is the global attractor. We can see that for $\delta$ just below $\delta_H$, a stable limit cycle grows in size and a new periodic solution emerges known as the canard cycle without a head (Fig. 2c, cyan color). This marks the onset of the canard explosion. Further decreasing $\delta$ slightly, we obtain another canard cycle known as canard with head (Fig. 2c, blue color). This cycle is special in the sense that from the vicinity of the fold point it follows the repelling slow manifold $C_1^r$, before jumping to another attracting manifold. A maximal canard is obtained at $\delta = \delta_c$. After crossing the maximal canard threshold, the system settles down to a large stable periodic solution called relaxation oscillation, which marks the end of canard explosion. This orbit is characterized by the fact that the slow flow on reaching the vicinity of the fold point directly jumps to another attracting slow manifold, as studied in the previous section. The strength of the Allee effect has a significant influence on the amplitude of stable
Fig. 5  The bifurcation diagram showing the change in the amplitude of the canard cycles is plotted against $\delta$ for $\alpha = 0.5, \gamma = 3, \varepsilon = 0.01, \beta = 0.22$.

Fig. 6  a The canard cycles for $\alpha = 0.5, \beta = 0.8, \gamma = 3, \varepsilon = 0.01$ and for different values of $\delta$, i.e., $\delta = 0.234$ (green), $\delta = 0.233$ (blue), $\delta = 0.231$ (magenta). b The bifurcation diagram showing the change in the size of the cycles (Color figure online)

oscillatory coexistence of both the species. The change in the amplitude of the limit cycle corresponding to canard explosion is shown in Fig. 5.

For smaller values of $\beta$, the size of the canard cycle is very large and the canard explosion occurs in an exponentially small interval. However, on increasing the value of $\beta$ the size of the limit cycle shrinks and instead of a sudden change in the size of the cycle, we observe a gradual increase in the amplitude of the periodic solution (Fig. 6). Though the transition from canard cycle to relaxation oscillation takes place in a much wider parametric interval, in this case, it is difficult to distinctively identify the different periodic solutions. For smaller values of $\beta$, when the prey population is almost absent, the predator population also slowly declines to an almost endemic level. But on increasing the strength of the Allee effect the predator density never collapses rather survives at a higher density. After which the system experience a sudden outbreak in the prey population within a very short interval of time. Again because of the abundance of resources, the predator population grows slowly and reaches the maximum capacity. Due to the exploitation of the resources, there is a fast decline in the prey density and this cycle continues.
5 Spatiotemporal Model

We now consider the spatiotemporal model corresponding to the model (2) with slow–fast timescale. Here, we consider that the prey and predator densities are functions of time and space, \(u(t, x)\) and \(v(t, x)\) denote prey and predator densities, respectively, at time \(t\) and at spatial location \(x\). In case of one-dimensional (1D) space \(x \in \mathbb{R}\) and for two-dimensional (2D) space \(x = (x, y) \in \mathbb{R}^2\). For simplicity, we assume that \(x\) belongs to a bounded domain \(D \subset \mathbb{R}\) and \(D \subset \mathbb{R}^2\), respectively. The spatiotemporal dynamics of the prey–predator interaction is described by the following reaction–diffusion equation

\[
\begin{align*}
\frac{\partial u}{\partial t} &= \gamma u(1 - u)(u + \beta) - \frac{uv}{1 + \alpha u} + \nabla^2 u, \\
\frac{\partial v}{\partial t} &= \varepsilon \left(\frac{uv}{1 + \alpha u} - \delta v\right) + d\nabla^2 v,
\end{align*}
\]

where \(d\) is the ratio of diffusivity coefficients of predator to prey and \(\nabla^2\) is the Laplacian operator. The above spatiotemporal model is subject to no-flux boundary condition and non-negative initial condition. The model (25) cannot produce any stationary Turing pattern and it can be proved that the Turing instability condition is not satisfied. However, instability of the coexistence steady state due to Hopf bifurcation combined with the diffusivity of two species leads to some dynamic pattern due to the formation of traveling wave, wave of invasion and spatiotemporal chaos. The mechanisms responsible for such kind of pattern formation are described in Lewis et al. (2016).

Analytical condition indicating the possible existence of traveling wave leads to successful invasion by specialist predator is discussed in the next subsection. For simplicity of mathematical calculation, we restrict ourselves to one-dimensional space to explain the existence of traveling wave. In case of two-dimensional spatial domain, the analogous patterns are presented separately.

5.1 Traveling Wave Solution

To study the successful invasion by the predator we consider the system (25) in one-dimensional space, we rewrite the above system as

\[
\begin{align*}
\frac{\partial u(t, x)}{\partial t} &= f(u, v) + \frac{\partial^2 u}{\partial x^2}, \\
\frac{\partial v(t, x)}{\partial t} &= \varepsilon g(u, v) + d\frac{\partial^2 v}{\partial x^2},
\end{align*}
\]

where \(f(u, v) = \gamma u(1 - u)(u + \beta) - \frac{uv}{1 + \alpha u}\), \(g(u, v) = \frac{uv}{1 + \alpha u} - \delta v\). The predator is introduced in a small domain where the prey density is at its carrying capacity. The successful invasion of the predator is characterized by the existence of a traveling wave joining the predator free steady state with the coexistence steady state. Depending upon the stability property of the coexistence steady state, we can find monotone traveling
wave, non-monotonic traveling wave, and periodic traveling wave as explained below with the help of numerical examples.

We begin with deriving the minimum speed of the traveling wave which result in the successful invasion of the specialist predator into the space already inhabited by its prey. For this, we first consider a single-species model with the linear growth:

\[
\frac{\partial v(t, x)}{\partial t} = \alpha v + D \frac{\partial^2 v}{\partial x^2},
\]

where \( \alpha, D > 0 \) are parameters with obvious meaning. Strictly speaking, the above equation does not possess a traveling wave solution. However, for a compact initial condition, it is known that the tail of the profile propagates with the constant speed given by \( c_{\text{min}} = 2\sqrt{D\alpha} \), see (Lewis et al. 2016), sometimes referred to as the Fisher spreading speed.

For the invasion of predator into space inhabited by its prey, we consider the tail of the profile where \( u \approx 1 \) and \( v \approx 0 \) and linearize (26b) around \((1, 0)\):

\[
\frac{\partial v(t, x)}{\partial t} = \varepsilon \left( \frac{1}{\alpha + 1} - \delta \right)v + d \frac{\partial^2 v}{\partial x^2}.
\]  
(27)

Clearly, the speed of the traveling wave, at the onset of successful invasion, is given by

\[
c_v = 2 \left( \varepsilon d \left[ \frac{1}{\alpha + 1} - \delta \right] \right)^{1/2}.
\]  
(28)

The feasibility condition is \( \delta(\alpha + 1) < 1 \). The expression for \( c_v \) indicates that the speed of traveling wave reduces in the order of \( \sqrt{\varepsilon} \). We consider the possibility of existence of traveling wave starting from the predator free steady state, which leads to the successful establishment of the predators, this requires the consideration of the system (26) with the following conditions

\[
\begin{align*}
    u(t, x) &= 1, \text{ and } v(t, x) = 0, \text{ as } x \to -\infty, \forall t, \\
    u(t, x) &= u_*, \text{ and } v(t, x) = v_*, \text{ as } x \to \infty, \forall t.
\end{align*}
\]

We consider the traveling wave solution of the system (26) in the form \( u(t, x) = \phi(\xi) \), \( v(t, x) = \psi(\xi) \) where \( \xi = x - ct \) and \( c \) is the wave speed. The functions \( \phi(\xi) \) and \( \psi(\xi) \) thus satisfy the equations

\[
\begin{align*}
    \frac{d^2 \phi}{d\xi^2} + c \frac{d\phi}{d\xi} + f(\phi, \psi) &= 0, \\
    \frac{d^2 \psi}{d\xi^2} + c \frac{d\psi}{d\xi} + \varepsilon g(\phi, \psi) &= 0.
\end{align*}
\]  
(29)
Substituting \( p(\xi) = -\frac{d\phi}{d\xi} \) and \( q(\xi) = -\frac{d\psi}{d\xi} \), from (29) we can derive four coupled ordinary differential equations as follows

\[
\begin{align*}
\frac{d\phi}{d\xi} &= -p, \\
\frac{dp}{d\xi} &= -cp + f(\phi, \psi), \\
\frac{d\psi}{d\xi} &= -q, \\
\frac{dq}{d\xi} &= \frac{1}{d}(-cq + \epsilon g(\phi, \psi)).
\end{align*}
\]

(30)

Three homogeneous steady states \((E_0, E_1, E_*)\) of the spatiotemporal model (26) corresponds to three steady states of system (30) are \(Q_0(0, 0, 0, 0)\), \(Q_1(1, 0, 0, 0)\) and \(Q_*(u_*, 0, v_*, 0)\). To ensure the successful invasion of the predator, we focus on the dynamics of the system (30) around \(Q_1\) and \(Q_*\). The Jacobian matrix of the system (30) evaluated at \(Q_1\) is

\[
J_{Q_1} = \begin{pmatrix}
0 & -1 & 0 & 0 \\
-\gamma(1 + \beta) & -c & -\frac{1}{1+\alpha} & 0 \\
0 & 0 & 0 & 1 \\
0 & 0 & \frac{c}{d}(1 + \alpha - \delta) & -\frac{c}{d}
\end{pmatrix}.
\]

(31)

The eigenvalues of the matrix \(J_{Q_1}\) are \(\lambda_{1,2} = \frac{c}{2} \pm \frac{\sqrt{c^2 + 4\epsilon g(1+\beta)}}{2}\) and \(\lambda_{3,4} = -\frac{c(1+\alpha)}{2} \pm \frac{\sqrt{\Gamma}}{d(1+\alpha)}\) where \(\Gamma = (1 + \alpha)^2 c^2 - 4\epsilon d(1 + \alpha)(1 - \delta - \alpha\delta)\). First two eigenvalues are real for all, whereas \(\lambda_{3,4}\) are real for \(c^2 \geq \frac{4\epsilon d(1 - \delta - \alpha\delta)}{1+\alpha}\). The traveling wave exist if all the eigenvalues are real, otherwise the trajectories will spiral around \(Q_1\) and leads to negative population density. Hence, the minimum speed of traveling wave originating from predator free steady state is

\[
c_{\text{min}} = \left[\frac{4\epsilon d(1 - \delta - \alpha\delta)}{1+\alpha}\right]^{1/2}.
\]

(32)

Note that \(c_{\text{min}}\) depends on \(\epsilon\), thus for \(\epsilon < 1\), the wave speed decreases. The minimum wave speed derived here is the same as it was derived earlier with the help of the linearized equation. The expressions for the eigenvalues of the Jacobian matrix \(J_{Q_*}\) are quite complicated and hence we avoid writing them here explicitly for the sake of brevity. For \(c \geq c_{\text{min}}\), the eigenvalues of \(J_{Q_*}\) can be real or complex depending on which we find monotone traveling wave and non-monotone as well as periodic traveling wave originating from the steady states \(E_1\).

To illustrate the existence of various types of traveling waves, we fix the parameter values \(\alpha = 0.5, \beta = 0.22, \gamma = 3, \epsilon = 1\) and consider \(\delta\) as variable parameter. From (32), we find that traveling wave exists for \(\delta < 2/3\). The eigenvalues of \(J_{Q_*}\) are real for \(0.52 < \delta < 0.667\) and the eigenvalues are complex conjugate for \(\delta \leq 0.52\). Complex
Fig. 7 Monotone traveling wave, non-monotone traveling wave and periodic traveling wave obtained for the model (26) with $\alpha = 0.5$, $\beta = 0.22$, $\gamma = 3$, $\epsilon = 1$ and $a\delta = 0.6$, $b\delta = 0.38$ and $c\delta = 0.3$ at different time as mentioned with the figures

conjugate eigenvalues with negative real parts correspond to non-monotone traveling wave and with positive real part correspond to periodic traveling wave. Three types of traveling waves are shown in Fig. 7 for three different values of $\delta$. For $\delta = 0.38$, the minimum wave speed $c_{\min} \approx 1.07$, and the complex conjugate eigenvalues with negative real part are $-1.22 \pm 0.423i$, whereas for $\delta = 0.3$, $c_{\min} \approx 1.211$ and the complex eigenvalues with positive real part are $0.034 \pm 0.405i$. The initial condition used in Fig. 7 is given by

$$u(0,x) = \begin{cases} u_*, & 0 \leq x \leq 3 \\ 1, & 3 < x \leq 300 \end{cases}, \quad v(0,x) = \begin{cases} v_*, & 0 \leq x \leq 3 \\ 0, & 3 < x \leq 300 \end{cases}.$$

The traveling wave emerging from the above initial conditions connects the prey-only steady state $E_1$ to the coexistence state $E_*$. Its shape depends on parameter values; for $\delta = 0.6$, its profile is monotone (see Fig. 7a). A non-monotone traveling wave is observed for $\delta = 0.38$ (see Fig. 7b). The range of spatiotemporal oscillation increases for values of $\delta$ close to the temporal Hopf bifurcation threshold. For $\delta = 0.3$, we find periodic traveling wave, with a plateau behind the oscillatory front corresponding to
Fig. 8  Periodic traveling waves for the model (26) with $\alpha = 0.5$, $\beta = 0.22$, $\gamma = 3$, $\varepsilon = 1$ and $a\delta = 0.3$, $b\delta = 0.2$ and $c\delta = 0.1$ at the same instant of time $t = 160$

steady state $E_*$ which is, for these parameter values, unstable: a phenomenon known as the dynamical stabilization (Malchow and Petrovskii 2002; Petrovskii and Malchow 2000, 2001; Sherratt 1998).

We mention here that the properties of emerging traveling wave are rather robust with regard to the choice of initial conditions. For instance, for a different initial condition as given by

$$u(0, x) = \begin{cases} 
1, & 0 \leq x \leq 3 \\
0, & 3 < x \leq 300
\end{cases}$$

$$v(0, x) = \begin{cases} 
0.2, & 0 \leq x \leq 2 \\
0, & 2 < x \leq 300
\end{cases}$$

the emerging periodic traveling waves shown in Figs. 7c and 8a are qualitatively similar. Mathematically, these two solutions are different as in Fig. 7c the traveling wave connects the steady state $E_1$ and $E_*$ whereas in Fig. 8a there is an additional connection between the steady states $E_0$ and $E_1$. Numerical simulation for smaller values of $\delta$ shows an increase in the magnitude and period of the oscillating front as shown in Fig. 8b, c. For numerical simulations we have chosen a spatial domain of size $[0, 300]$, further increase in domain size does not affect the qualitative property of the traveling waves.
Fig. 9 Periodic traveling waves for the model (26) with $\alpha = 0.5$, $\beta = 0.22$, $\gamma = 3$, $\delta = 0.3$ and $\epsilon = 0.75$, $\epsilon = 0.5$ and $\epsilon = 0.25$ at the same instant of time $t = 160$

To understand the effect of slow–fast timescale on the resulting pattern formation, here we consider the change in periodic traveling wave shown in Fig. 8a for $\epsilon < 1$. The model (26) is simulated for three different values of $\epsilon$ as mentioned at the caption of Fig. 9. With the decrease in $\epsilon$, we observe that the oscillatory wake of the invading predator front separating the predator-free area and the onset of spatiotemporal oscillation shrinks and eventually disappears for smaller values of $\epsilon$, so that dynamical stabilization does not occur. Also the size of predator-free area where prey exists at its carrying capacity increases with the decrease in $\epsilon$.

5.2 Patterns in Two Dimensions

Finally, we consider the spatiotemporal pattern formation over two-dimensional spatial domain. The nonlinear reaction–diffusion system (25) is solved numerically using five-point finite difference scheme for the Laplacian operator and forward Euler scheme for the temporal part with the initial conditions (33) and (34). Equal diffusivities are considered throughout, i.e., $d = 1$. Two types of initial conditions are used to study the successful invasion and establishment of both species. Morozov et al. (2006) used
the following initial condition which explains that a small amount of population of both the species are introduced within a small elliptic domain

\[
\begin{align*}
    u(0, x, y) &= \begin{cases} 
        u_0, & \frac{(x-x_1)^2}{A_{11}} + \frac{(y-y_1)^2}{A_{12}} \leq 1, \\
        0, & \text{otherwise}
    \end{cases}, \\
    v(0, x, y) &= \begin{cases} 
        v_0, & \frac{(x-x_2)^2}{A_{21}} + \frac{(y-y_2)^2}{A_{22}} \leq 1, \\
        0, & \text{otherwise}
    \end{cases}
\end{align*}
\]

where \(u_0\) and \(v_0\) measure the initial densities of prey (native) and predator (invasive) species, respectively. The other initial condition we consider here, is a small-amplitude heterogeneous perturbation from the homogeneous steady state (see (Medvinsky et al. 2002) for details), is

\[
\begin{align*}
    u(x, y, 0) &= u_\ast - e_1(x - 0.1y - 225)(x - 0.1y - 675), \\
    v(x, y, 0) &= v_\ast - e_2(x - 450) - e_3(y - 450),
\end{align*}
\]

where \((u_\ast, v_\ast)\) is the homogeneous steady state and for numerical simulation we choose \(e_1 = 2 \times 10^{-7}\), \(e_2 = 3 \times 10^{-5}\) and \(e_3 = 2 \times 10^{-4}\).

First we simulate the spatiotemporal model with the initial condition (33) in a square domain \(L \times L\) with \(L = 300\), with grid spacing \(\Delta x = \Delta y = 1\) and time step \(\Delta t = 0.01\). The simulation results are verified with other choices of \(\Delta x\) and \(\Delta t\) to ensure that the obtained results are free from numerical artifact. We consider a small elliptic domain within which the prey is at its carrying capacity \((u_0 = 1)\) and a small amount of population \((v_0 = 0.2)\) is introduced. Other parameter values are \(x_1 = 153.5, y_1 = 145, x_2 = 150, y_2 = 150, A_{11} = 12.5, A_{12} = 12.5, A_{21} = 5, A_{22} = 10\). We simulate the model for a sufficiently long time so that the invading waves can cover the whole domain and hits the domain boundary. Parameter values of \(\alpha, \beta, \gamma\) and \(\epsilon\) are same as mentioned in the previous subsection. We will first check the change in resulting pattern by varying the parameter \(\delta\). In Fig. 10, two-dimensional spatial distribution of prey population density at two different time points are shown for \(\delta = 0.3\). We have omitted the spatial distribution of the predator population as they exhibit similar patterns as exhibited by the prey species. Choosing \(\delta = 0.3\), just below the temporal Hopf bifurcation threshold \((\delta_H = 0.3768)\), we observe concentric circular rings as the initial transient pattern which eventually settle down to an interacting spiral pattern once the transients are over. With the advancement of time, the expanding circular rings hit the domain boundary and break into irregular patches. These irregular spiral patches cover the whole domain, and the system dynamics can be identified as interacting spiral chaos (see Fig. 10b). Note that the initial invading waves are the periodic traveling waves (Fig. 10a) but in large-time we observe irregular spatiotemporal oscillations (Fig. 10b). This type of chaotic dynamics persists in the vicinity of temporal Hopf bifurcation threshold \((0.2 < \delta < \delta_H = 0.3768)\).

Keeping other parameters fixed, we further decrease \(\delta\) \((\leq 0.2)\) and find propagating circular rings which are periodic traveling waves. The number of rings, that is the number of population patches within the fixed domain, decreases with the decrease in magnitude of \(\delta\). These periodic traveling waves do not break after hitting the boundary and the spatiotemporal dynamics remains unaltered. This result is in agreement with
Sherratt et al. (1997) that the system exhibits oscillatory dynamics as a successful invasion. Periodic traveling fronts for $\delta \leq 0.2$. are shown in Fig. 11.

Now we consider the effect of the slow–fast timescale on the resulting patterns. In the previous subsection, we have explained the reduction of traveling wave speed with the decrease in the magnitude of $\varepsilon$. As a result, the time taken by the predators to invade over the entire domain for $\varepsilon \ll 1$ is much longer as compared to $\varepsilon = 1$. For $\varepsilon < 1$, we find two kinds of distinctive changes in the resulting patterns. The width of the population patches increase (see Fig. 12a), and the spatiotemporal chaotic dynamics changes to periodic temporal oscillation of nearly homogeneous distribution of prey and predator densities (see Fig. 12d). The time evolution of the spatial average of the prey and predator population is analogous to the temporal canard cycle.

The choice of the initial condition and the domain size plays an important role in pattern formation. We simulate the system (25) with the second kind of initial condition (34) and over a square domain $L \times L$ with $L = 900$. The initial condition indicates a small heterogeneous perturbation from the homogeneous steady state $(u^*, v^*)$. Choosing the same parameter set as Fig. 10, initially, we find two spirals rotating about their fixed centers. The regular spirals are destroyed with the advancement of time and the interacting spiral pattern engulfs the whole domain (see Fig. 13b, c). These patches move, break and form new patches, but qualitatively, the dynamics of the system does not alter with time.

Exhaustive numerical simulation indicates that for $\delta$ close to the temporal Hopf bifurcation threshold, the system always exhibits spatiotemporal chaos. The duration and type of transient patterns depend upon the initial condition and the size of the domain. Now considering $\varepsilon < 1$, we found the persistent interacting spirals with thick arms (see Fig. 14a for $\varepsilon = 0.1$). The regular spiral grows in size and does not breakdown even after hitting the boundary when $\varepsilon$ is significantly small, say $\varepsilon = 0.01$. The irregularity of the temporal evolution of spatial averages of both the population decreases and moves toward periodic or quasi-periodic oscillation with the decrease in the magnitude of $\varepsilon$. This claim is justified from the time evolution of spatial averages as presented in the lower panel of Fig. 14.
Discussion and Conclusions

Understanding the effects that the existence of multiple timescales may have on the population dynamics of corresponding interacting species, in particular by promoting or hampering their persistence, has been attracting an increasing attention over the last two decades. In particular, some preliminary yet significant work has been done to understand changes in the oscillatory coexistence in the presence of slow–fast timescales (Hek 2010; Kooi and Poggiale 2018; Muratori and Rinaldi 1989; Rinaldi and Muratori 1992). However, the effects of the slow–fast dynamics in the spatially explicit systems, e.g., as given by the corresponding reaction–diffusion equations, remains poorly investigated. This paper aims to bridge this gap, at least partially. As our baseline system, we consider the classical Rosenzweig–MacArthur prey–predator model with the multiplicative weak Allee effect in prey’s growth. We pay particular attention to the interplay between the strength of the weak Allee effect (quantified by parameter $0 < \beta < 1$) and the difference in the timescales for prey and predator (quantified by $\epsilon \leq 1$).

Fig. 11  Spatial distribution of prey population with initial condition (33) for $\alpha = 0.5$, $\beta = 0.22$, $\gamma = 3$, $\epsilon = 1$ at $t = 200$
Fig. 12 Spatial distribution of prey population and plot of spatial average of prey and predator population for $\alpha = 0.5$, $\beta = 0.22$, $\gamma = 3$, $\delta = 0.3$ for $\epsilon = 0.1$ (left) and $\epsilon = 0.01$ (right). Upper panel shows the pattern at $a \ t = 10,000$, $b \ t = 5000$; lower panel shows the phase trajectory of spatially averaged densities $c \ t \in [2000, 10,000]$, $d \ t \in [5000, 10,000]$

We first provide a detailed slow–fast analysis for the corresponding non-spatial system. In doing that, we have obtained the following results:

- In the presence of slow–fast dynamics ($\epsilon \ll 1$) and a weak Allee effect, a decrease in the predator mortality may lead to a regime shift where small-amplitude oscillations in the population abundance change to large-amplitude oscillations (see Fig. 5). This change becomes more abrupt in case the Allee effect is ‘not too weak’ (i.e., $\beta$ is sufficiently small), cf. Figs. 5 and 6.

On a more technical side, we have derived an asymptotic expansion in $\epsilon$ for the invariant approximated manifolds and have explained the dynamics of the system near the hyperbolic submanifolds. Note that this theory cannot be extended at non-hyperbolic points. To unravel the complete geometry of the manifolds and their intersection as they pass through the non-hyperbolic points we followed the blow-up technique (Dumortier and Roussarie 1996; Krupa and Székely 2001a, b). We considered the slow–fast normal form of the model by translating the fold point to the origin. As the transformed system has a singularity at the origin, it is then blown up to a sphere $S^3$ and the trajectories of the blow-up system are mapped on and around
the sphere. Using the blow-up analysis we have found the analytical expression for the singular Hopf bifurcation curve \( \lambda_H(\sqrt{\epsilon}) \) along which the eigenvalues become singular as \( \epsilon \to 0 \). A particular kind of slow–fast solution known as canards (with or without head) has been found explicitly with the help of Melnikov’s distance function in the blow-up space. We have also calculated an analytical expression for the maximal canard curve \( \lambda_c(\sqrt{\epsilon}) \). Another type of periodic solution is obtained which consists of two concatenated slow and fast flow, known as relaxation oscillation. We have proved the existence and uniqueness of the relaxation oscillation cycle analytically using the entry–exit function (Rinaldi and Muratori 1992; Wang and Zhang 2019b) and validated our results numerically.

The difference in the timescale for the growth and decay in prey and predator species capture some interesting feature of respective populations. If the prey population growth takes place on a faster timescale, the predator population remains unchanged during the rapid growth and the decay of prey population. On the other hand, the change in predator population occurs slowly compared to the prey population. This type of growth and decay in two constituent species is observed for steady-state coexistence as well as oscillatory coexistence. The presence of weak Allee effect in prey growth acts as a system saver, that is, it prevents the system from collapsing.

Fig. 13 Spatial distribution of prey density for \( \alpha = 0.5, \beta = 0.22, \gamma = 3, \delta = 0.3, \epsilon = 1 \), at different time intervals

(a) \( t = 360 \)  
(b) \( t = 900 \)  
(c) \( t = 1500 \)
The size of the limiting relaxation oscillation cycle is smaller when the magnitude of Allee effect is comparatively large (cf. Fig. 6). Therefore, it reduces the chance of population extinction, as the periodic attractor remains away from both the axes.

To understand the change in dynamic behavior, we have chosen the predator mortality rate $\delta$ as the bifurcation parameter. For the predator mortality rate greater than the Hopf threshold, the system stabilizes at coexistence steady state, whereas for mortality rate below the threshold the system shows oscillatory dynamics. For the model under consideration, the Hopf threshold is independent of the timescale parameter ($0 < \varepsilon \ll 1$). But the interplay between the mortality rate and the timescale parameter has enormous effect on the nature of the oscillatory coexistence. For a fixed $\varepsilon > 0$, as we decrease $\delta$ below the Hopf threshold, we observe a fast transition from small-amplitude oscillatory coexistence to relaxation oscillation within an exponentially small range of the parameter $\delta$ via a family of canard cycles (Fig. 5), known as canard explosion. We also mention here that this type of dynamics has been observed in an ecosystem where the growth rates of the interacting species (resource–consumer type) differ by orders of magnitude (Ludwig et al. 1978; Scheffer et al. 1997, 2000; Stenseth et al. 1997).

We then considered the effect of multiple timescales in 1D and 2D spatial extension of our slow–fast system. In the 1D case, the minimum speed of the traveling wave of predator invading into the space already occupied by its prey (observed in case of compact initial conditions) is found analytically, while the patterns emerging in the wake of the front are investigated by means of numerical simulations. In the 2D case,
the effect of the interplay between the weak Allee effect and the multiple timescales is studied in simulations.

The following result is worth of highlighting:

– in the presence of a weak Allee effect, a decrease in the timescale ratio (i.e., $\epsilon \ll 1$) may lead to a regime shift where the pattern becomes correlated across the whole spatial domain, thus resulting in large-amplitude oscillations of spatially average population density; see Fig. 14. Since the corresponding trajectory in the phase plane ($<u>, <v>$) comes close to the vertical axis, the immediate ecological implication of this is a likely extinction of prey.

On a more technical side, our main interest was to study how the invasion of the species, as described by traveling fronts (Lewis et al. 2016), and the corresponding pattern formation in the wake (cf. (Sherratt et al. 1995, 1997)) are getting affected in the presence of the timescale parameter $\epsilon \ll 1$. For the values of $\delta$ below the Hopf bifurcation threshold ($\delta < \delta_H$), we find chaotic spatiotemporal patterns. The onset of spatiotemporal chaos and the duration of transient oscillation appear to be rather sensitive to the initial distribution of the two species. Fig. 10 shows periodic traveling waves as transient dynamics before spatiotemporal chaos sets in. However, small-amplitude heterogeneous perturbation around the homogeneous steady states reduces the time length for transient dynamics and the system quickly enters spatiotemporal chaotic regime. For $\delta$ significantly less than $\delta_H$ (see Fig. 11), we find only periodic traveling waves which indicate that continuous alteration of population patches mimics the temporal dynamics of large-amplitude oscillations.

Altogether, the existence of different timescales has a somewhat stabilizing effect on the dynamics of the spatiotemporal system. On one hand, it increases the size of the coexisting population patches over the domain, and on other hand, it drives the spatiotemporal chaotic pattern to periodic or quasi-periodic oscillatory dynamics (e.g., see Fig. 14). The speed of the traveling front decreases with a decrease in $\epsilon$. Also, a decrease in $\epsilon$ reduces the magnitude of irregular oscillation but enhances the duration of transient oscillations.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Appendix A

Here, we will follow geometric singular perturbation technique as given by Fenichel (1979) to find the analytical expression of locally perturbed invariant manifold $C^1_\varepsilon$. Since $v = q(u, \varepsilon)$, from the invariance condition we have

$$\frac{dv}{dt} = \frac{dq(u, \varepsilon)}{du} \frac{du}{dt}.$$
Using the explicit expression for $\frac{du}{dt}$ and $\frac{dv}{dt}$ from (2), we get

$$\varepsilon q(u, \varepsilon)(u(1 - \alpha \delta) - \delta) = u \frac{dq(u, \varepsilon)}{du}(\gamma(1 - u)(u + \beta)(1 + \alpha u) - q(u, \varepsilon)).$$  \hspace{1cm} (35)$$

Substituting the asymptotic expansion of $q(u, \varepsilon)$ from (9 and assuming $u \neq 0, \dot{q}_0(u) \neq 0$, we equate $\varepsilon$ free terms from both sides to obtain

$$q_0(u) = \gamma(1 - u)(u + \beta)(1 + \alpha u),$$  \hspace{1cm} (36)$$

which is exactly the critical manifold. Now equating the coefficients of $\varepsilon$ from both sides of (35) we get

$$q_1(u) = \frac{q_0(u)(u(1 - \alpha \delta) - \delta)}{-u\dot{q}_0(u)}.$$  \hspace{1cm} (37)$$

Similarly, we obtain $q_2(u)$ by equating the coefficients of $\varepsilon^2$,

$$q_2(u) = \frac{q_1(u)(u(1 - \alpha \delta) - \delta) + uq_1\dot{q}_1(u)}{-u\dot{q}_0(u)}.$$  \hspace{1cm} (38)$$

Proceeding as above, we find $q_r(u), r = 3, 4, \ldots$ by equating the coefficients of $\varepsilon^r$ from (35). Therefore, the second-order approximation of the perturbed invariant manifold is given by

$$q(u, \varepsilon) = q_0(u) + \varepsilon q_1(u) + \varepsilon^2 q_2(u),$$

where $q_0, q_1, q_2$ are given in Eqs. (36)–(38).

**Appendix B**

We apply the blow-up transformation in the slow–fast normal form (12) where

$$
\begin{align*}
    h_1(U, V) &= u_* + U, \quad h_3(U, V) = 0, \quad h_5(U, V) = (v_* + V)(1 + \alpha u_*) + U v_* \alpha, \\
    h_2(U, V) &= -\gamma(-1 + 6u_*^2 \alpha + 3u_*(1 + \alpha(\beta - 1)) + \beta - \alpha \beta) - U \gamma(1 + \alpha(4u_* + \beta - 1)), \\
    h_4(U, V) &= (v_* + V)(1 - \alpha \delta_*), \quad h_6(U, V) = u_* - (1 + u_* \alpha) \delta_*,
\end{align*}
$$

\(\bar{\varepsilon} = 1\) the blow-up transformation as defined in (13) reduces to

$$\bar{r} = \sqrt{\varepsilon}, \quad U = \sqrt{\varepsilon} \bar{U}, \quad V = \varepsilon \bar{V}, \quad \lambda = \sqrt{\varepsilon} \bar{\lambda}.$$  \hspace{1cm} (39)$$

Using the transformation (39), we can write the system (15) by removing the overbars as

$$
\begin{align*}
    U_t &= -b_1 V + b_2 U^2 + \sqrt{\bar{\varepsilon}} G_1(U, V) + O(\sqrt{\varepsilon}(\lambda + \sqrt{\varepsilon})), \\
    V_t &= b_3 U - b_4 \lambda + \sqrt{\bar{\varepsilon}} G_2(U, V) + O(\sqrt{\varepsilon}(\lambda + \sqrt{\varepsilon})),
\end{align*}$$  \hspace{1cm} (40)$$
where
\[ b_1 = u_*, \quad b_2 = -\gamma(-1 + 6u_*^2\alpha + 3u_*(1 + \alpha(\beta - 1)) + \beta - \alpha\beta), \]
\[ b_3 = v_*(1 - \alpha\delta_*), \quad b_4 = v_*(1 + \alpha u_*), \]
and
\[ G_1(U, V) = a_1 U - a_2 UV + a_3 U^3, \quad G_2(U, V) = a_4 U^2 + a_5 V. \]

Let the equilibrium point of the system (40) is \((U_e, V_e)\), \(U_e = \frac{b_4\lambda}{b_3} + O(2)\) and \(V_e = O(2)\) where \(O(2) := O(\lambda^2, \sqrt{\epsilon}, \lambda)\). Linearizing the system about this equilibrium point we have the Jacobian matrix as
\[
\mathcal{J} := \begin{pmatrix}
2U_e b_2 + a_1 \sqrt{\epsilon} + O(2) & -b_1 + O(2) \\
b_3 + O(2) & a_5 \sqrt{\epsilon} + O(2)
\end{pmatrix}.
\]

At the Hopf bifurcation, we have Trace \(\mathcal{J} = 0\) which implies
\[
\frac{2b_2b_4\lambda}{b_3} + \sqrt{\epsilon}(a_1 + a_5) + O(2) = 0.
\]

and applying the blow-down map \(\lambda_H = \lambda\sqrt{\epsilon}\) we get the singular Hopf bifurcation curve \(\lambda_H(\sqrt{\epsilon})\) for the slow–fast normal form (12) as
\[
\lambda_H(\sqrt{\epsilon}) = -\frac{b_3(a_1 + a_5)}{2b_2b_4}\sqrt{\epsilon} + O(\epsilon^{3/2}).
\]

**Appendix C**

Here, we prove the existence of maximal canard curve and will give an analytical expression for the same. For that we will first prove the following proposition. In chart \(K_2\) of the blow-up space, we consider the desingularized system (40) as
\[
U_t = -b_1 V + b_2 U^2 + rG_1(U, V) + O(\lambda r, r), \quad V_t = b_3 U - b_4 \lambda + rG_2(U, V) + O(\lambda r, r), \quad r_t = 0, \quad \lambda_t = 0,
\]
where \(b_1, b_2, b_3, b_4, G_1\) and \(G_2\) are computed above (41), (42). The dynamics of the system on the sphere is obtained by putting \(r = 0\) in (46) for different values of \(\lambda\) in the vicinity of 0. Thus, by taking \(r = 0, \lambda = 0\), the above system is integrable and we have
\[
U_t = -b_1 V + b_2 U^2, \quad V_t = b_3 U.
\]
This is a Riccati equation and the solution of this equation helps in proving our main
theorem.

**Proposition 1**  *The solution of the system (47) is given by* \( H(U, V) = c \), *where*

\[
H(U, V) = e^{-\frac{2b_2}{b_3}V \left(\frac{b_3}{2}U^2 - \frac{b_1b_3^2}{4b_2^2} - \frac{b_1b_3}{2b_2}V\right)}
\]

and

\[
\begin{align*}
\frac{dU}{dt} &= -e^{\frac{2b_2}{b_3}V} \frac{\partial H}{\partial V}, \\
\frac{dV}{dt} &= e^{\frac{2b_2}{b_3}V} \frac{\partial H}{\partial U}.
\end{align*}
\]

(48)

**Proof**  We can write the above Riccati system (47) as

\[
\frac{dV}{dU} = \frac{b_3U}{-b_1V + b_2U^2}
\]

(49)

where the integrating factor is \( e^{-\frac{2b_2}{b_3}V} \). Multiplying both sides with the I.F and integrating we get

\[
e^{-\frac{2b_2}{b_3}V} \left( U^2 - \frac{b_1}{b_2}V - \frac{b_1b_3}{2b_2} \right) = c_0.
\]

Multiplying with \( \frac{b_3}{2} \), we obtain the solution of the system (47) as

\[
e^{-\frac{2b_2}{b_3}V} \left( \frac{b_3}{2}U^2 - \frac{b_1b_3^2}{4b_2^2} - \frac{b_1b_3}{2b_2}V \right) = c,
\]

where \( c = c_0 \frac{b_3}{2} \) is a constant. The solution determined by \( c = 0 \) is a parabola of the form

\[
U^2 = \frac{b_1b_3}{2b_2^2} + \frac{b_1}{b_2}V.
\]

\( \square \)
**Proof of theorem 4.2:** We write the solution of the system (47) in the parametric form
\[
\eta(t) = (U(t), V(t)) = \left( t, \frac{b_2}{b_1} t^2 - \frac{b_3}{2b_2} \right), \quad t \in \mathbb{R}
\] (50)

For \( \varepsilon = 0 \), the attracting and repelling submanifolds of the critical manifold \( \mathcal{M}_0^1 \) intersect along the equator of the blow-up space \( S^3 \). From Fenichel’s theory, for \( \varepsilon > 0 \) there exist invariant perturbed attracting \((\mathcal{M}_0^{1,a})\) and repelling submanifold \((\mathcal{M}_0^{1,r})\). Along the curve (50), the attracting \((\mathcal{M}_0^{1,a})\) and repelling \((\mathcal{M}_0^{1,r})\) invariant submanifolds in the blow-up space intersect and the solution trajectory lying in that intersection is called maximal canard. We use Melnikov function to calculate the distance between these invariant manifolds (Krupa and Szmolyan 2001a; Kuehn 2015), which is given by
\[
D_{r,\lambda} = d_r r + d_\lambda \lambda + O(r^2),
\] (51)

where
\[
d_r = \int_{-\infty}^{\infty} \nabla H(\eta(t))^T \mathcal{G}(\eta(t)) dt,
\]
\[
d_\lambda = \int_{-\infty}^{\infty} \nabla H(\eta(t))^T \begin{pmatrix} 0 \\ -b_4 \end{pmatrix} dt,
\] (52)

where \( \mathcal{G}, H \) and \( b_4 \) are defined in (42), (48) and (41), respectively. The distance between the submanifolds \( \mathcal{M}_0^{1,a} \) and \( \mathcal{M}_0^{1,r} \) is given by Eq. (51). And since the maximal canard lie in the intersection of these manifolds, so we must have \( D_{r,\lambda} = 0 \). For that, we now calculate the Melnikov-type integrals \( d_r \) and \( d_\lambda \) (50) and (52). Therefore,
\[
\begin{align*}
    d_r &= \int_{-\infty}^{\infty} \left[ (a_1 U - a_2 UV + a_3 U^3) \frac{\partial H(\eta(t))}{\partial U} + (a_4 U^2 + a_5 V) \frac{\partial H(\eta(t))}{\partial V} \right] dt \\
    &= \int_{-\infty}^{\infty} e^{-\frac{2b_2}{b_3} V} \left[ (a_1 U - a_2 UV + a_3 U^3)b_3 U + (a_4 U^2 + a_5 V)(b_1 V - b_2 U^2) \right] dt \\
    &= e \int_{-\infty}^{\infty} e^{-A_4 t^2} \left( A_1 t^4 + A_2 t^2 + A_3 \right) dt \tag{53}
\end{align*}
\]

where
\[
A_1 = a_3 b_3 - \frac{a_2 b_2 b_3}{b_1}, \quad A_2 = a_1 b_3 + \frac{a_2 b_2^2}{2b_2} - \frac{a_4 b_1 b_3}{2b_2} - \frac{a_5 b_3}{2}, \quad A_3 = \frac{a_5 b_1 b_3^2}{4b_2^2}, \quad A_4 = \frac{2b_2}{b_1 b_3}.
\]

Now substituting \( z = t^2 \) and by repeated integration by parts, we obtain
\[
d_r = e \left( \frac{3A_1}{4A_4^2} + \frac{A_2}{2A_4} + A_3 \right) \int_{-\infty}^{\infty} e^{-A_4 t^2} dt, \tag{54}
\]
and

\[
d_s = - \int_{-\infty}^{\infty} b_4 \frac{\partial H}{\partial V} dt
= b_4 \int_{-\infty}^{\infty} e^{2 b_2 V} \left(-b_1 V + b_2 U^2\right) dt
= e A_5 \int_{-\infty}^{\infty} e^{-A_4 t^2} dt,
\]

(55)

where \( A_5 = \frac{b_1 b_3 b_4}{2b_2} \). Since \( d_s \neq 0 \) therefore using implicit function theorem we can explicitly solve for \( \lambda \) from (51)

\[
\lambda(r) = -\frac{d_r}{d_s} r + O(r^2) = -\frac{1}{A_5} \left(\frac{3A_1}{4A_4^2} + \frac{A_2}{2A_4} + A_3\right) r + O(r^2).
\]

(56)

Now using blow down map \( \lambda_c = \lambda \sqrt{\varepsilon} \), we obtain the maximal canard curve for the slow–fast normal form (12).

\[
\lambda_c(\sqrt{\varepsilon}) = -\frac{1}{A_5} \left(\frac{3A_1}{4A_4^2} + \frac{A_2}{2A_4} + A_3\right) \varepsilon + O(\varepsilon^{3/2}).
\]

(57)

\[\square\]

**Appendix D**

Here, we prove the existence of a unique attracting limit cycle called relaxation oscillation. To study the dynamics of the system (21), we define two sections of the flow as

\[
\Delta_{\text{in}} = \{(u_+, v) : u_+ << u_{\text{max}}, v \in (v_1 - \rho, v_1 + \rho)\},
\]

\[
\Delta_{\text{out}} = \{(u_+, v) : u_+ << u_{\text{max}}, v \in (v_0 - \rho^2, v_0 + \rho^2)\},
\]

where \( u_{\text{max}}, v_1, v_0 \) are defined in Sect. 4.3 and \( \rho \) is sufficiently small positive number.

Let us define a return map \( \Pi : \Delta_{\text{in}} \to \Delta_{\text{in}} \) which is a composition of two maps

\[
\Phi : \Delta_{\text{in}} \to \Delta_{\text{out}}, \quad \Psi : \Delta_{\text{out}} \to \Delta_{\text{in}},
\]

such that \( \Pi = \Psi \circ \Phi \). Let us fix \( \varepsilon > 0 \) and we take a point \( (u_+, v_+) \) on the section \( \Delta_{\text{in}} \). Now we consider a trajectory of the system (21) starting from the initial point \( (u_+, v_+) \). From the analysis of the entry–exit function, we can say that this trajectory will be attracted to \( V_+ \) and will leave \( V_- \) at point \( (0, p(v_+)) \), where \( p \) is the entry–exit function. The trajectory then jumps into the section \( \Delta_{\text{out}} \) at the point \( (u_+, p(v_+)) \). Thus, the map \( \Phi \) is defined with the help of entry–exit function as \( \Phi(u_+, v_+) = (u_+, p(v_+)) \).
Now to study the map $\Psi$ we consider two trajectories $\gamma^1_\epsilon, \gamma^2_\epsilon$ starting from the section $\Delta^{\text{out}}$. These trajectories get attracted toward $C^a_\epsilon$, where the slow flow is given by:
\[
\frac{du}{d\tau} = g(u, q(u, \epsilon)) \quad \dot{q}(u, \epsilon).
\]
They follow the slow perturbed manifold until the vicinity of the fold point where they contract exponentially toward each other (Wang and Zhang 2019b) and jump into $\Delta^{\text{in}}$. From Theorem 2.1 of Krupa and Szmolyan (2001a), we have that the map $\Pi$ is a contraction. Using contraction mapping theorem, we conclude that $\Pi$ has a unique fixed point which gives rise to a unique relaxation oscillation cycle $\gamma_\epsilon$. Further from Fenichel’s theory, we infer that $\gamma_\epsilon$ converges to $\gamma_0$ as $\epsilon \to 0$.

For the parameter values $\alpha = 0.5, \beta = 0.2, \delta = 0.3$, the unique attracting cycle $\gamma_\epsilon$ for $\epsilon = 0.1$, is shown in Fig. 15 which converges to $\gamma_0$ as $\epsilon \to 0$.

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