Journal of Dynamics and Differential Equations (2020) 32:979–1002
https://doi.org/10.1007/s10884-019-09757-y

Diffusive Spatial Movement with Memory

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Received: 19 December 2018 / Revised: 10 April 2019 / Published online: 6 May 2019

Abstract
Animal movements and their underlying mechanisms are an extremely important research area in biology and have been extensively studied for centuries. However, spatial memory and cognition, which is the most significant difference between animal movements and chemical movements, has been ignored in the modeling of animal movements. To incorporate cognition and memory of "clever" animals in the simplest and self-contained way, we propose a delayed diffusion model via a modified Fick's law, whereas in literature the standard diffusion for chemical movements was applied to describe "drunk" animal movements. Our mathematical model is expressed by a reaction–diffusion equation with an additional delayed diffusion term, which makes rigorous analysis intriguing and challenging. We show the wellposedness and analyze the asymptotic stability of steady state in the spatial memory model. It is shown that for the three possible reaction schemes, the stability of a spatially homogeneous steady state fully depends on the relationship between the two diffusion coefficients but is independent of the time delay. Finally, we numerically illustrate possible spatialtemporal patterns when the system is divergent.

Keywords Animal movement · Spatial memory · Cognition · Delay · Reaction–diffusion · Functional partial differential equation · Stability analysis · Pattern

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1 Introduction

Diffusion is one of fundamental physical processes in which substances or organisms move in space. It was first used to describe the heat conduction in early nineteenth century, and since then it has been used in numerous movement processes in physics, chemistry and biology [7,15,16]. Diffusion equation is based on the basic mass balance law and the Fick's law, which assumes that the movement flux is in the direction of negative gradient of the density distribution function, that is

$$\mathbf{J}(x,t) = -D\nabla u(x,t). \tag{1.1}$$

On the other hand, if the movement is in an advective environment like a river or stream, then the flux is also affected by the fluid velocity and the flux in (1.1) can be modified as

$$\mathbf{J}(x,t) = -D_1\nabla u(x,t) - \mathbf{v}(x,t)\cdot u(x,t), \tag{1.2}$$

where $\mathbf{v}(x,t)$ is a vector field indicating the fluid flow. Using the flux law in (2.2) and the continuity equation, one arrives at the typical diffusion–advection equation to describe movement:

$$\frac{\partial u(x,t)}{\partial t} = D_1\Delta u(x,t) + div(\mathbf{v}(x,t)\cdot u(x,t)). \tag{1.3}$$

However, the direct application of this physical process to animal movement has a severe drawback. The main feature of animals, especially highly developed animals, is their cognition and memory. A recent review paper [9] emphasized the importance of integrating spatial memory into animal movements. Spatial memory is an extremely complicated and poorly understood phenomenon in the study of animal movements, however, it is clearly the most significant difference between chemical movements and animal movements. The review paper summarized nine well-demonstrated memory mechanisms. Here we consider the episodic-like spatial memory of animals. For example, an animal in a polar region usually judges footprints to decide its spatial movement, and footprints record a history of species distribution and movements, in which time delay is involved. Waning of footprints leads to a finite delay. Apparently, highly developed animals can even remember the historic distribution or clusters of the species in space. Spatial memories decay over time, and these decays may include decreases in intensity and/or spatial precision [9]. To incorporate this kind of cognition and memory in the simplest and self-contained way, we propose a modified Fick's law that in addition to the negative gradient of the density distribution function at the present time, there is a directed movement toward the negative gradient of the density distribution function at *past time*. Such movement is based on the memory (or history) of a particular past time density distribution.

The paper is organized as follows. The next section is to derive the animal movement model with spatial memory (or history) and discuss the wellposedness of the proposed model. The third section is to analyze the stability of a spatially homogeneous steady state solution. The fourth section is to discuss three examples with different forms of the reaction function. The last section is the summary and discussion. Throughout the paper, $\mathbb{N}$ is the set of all positive integers, and $\mathbb{N}_0 = \mathbb{N}\cup\{0\}$ is the set of all non-negative integers.

2 Model of Diffusion with Spatial Memory

Suppose that Ω is a bounded, connected open region in $\mathbb{R}^N$, and $u(x,t)$ is the population density of a biological species for location $x \in \Omega$ and time $t \geq 0$. Then by using the principle of mass conservation and divergence theorem in calculus, we know that the rate of change of the population density satisfies the following continuity equation:

$$\frac{\partial u}{\partial t}(x,t) = -div(\mathbf{J}(x,t)), \tag{2.1}$$

where $\mathbf{J}(x,t)$ is the population flux of u. Here instead of the classical Fick's law, we propose the following modified Fick's law which suggests a flux in the form of

$$\mathbf{J}(x,t) = -D_1\nabla u(x,t) - D_2 u(x,t) f(\nabla u(x,t-\tau)), \tag{2.2}$$

where D_1 is the Fickian diffusion coefficient, D_2 is the memory-based diffusion coefficient, the time delay $\tau > 0$ represents the averaged memory period, and $f : \mathbb{R}^N \to \mathbb{R}^N$ is a function showing the dependence of memory-based diffusion on the gradient of concentration at τ time units before the present time. The memory-based diffusion flux is proportional to the population density at present time and the spatial gradient at a particular past time. When $\tau = 0$ and $f(U) = U$, the form of flux in (2.2) has been suggested in [19] to model the dispersive force due to population pressure. Hence the form of flux in (2.2) is also an extension of the derivation in [19] of instantaneous pressure to memory-based pressure.

By using the modified Fick's law in (2.2) and combining the chemical/biological processes of the species, the density function $u(x,t)$ satisfies the following reaction–diffusion equation:

$$\frac{\partial u}{\partial t}(x,t) = D_1\Delta u(x,t) + D_2 div(u(x,t) f(\nabla u(x,t-\tau))) + g(x,t,u(x,t)), \tag{2.3}$$

where g describes the chemical reaction or biological birth/death. For simplicity, in the following we shall assume that f is the identity function, g is independent of x and t, and the movement is confined to a bounded, connected open region Ω in $\mathbb{R}^N$ with C^2 boundary $\partial\Omega$. Then we have the following autonomous initial-boundary value problem:

$$\begin{cases} \dfrac{\partial u}{\partial t} = D_1\Delta u + D_2 div(u\nabla u_\tau) + g(u), & x \in \Omega, t > 0, \\ \dfrac{\partial u}{\partial n}(x,t) = 0, & x \in \partial\Omega, t > 0, \\ u(x,t) = \varphi(x,t), & x \in \Omega, -\tau \leq t \leq 0. \end{cases} \tag{2.4}$$

Here $u = u(x,t)$, $u_\tau = u(x,t-\tau)$; Ω is a bounded domain in $\mathbb{R}^N$ ($N \geq 1$) with C^2 boundary $\partial\Omega$; a homogeneous Neumann boundary condition is imposed so that there is no population movement across the boundary $\partial\Omega$. The initial condition $\varphi(x,t)$ satisfies

$$\varphi(x,t) \in C^{2,\alpha}(\overline{\Omega} \times [-\tau,0]), \quad \frac{\partial\varphi}{\partial n}(x,t) = 0, \quad (x,t) \in \partial\Omega \times [-\tau,0], \quad \alpha \in (0,1). \tag{2.5}$$

The growth rate $g(u)$ is always assumed to satisfy

$$g \in C^1([0,\infty),\mathbb{R}), \;\; g(0) = g(1) = 0, \;\; g(u) < 0, \quad \text{for } u > 1. \tag{2.6}$$

When $D_2 = 0$, Eq. (2.4) is the Fisher-KPP type scalar reaction–diffusion equation which is well understood [4,15]. Hence in Eq. (2.4), we assume that $D_1 > 0$ and $D_2 \neq 0$. Normally we have $D_2 > 0$, that is, animals leave away from high density to low density. This is a natural phenomenon. However, some social animals have aggregations for group defense or group working (see Sect. 5 for more details). In this case, we have $D_2 < 0$. Similar to the classical Fisher–KPP equation with non-flux boundary condition, Eq. (2.4) is a closed system with no population loss or gain through the boundary.

We remark that when the memory-based diffusion term $D_2 div(u\nabla u_\tau)$ is replaced by a chemotaxis term $-D_2 div(u\nabla v)$ and v represents the density of a chemical signal, then the system (2.4) becomes the well-known Keller–Segel chemotaxis model with growth if v also satisfies a reaction–diffusion equation [2,13,22]:

$$\begin{cases} \dfrac{\partial u}{\partial t} = D_1\Delta u - D_2\nabla\cdot(u\nabla v) + g(u), & x\in\Omega,\ t>0, \\ \dfrac{\partial v}{\partial t} = \Delta v - \alpha v + \beta u, & x\in\Omega,\ t>0, \\ \dfrac{\partial u}{\partial n}(x,t) = \dfrac{\partial v}{\partial n}(x,t) = 0, & x\in\partial\Omega,\ t>0. \end{cases} \tag{2.7}$$

The system (2.4) can also be viewed as a taxis type system but with its past distribution as the cue. In the classical Keller–Segel chemotaxis model (2.7), the cells are attracted to the higher density location of the chemical signal, thus the term with D_2 is negative. In other word, the memory-based diffusion with $D_2 > 0$ can be viewed as a repulsive taxis that the substances u move away from higher density location of its own past distribution. This is in consistence with the Fick's law that substances move from high density locations to low density ones. The dynamical behavior of (2.7) with logistic type g is still not fully understood, and numerical simulations show that chaotic dynamics could exist for (2.7) [8,17]. On the other hand, when $D_2 < 0$ in system (2.4), the model resembles the classical chemo-attractive chemotaxis model (2.7) for which the substances u is attracted by high concentration locations in the past. However, as will also be seen from simulations, the pattern generated by the model seems quite different from the case of $D_2 > 0$.

To conclude this section, we prove the wellposedness (existence, uniqueness, and positivity) of solutions to Eq. (2.4).

Proposition 2.1 *Suppose that $D_1 > 0$, $D_2 \in \mathbb{R}$, $\tau > 0$, Ω is a bounded, connected open subset of $\mathbb{R}^N$ with C^2 boundary $\partial\Omega$, $\varphi(x,t)$ satisfies (2.5) and $g(u)$ satisfies (2.6). Then, Eq. (2.4) possesses a unique solution $u(x,t)$ for $(x,t)\in\overline{\Omega}\times[0,\infty)$, and $u\in C^{2,1}(\bar{\Omega}\times[0,\infty))$. Moreover if $\varphi(x,t)\geq 0$ for $(x,t)\in\partial\Omega\times[-\tau,0]$, then $u(x,t)>0$ for $(x,t)\in\overline{\Omega}\times(0,\infty)$.*

Proof For $t\in[0,\tau]$, u_τ coincides with the initial function $\varphi(t-\tau,x)$. Set

$$F(t,x,u,\nabla u) = D_2\nabla\cdot(u\nabla\varphi(t-\tau,x)) + g(u)$$

From (2.5) and (2.6), we know F is continuous and satisfies a Hölder condition with respect to t, a Lipschitz condition with respect to $(u,\nabla u)$. Since $\partial\Omega$ is C^2, it then follows from [14, Proposition 7.3.3] that (2.4) has a unique solution $u\in C^{2,1}(\bar{\Omega}\times[0,T))$ for some $T>0$. The condition $g(u)<0$ for $u>1$ guarantees that the solution can be extended to $[0,\tau]$ if $\tau > T$. Then this process can be repeated for $t\in[\tau,2\tau]$ and further to any $[k\tau,(k+1)\tau]$ for $k\in\mathbb{N}$ as the step method for the existence of solutions to delay differential equations. Thus the solution can be extended to $t\in[0,\infty)$.

To prove the solution $u(x,t)$ is positive, we observe that u is the solution of the initial-boundary value problem

$$\begin{cases} \dfrac{\partial u}{\partial t} = D_1 \Delta u + D_2 div(u \nabla_x \varphi(x, t-\tau)) + g(u), & x \in \Omega, 0 < t < \tau, \\ \dfrac{\partial u}{\partial n}(x,t) = 0, & x \in \partial\Omega, t > 0, \\ u(x,0) = \varphi(x,0), & x \in \Omega. \end{cases} \tag{2.8}$$

Since $g(0) = 0$, then $u(x,t) > 0$ for $x \in \overline{\Omega} \times (0, \tau)$ from the standard maximum principle of parabolic equations. Repeating this argument, we obtain that $u(x,t) > 0$ for $(x,t) \in \overline{\Omega} \times (0, \infty)$. □

Note that in Proposition 2.1, we show that the solution $u(x,t)$ of (2.4) exists for all $t > 0$, so it exists globally. It is unknown whether the solution is bounded for $t \in (0, \infty)$ or even bounded by a constant independent of initial conditions. Such question is not completely solved for chemotaxis model (2.7) either. When there is a logistic growth term in (2.7), it is known that the solution is bounded under some conditions [26], or even converges to a constant equilibrium [28], but it is also known that solutions can blow up in finite time despite logistic growth [27], or have other interesting dynamics [29,30]. Here Proposition 2.1 excludes the possibility of finite-time blowup of solutions when $\tau > 0$, and it is not known whether the blowup can occur when $\tau = 0$.

3 Stability of Homogeneous States

Suppose that $u = u^*$ is a constant (spatially homogeneous) steady state solution of (2.4). We analyze the asymptotic stability of the constant steady state u^* with respect to the model (2.4). Here we always assume that $D_1 > 0$, $D_2 \in \mathbb{R}$ and $u^* \geq 0$. The linearization of (2.4) at $u = u^*$ is given by

$$\begin{cases} \dfrac{\partial \psi}{\partial t} = D_1 \Delta \psi + D_2 u^* \Delta \psi_\tau + g'(u^*)\psi, & x \in \Omega, t > 0, \\ \dfrac{\partial \psi}{\partial n}(x,t) = 0, & x \in \partial\Omega, t > 0, \\ \psi(x,t) = \varphi_0(x,t), & x \in \Omega, -\tau \leq t \leq 0, \end{cases} \tag{3.1}$$

where $\psi = \psi(x,t)$, $\psi_\tau = \psi(x, t-\tau)$ and φ_0 also satisfies (2.5).

3.1 Linear Stability

In this subsection, we show that the solution operator of (3.1) is an α-contraction, then from Lemma 7.4.2 in [11], one can assert that the stability of the constant solution $u = u^*$ is determined by the set of eigenvalues of (3.1). Let $\mathcal{C} := C([-\tau, 0], L^2(\Omega))$, and define the difference operator $\mathcal{D} : \mathcal{C} \to \mathcal{C}$ by $\mathcal{D}\phi = D_1\phi(0) + D_2 u^* \phi(-\tau)$. Then, we can rewrite (3.1) as an abstract ODE:

$$\frac{d\psi_t}{dt} = A\psi_t \tag{3.2}$$

where $A\phi = \phi'$ for $\phi \in \mathrm{Dom}(A)$ with

$$\mathrm{Dom}(A) = \{\phi' \in \mathcal{C} : \mathcal{D}\phi \in \mathrm{Dom}(\Delta), \phi'(0) = \Delta\mathcal{D}\phi(\theta) + g'(u^*)\phi(0)\}.$$

First we show that the spectral set $\sigma(A)$ of A is consisted of eigenvalues only.

Lemma 3.1 *For the linear operator A defined above, we have $\sigma(A) = \sigma_P(A)$, the set of eigenvalues of A, and $\mu \in \sigma_P(A)$ if and only if the operator $\triangle(\mu) : L^2(\Omega) \supset H^2(\Omega) \to L^2(\Omega)$ defined by*

$$\triangle(\mu)b = \mu b - (D_1 + D_2 u^* e^{-\mu\tau})\Delta b - g'(u^*)b,$$

for $b \in H^2(\Omega)$, is non-invertible.

Proof Let $\rho(A)$ be the resolvent set of A. The constant $\mu \in \rho(A)$ if and only if the equation

$$A\phi - \mu\phi = \eta, \tag{3.3}$$

has a solution $\phi \in \mathrm{Dom}(A)$ for every $\eta \in C([-\tau, 0], H^2(\Omega))$ (which is dense in $\mathcal{C}$), and the solution depends continuously on η. Recall that $A\phi = \phi'$ for $\phi \in \mathrm{Dom}(A)$. Solving (3.3), we have

$$\phi(\theta) = e^{\mu\theta} b + \int_0^\theta e^{\mu(\theta-\xi)}\eta(\xi)d\xi, \tag{3.4}$$

for some $b \in H^2(\Omega)$. In order to ensure $\phi \in \mathrm{Dom}(A)$, it requires that

$$\mu\phi(0) + \eta(0) = \Delta\mathcal{D}\phi(\theta) + g'(u^*)\phi(0). \tag{3.5}$$

Combining (3.4) and (3.5), we get

$$\begin{aligned} \mu b - \Delta\mathcal{D}(e^{\mu\cdot}b) - g'(u^*)b &= \mu b - (D_1 + D_2 u^* e^{-\mu\tau})\Delta b - g'(u^*)b \\ &= -\eta(0) + \Delta\mathcal{D}\left(\int_0^\theta e^{\mu(\theta-\xi)}\eta(\xi)d\xi\right), \end{aligned}$$

which has a solution for $b \in H^2(\Omega)$ if and only if the operator $\triangle(\mu)$ is invertible. On the other hand, it follows from $b \in H^2(\Omega)$, $\eta \in C([-\tau, 0], H^2(\Omega))$ and (3.4) that $\phi(\theta)$ also satisfies $\mathcal{D}\phi \in \mathrm{Dom}(\Delta)$. Therefore,

$$\{\mu \in \mathbb{C} : \triangle(\mu) \text{ is invertible}\} \subseteq \rho(A).$$

On the other hand, if there exists $\mu \in \mathbb{C}$ such that $\triangle(\mu)$ is non-invertible, i.e., $\mu b - \Delta\mathcal{D}(e^{\mu\cdot}b) - g'(u^*)b = 0$ always has a nontrivial solution for $b \in H^2(\Omega)$, then by a similar argument, we can show that $A\phi - \mu\phi = 0$ has a unique solution, given by $e^{\mu\theta}b$. Therefore, $\mu \in \sigma_P(A)$. □

In order to show that the asymptotical stability of zero solution of (3.2) is completely determined by the distribution of $\sigma_P(A)$, one has to show that the solution operator of (3.2) possesses some compactness property. For that purpose, we assume that

$$|q| < 1, \quad \text{where} \quad q = \frac{D_2 u^*}{D_1}. \tag{3.6}$$

Now we make the following change of variable

$$D_1\psi(x, t) + D_2 u^* \psi(x, t - \tau) = v(x, t), \tag{3.7}$$

and assuming (3.6), we can invert ψ from v in (3.7) by setting

$$\psi(x,t) = \frac{1}{D_1}\sum_{n=0}^{\infty}(-1)^n q^n v(x,t-n\tau) =: \frac{1}{D_1}\bar{\mathcal{D}}v_t(x,\cdot). \tag{3.8}$$

By using (3.8), we can rewrite (3.2) as the following linear neutral partial functional differential equation with infinitely but countably many delays:

$$\frac{\partial \bar{\mathcal{D}}v_t(x,\cdot)}{\partial t} = D_1\Delta v(x,t) + g'(u^*)\bar{\mathcal{D}}v_t(x,\cdot). \tag{3.9}$$

subject to the initial condition

$$v(x,t) = \begin{cases} D_1\varphi_0(x,0) + D_2u^*\varphi_0(x,-\tau), & t=0,\\ D_1\varphi_0(x,t), & t\in[-\tau,0),\\ 0, & t<-\tau. \end{cases} \tag{3.10}$$

A typical choice of the phase space for (3.9) is

$$\mathcal{L} = \left\{\nu \in L^1((-\infty,0),L^2(\Omega)) : \|\nu\|_{\mathcal{L}} := \int_{-\infty}^{0}\|\nu(s)\|_{L^2(\Omega)}e^{\varepsilon s}ds < \infty\right\}, \tag{3.11}$$

where $\varepsilon > 0$ is fixed, see [21]. Let $T_\Delta(t)$ be the semigroup generated by the diffusion operator $D_1\Delta$. Then, the associated integral form of (3.9) subject to the initial condition (3.10) is

$$\bar{\mathcal{D}}v_t(x,\cdot) = T_\Delta(t)v(0) + g'(u^*)\int_0^t T_\Delta(t-s)\bar{\mathcal{D}}v_s(x,\cdot)ds. \tag{3.12}$$

As shown in [11,31], for neutral differential equations, the associated difference equation plays a key role on the dynamics of the original neutral type equations. Here we also consider the following associated difference equation of (3.9) on $L^2(\Omega)$:

$$\mathbb{D}w_t := \sum_{n=0}^{\infty}(-1)^n q^n w(t-n\tau) = h(t), \quad t\ge 0, \tag{3.13}$$

with $w_0 \in \mathcal{L}$ such that $\mathbb{D}w_0 = h(0)$ and $h \in C([0,\infty), L^2(\Omega))$. Define $\zeta : (-\infty,0] \to B(L^2(\Omega))$ by

$$\zeta(\theta) = \begin{cases} 0, & \theta\in(-\tau,0],\\ \sum_{i=1}^{n}(-1)^{i-1}q^i, & \theta\in(-(n+1)\tau,-n\tau], n\in\mathbb{N}, \end{cases} \tag{3.14}$$

where $B(L^2(\Omega))$ is the set of bounded linear operators from $L^2(\Omega)$ to itself. Then, (3.13) can be written as

$$w(t) + \int_{-\infty}^{0} w_t(\theta)d\zeta(\theta) = h(t),$$

which is equivalent to

$$w(t) + \eta * w = f(t) + h(t), \qquad t\ge 0, \tag{3.15}$$

where $(\eta * w)(t) = \int_0^t w(t-s)d\eta(s)$, $\eta : [0,\infty) \to B(L^2(\Omega))$ is given by $\eta(s) = -\zeta(-s)$, and $f(t) = -\int_t^{+\infty} w_0(t-s)d\eta(s)$. For the integral equation (3.15), we first show the existence of resolvent ς of η in the following lemma.

Lemma 3.2 *Assume that* (3.6) *holds. For* $\eta(s) = -\zeta(-s)$*, the system*

$$\varsigma(t) + (\eta * \varsigma)(t) = \eta(t), \qquad \varsigma(t) + (\varsigma * \eta)(t) = \eta(t) \tag{3.16}$$

has a unique solution for $\varsigma : [0, \infty) \to B(L^2(\Omega))$*, which is given by*

$$\varsigma(t) = \begin{cases} 0, & t \in [0, \tau), \\ -q, & t \in [\tau, +\infty). \end{cases} \tag{3.17}$$

Proof We first prove the existence and uniqueness of solution of (3.16) by using the contraction mapping principle. Let $BV([0,\infty), B(L^2(\Omega)))$ be the space of functions from $[0,\infty)$ to $B(L^2(\Omega))$ with bounded variation. For any $\vartheta \in BV([0,\infty), B(L^2(\Omega)))$, define

$$\|\vartheta\|_{BV} = \operatorname*{Var}_{s\in\mathbb{R}^+} \vartheta(s) := \sup \left\| \sum_i (\vartheta(s_i) - \vartheta(s_{i-1})) \right\|_{B(L^2(\Omega))}.$$

Then, $BV([0,\infty), B(L^2(\Omega)))$ equipped with $\|\cdot\|_{BV}$ is a Banach space. Note that $\operatorname*{Var}_{s\in\mathbb{R}^+} \eta(s) = |q|/(1-q)$. Let $\tilde{\eta}(t) = \eta(s)e^{-\kappa t}$. Then, we can always choose $\kappa > 0$ large enough so that $\operatorname*{Var}_{s\in\mathbb{R}^+} \tilde{\eta}(s) < 1/2$. Consider the operator $\mathcal{F} : BV([0,\infty), B(L^2(\Omega))) \to BV([0,\infty), B(L^2(\Omega)))$, given by

$$\mathcal{F}\tilde{\varsigma}(t) := \tilde{\eta}(t) - (\tilde{\eta} * \tilde{\varsigma})(t).$$

Then, for any $\tilde{\varsigma}_1, \tilde{\varsigma}_2 \in BV([0,\infty), B(L^2(\Omega)))$, we have

$$\begin{aligned} \|\mathcal{F}\tilde{\varsigma}_1 - \mathcal{F}\tilde{\varsigma}_2\|_{BV} &\le \operatorname*{Var}_{s\in[0,t]} \tilde{\eta}(s) \|\tilde{\varsigma}_1 - \tilde{\varsigma}_2\|_{BV} \\ &< \operatorname*{Var}_{s\in\mathbb{R}^+} \tilde{\eta}(s) \|\tilde{\varsigma}_1 - \tilde{\varsigma}_2\|_{BV} < \frac{1}{2}\|\tilde{\varsigma}_1 - \tilde{\varsigma}_2\|_{BV}, \end{aligned}$$

which implies that $\mathcal{F}$ is a contraction mapping, and it admits a unique fixed point in $BV([0,\infty), B(L^2(\Omega)))$, or equivalently, there exists a unique $\tilde{\varsigma}(t)$ such that

$$\tilde{\varsigma}(t) + (\tilde{\eta} * \tilde{\varsigma})(t) = \tilde{\eta}(t).$$

Let $\varsigma(t) = \tilde{\varsigma}(t)e^{\kappa t}$. It can be verified that $\varsigma(t)$ is the solution of the first equation of (3.16).

It remains to check that the solution of (3.16) is indeed given by (3.17). For $t \in [n\tau, (n+1)\tau)$ with any $n \ge 1$, we have

$$\begin{aligned} &\varsigma(t) + \int_0^t \varsigma(t-s)d\eta(s) \\ &\quad = -q + (-q)\varsigma(t-\tau) + q^2\varsigma(t-2\tau) + (-q)^3\varsigma(t-3\tau) + \cdots + (-q)^n\varsigma(t-n\tau) \\ &\quad = -q + q^2 + \cdots + (-q)^n \\ &\quad = \eta(t), \end{aligned}$$

that is, $\varsigma(t)$ is a solution of the first equation of (3.16). Using (3.14) and (3.17), we can verify $(\eta * \varsigma)(t) = (\varsigma * \eta)(t)$. Hence, $\varsigma(t)$ also satisfies the second equation of (3.16). □

By using the resolvent ς, we can obtain the solution of (3.15).

Lemma 3.3 *Assume that* (3.6) *holds. For* $w_0 \in \mathcal{L}$*, the integral equation* (3.15) *admits a unique solution* $w(t)$ *such that* $w(t) = w_0(t)$ *for* $t \in (-\infty, 0]$*, which can be represented as*

$$w(t) = (f+h) - \varsigma * (f+h) = f(t) + h(t) - \int_0^t d\varsigma(s)[f(t-s) + h(t-s)],$$

where ς is defined in (3.17).

Proof Let $w(t) = (f+h) - \varsigma * (f+h)$. It then follows from (3.3) and the first equation of (3.16) that

$$\begin{aligned} w + \eta * w &= w + \eta * ((f+h) - \varsigma * (f+h)) = w + \eta * (f+h) - (\eta * \varsigma) * (f+h) \\ &= w + \eta * (f+h) - (\eta - \varsigma) * (f+h) = w + \varsigma * (f+h) = f + h. \end{aligned}$$

This implies that $w(t) = (f+h) - \varsigma * (f+h)$ is a solution of (3.15). Conversely, if $w(t)$ is a solution, i.e., $w + \eta * w = f + h$, then we have

$$\varsigma * w + (\varsigma * \eta) * w = \varsigma * (f+h).$$

Using the second equation of (3.16), we have $\eta * \omega = \varsigma * (f+h)$, and therefore,

$$w(t) = -\eta * w + (f+h) = (f+h) - \varsigma * (f+h).$$

Note that, for $t \in (n\tau, (n+1)\tau]$ with any $n \geq 0$, we have

$$f(t) = -\sum_{i=n+1}^{+\infty} w_0(t - i\tau)(-q)^i.$$

If $w_0(t)$ satisfies (3.10), then $w_0(t) = 0$ for $t < -\tau$, and therefore, for $t \in (n\tau, (n+1)\tau]$ with $n \geq 0$,

$$\begin{aligned} &\|w(t)\|_{L^2(\Omega)} \\ &= \left\| f(t) + h(t) - \int_0^t [f(t-s) + h(t-s)] d\varsigma(s) \right\|_{L^2(\Omega)} \\ &= \begin{cases} \|f(t) + h(t) + qf(t-\tau) + qh(t-\tau)\|_{L^2(\Omega)}, & n \geq 1, \\ \|f(t) + h(t)\|, & n = 0, \end{cases} \\ &\leq \begin{cases} (1+q) \sup\limits_{t-\tau \leq s \leq t} \|h(s)\|_{L^2(\Omega)}, & n \geq 1, \\ \sum\limits_{i=1}^{+\infty} \|w_0(t - i\tau)\|_{L^2(\Omega)} |q|^i + \sup\limits_{0 \leq s \leq \tau} \|h(s)\|_{L^(\Omega)}, & n = 0. \end{cases} \end{aligned} \tag{3.18}$$

□

Now we have the main result of this subsection.

Theorem 3.4 *Assume that* (3.6) *holds. If* $\sigma_P(A) \subset \{z \in \mathbb{C} : \mathrm{Re} z < 0\}$, *then for any* $\epsilon > 0$, *there exists* $K(\epsilon) > 0$ *such that the solution operator* $T(t)$ *of* (3.2) *satisfies*

$$\|T(t)\psi_0\|_{\mathcal{C}} \leq K(\epsilon) e^{-\epsilon t} \|\psi_0\|_{\mathcal{C}}, \quad \forall\, t \geq 0,\ \psi_0 \in \mathcal{C}. \tag{3.19}$$

Proof It can be verified that $v(t)$ is a solution of (3.12) if and only if $v(t)$ satisfies

$$\bar{\mathcal{D}} v_t = e^{-\gamma t} T_\Delta(t) v(0) + \int_0^t e^{-\gamma(t-s)} T_\Delta(t-s) \bar{\mathcal{D}} v_s ds =: h_1(t) + h_2(t, v_s).$$

for some $\gamma > \varepsilon$. Then, v_t can be decomposed as $v_t = v_t^1 + v_t^2$, where v_t^1 and v_t^2 are the solutions of $\bar{\mathcal{D}} v_t^1 = h_1$ with $v_0^1 = v_0$ and $\bar{\mathcal{D}} v_t^2 = h_2$ with $v_0^2 = 0$, respectively.

Let $S(t)$ be defined in such a way that $S(t)v_0 = v_t^1$. For h_1, we have

$$\|h_1(t)\|_{L^2(\Omega)} \le \|e^{-\gamma t}T_\Delta(t)v(0)\|_{L^2(\Omega)} \le e^{-\gamma t}\|v(0)\|_{L^2(\Omega)}, \quad t \ge 0. \tag{3.20}$$

It then follows from (3.10) and (3.18) that, for $t > \tau$,

$$\begin{aligned}\|v_t^1\|_{\mathcal{L}} &= \left(\int_{-\infty}^0 + \int_0^t\right)\|v^1(\theta)\|_{L^2(\Omega)}e^{\varepsilon(\theta-t)}d\theta\\ &\le e^{-\varepsilon t}\|v_0^1\|_{\mathcal{L}} + \int_0^\tau\left(\sum_{i=1}^{+\infty}\|w_0(\theta-i\tau)\|_{L^2(\Omega)}|q|^i + \sup_{0\le s\le\tau}\|h(s)\|_{L^(\Omega)}\right)e^{\varepsilon(\theta-t)}d\theta\\ &\quad + (1+q)\int_\tau^t \sup_{\theta-\tau\le s\le\theta}\|h_1(s)\|_{L^2(\omega)}e^{\varepsilon(\theta-t)}d\theta\\ &\le e^{-\varepsilon t}\|v_0^1\|_{\mathcal{L}} + e^{-\varepsilon t}\|v_0^1\|_{\mathcal{L}} + \left(\frac{e^{\varepsilon\tau}-1}{\varepsilon} + \frac{(1+q)e^{\gamma\tau}}{\gamma-\varepsilon}\right)e^{-\varepsilon t}\|v(0)\|_{L^2(\Omega)},\end{aligned} \tag{3.21}$$

that is, there exists $\mathcal{K} > 0$ and $\varrho > 0$ such that

$$\|S(t)v_0^1\|_{\mathcal{L}} \le \mathcal{K}e^{-\varrho t}\|v_0^1\|_{\mathcal{L}}.$$

Therefore, $S(t)$ is an α-contraction, in the sense that $\alpha(S(t)) < 1$, where $\alpha(T) := \inf\{c : \alpha(TP) \le c\alpha(P), \forall \text{ bounded set } P\}$, and $\alpha(P)$ is the Kuratowskii's measure of a bounded set P in a Banach space.

Let $V(t)v_0^2 = v_t^2 = v_t - S(t)v_0^1$. Then, $V(t)v_0^2$ is the solution of $\bar{\mathcal{D}}v_t^2 = h_2$ with $v_0^2 = 0$. By a similar argument of Theorem 2.2 in [12], one can show that $V(t)$ is compact. In fact, from the regularity theory of parabolic equations, we know that $h_2(t,\cdot) : \mathcal{L} \to L^2(\Omega)$ is completely continuous for any $t \ge 0$. Suppose that $\{\chi_k\}$ be a bounded sequence in $\mathcal{L}$. Then, there is a subsequence of $h_2(t,\chi_k)$, still denoted by $h_2(t,\chi_k)$, converging to some $h_2(t) \in L^2(\Omega)$. Let v_{tk}^2 be the solution of $\bar{\mathcal{D}}v_t^2 = h_2(t,\chi_k)$. From (3.21), we know that $\{v_{tk}^2\}_{k=1}^\infty$ is a Cauchy sequence. This proves the compactness of $V(t)$. Thus, $U(t) := S(t) + V(t)$, the solution operator defined by (3.12), is an α-contraction for $t > \tau$. Using (3.7) and (3.6), we know that $T(t)$ is also an α-contraction. Recall that the radius of essential spectra $\sigma_{ess}(T(t))$ of $T(t)$ is bounded above by $\alpha(T(t))$, If $\sigma_P(A) \subset \{z \in \mathbb{C} : \mathrm{Re}z < 0\}$, then the spectral radius of $T(t)$ is less than 1 for large t, and therefore (3.19) follows directly from Lemma 7.4.2 in [11]. □

Finally we remark that if there exists $\lambda \in \sigma_P(A)$ such that $\mathrm{Re}\lambda > 0$, then the zero solution of (3.1) is always unstable. In fact, in this case, (3.9) will always have an unstable manifold in $\mathcal{C}_\alpha$, and therefore, there is a solution $\bar{v}(t)$ of (3.9) approaching to infinity. Recall that the solutions of (3.9) and (3.1) are correlated by (3.7). It then follows from Lemma 3.3 that there exists a solution (associated with $\bar{v}(t)$) of (3.1) tending to infinity, that is, the zero solution of (3.1) is unstable.

3.2 Spectral Set

In what follows, we will analyze $\sigma_P(A)$ in detail. Define the real-valued Sobolev space X by

$$X = \left\{u \in H^2(\Omega) : \frac{\partial u(x)}{\partial n} = 0, \quad x \in \partial\Omega\right\},$$

and the complexification of X is given by

$$X_{\mathbb{C}} = X \oplus iX = \{x_1 + ix_2 : x_1, x_2 \in X\}.$$

Let $0 = \lambda_0 < \lambda_1 \le \lambda_2 \le \cdots \le \lambda_n \le \cdots$ be the sequence of eigenvalues of the linear eigenvalue problem

$$\begin{cases} \Delta\phi + \lambda\phi = 0, & x \in \Omega, \\ \dfrac{\partial\phi}{\partial n}(x) = 0, & x \in \partial\Omega. \end{cases} \tag{3.22}$$

Then $\lim_{n\to\infty} \lambda_n = \infty$. By assuming that $\psi(x,t) = e^{\mu t} y(x)$, we obtain that the characteristic equation of (3.1) is given by

$$\mu y - D_1\Delta y - D_2 u^* e^{-\mu\tau}\Delta y - g'(u^*) y = 0, \tag{3.23}$$

where $0 \ne y \in X_{\mathbb{C}}$ and $\mu \in \mathbb{C}$.

For $n \in \mathbb{N}_0$, define $E(n,\tau,\mu)$ by

$$E(n,\tau,\mu) = \mu + D_1\lambda_n + D_2 u^* \lambda_n e^{-\mu\tau} - g'(u^*). \tag{3.24}$$

Then we have the following basic property.

Lemma 3.5 *$\mu \in \mathbb{C}$ is an eigenvalue of the characteristic equation (3.23) if and only if there exists some $n_0 \in \mathbb{N}_0$ such that $E(n_0,\tau,\mu) = 0$ and y is an eigenvector of (3.22) with $\lambda = \lambda_{n_0}$.*

Proof Assume that $\mu \in \mathbb{C}$ is an eigenvalue of the characteristic equation (3.23) and the corresponding eigenfunction is $0 \ne y_\mu(x) \in X_{\mathbb{C}}$. Then

$$\mu y_\mu - D_1\Delta y_\mu - D_2 u^* e^{-\mu\tau}\Delta y_\mu - g'(u^*) y_\mu = 0. \tag{3.25}$$

Let $\{\phi_{nj} : 1 \le j \le \dim E_n\}$ be an orthonormal basis of the eigenspace E_n of the linear eigenvalue problem (3.22) corresponding to the eigenvalue λ_n. Then $y_\mu(x)$ can be decomposed as

$$y_\mu(x) = \sum_{n=1}^{\infty} \sum_{j=1}^{\dim E_n} a_{nj}\phi_{nj}(x), \tag{3.26}$$

where $a_{nj} \in \mathbb{C}$. Substituting (3.26) into (3.25) and noticing that $\Delta\phi_{nj} = -\lambda_n\phi_{nj}$ yields

$$\begin{aligned} &\sum_{n=1}^{\infty} \sum_{j=1}^{\dim E_n} (\mu + D_1\lambda_n + D_2 u^*\lambda_n e^{-\mu\tau} - g'(u^*)) a_{nj}\phi_{nj}(x) \\ &= \sum_{n=1}^{\infty} \sum_{j=1}^{\dim E_n} E(n,\tau,\mu) a_{nj}\phi_{nj}(x) = 0. \end{aligned} \tag{3.27}$$

Multiplying the two sides of (3.27) by $\phi_{nj}(x)$ and integrating the resulted equality on Ω gives

$$E(n,\tau,\mu) a_{nj} = 0, \quad n \in \mathbb{N}_0, \quad 1 \le j \le \dim E_n. \tag{3.28}$$

In addition, from $y_\mu \ne 0$ we know that there exists a certain $a_{n_0 j_0} \in \mathbb{C}$ such that $a_{n_0 j_0} \ne 0$ and hence (3.28) leads to $E(n_0,\tau,\mu) = 0$. That is, μ is an eigenvalue of $E(n_0,\tau,\mu)$.

Now we suppose that μ is an eigenvalue of $E(n_0,\tau,\mu)$, that is, $E(n_0,\tau,\mu) = 0$. Take

$$y_\mu(x) = \phi_{n_0 1}(x).$$

Then $y_\mu \neq 0$ and

$$\begin{aligned}&\mu y_\mu - D_1 \Delta y_\mu - D_2 u^* e^{-\mu\tau} \Delta y_\mu - g'(u^*) y_\mu \\ &\quad = (\mu + D_1 \lambda_{n_0} + D_2 u^* \lambda_{n_0} e^{-\mu\tau} - g'(u^*)) \phi_{n_0 1}(x) = E(n_0, \tau, \mu) \phi_{n_0 1}(x) = 0.\end{aligned}$$

Therefore μ is also an eigenvalue of the Eq. (3.23). This completes the proof. □

Let $\sigma_n(\tau)$ be defined by

$$\sigma_n(\tau) \equiv \{\mu \in \mathbb{C} : E(n, \tau, \mu) = 0\}. \tag{3.29}$$

Then Lemma 3.5 demonstrates that the spectral set of (3.23) can be expressed by

$$\sigma(\tau) = \bigcup_{n=0}^{\infty} \sigma_n(\tau). \tag{3.30}$$

From (3.30) one can say that the constant steady state $u = u^*$ of the model (2.4) is linearly (or locally asymptotically) stable for the delay $\tau \geq 0$ if for all $n \in \mathbb{N}_0$, $\sigma_n(\tau) \subseteq \mathbb{C}^- = \{\alpha + \beta i : \alpha < 0\}$. However, if there exists some $n \in \mathbb{N}_0$ such that $\sigma_n \cap \mathbb{C}^+ \neq \emptyset$ where $\mathbb{C}^+ = \{\alpha + \beta i : \alpha > 0\}$, then the steady state $u = u^*$ of the model (2.4) is unstable and we also say that $u = u^*$ is unstable for the delay $\tau \geq 0$ in mode-n. In particular, the constant steady state $u = u^*$ of the model (2.4) is unstable for any delay $\tau \geq 0$ when $g'(u^*) > 0$ since in this case it is unstable in mode-0.

We remark that instead of assuming $\psi(x,t) = e^{\mu t} y(x)$ to derive (3.23), one can also solve (3.1) by using Fourier series. Indeed we write the solution of (3.1) as

$$\psi(x,t) = \sum_{n=0}^{\infty} T_n(t) \phi_n(x),$$

where $\{\phi_n(x) : n \in \mathbb{N}_0\}$ is an orthonormal basis of $L^2(\Omega)$ consisting of normalized eigenfunctions of (3.22) satisfying $\int_\Omega \phi_n^2(x)dx = 1$. Then $T_n(t)$ satisfies the delay differential equation

$$\begin{cases} T_n'(t) = (-D_1 \lambda_n + g'(u^*)) T_n(t) - D_2 u^* \lambda_n T_n(t-\tau), & t > 0, \\ T_n(t) = \tilde{\varphi}_n(t) := \int_\Omega \varphi_0(x,t) \phi_n(x) dx, & -\tau \leq t \leq 0. \end{cases} \tag{3.31}$$

Well-known theory [20] can be used to established the existence and uniqueness of solution to (3.31). In particular, the stability of equilibrium $T_n = 0$ with respect to (3.31) is equivalent to that all roots μ of $E(n, \tau, \mu) = 0$ have negative real parts. Hence the stability of u^* with respect to (2.4) is again reduced to the characteristic equation $E(n, \tau, \mu) = 0$.

To determine the stability, we give the description of the spectral set $\sigma(\tau)$ and $\sigma_n(\tau)$. First we consider the case that $D_2 > 0$.

Theorem 3.6 *Suppose that $D_1, D_2 > 0$. Let $\sigma_n(\tau)$ be the spectral set of* (3.1) *defined as in* (3.29). *Then $\sigma_0(\tau) = \{g'(u^*)\}$ for any $\tau \geq 0$; for any $n \in \mathbb{N}$, define*

$$\bar{\mu}_n := g'(u^*) - (D_1 + D_2 u^*) \lambda_n, \quad \tau_n^* = \sup_{\mu \leq \bar{\mu}_n} F_n(\mu), \tag{3.32}$$

where

$$F_n(\mu) := -\frac{1}{\mu} \ln \left(\frac{g'(u^*) - D_1 \lambda_n - \mu}{D_2 u^* \lambda_n} \right), \quad \mu \in (-\infty, \bar{\mu}_n]. \tag{3.33}$$

Then

1. $\sigma_n(0) = \{\bar{\mu}_n\}$;
2. *for* $\tau \in (0, \tau_n^*)$, $\sigma_n(\tau) \cap \mathbb{R} = \{\mu_{1,n}, \mu_{2,n}\}$ *with* $-\infty < \mu_{2,n} < \mu_{1,n} < \bar{\mu}_n$ *satisfying* $F_n(\mu_{1,n}) = F_n(\mu_{2,n}) = \tau$; $\sigma_n(\tau_n^*) \cap \mathbb{R} = \{\mu_{1,n}\} \subseteq \mathbb{R}$ *with* $-\infty < \mu_{1,n} < \bar{\mu}_n$ *satisfying* $F_n(\mu_{1,n}) = \tau_n^*$; *and for* $\tau \in (\tau_n^*, \infty)$, $\sigma_n(\tau) \cap \mathbb{R} = \emptyset$;
3. *for* $\tau \in (0, \infty)$, $\sigma_n(\tau) \cap (\mathbb{C} - \mathbb{R}) = \bigcup_{k=0}^{\infty} \sigma_{n,k}(\tau)$, *and* $\sigma_{n,k}(\tau) = \{\alpha_{n,k}(\tau) \pm i\beta_n(\alpha_{n,k}, \tau)\}$, *where* $\alpha_{n,k}(\tau)$ *satisfies*

$$D_2 u^* \lambda_n \tau = e^{\tau\alpha} \frac{\cos^{-1}(p_n(\alpha, \tau)) + 2k\pi}{\sqrt{1 - p_n^2(\alpha, \tau)}} := q_{n,k}(\alpha, \tau), \quad k \in \mathbb{N}_0, \tag{3.34}$$

and $p_n(\alpha, \tau)$ *and* $\beta_n(\alpha, \tau)$ *are defined by*

$$\begin{aligned} p_n(\alpha, \tau) &:= \frac{e^{\tau\alpha}[g'(u^*) - \alpha - D_1\lambda_n]}{D_2 u^* \lambda_n}, \\ \beta_n(\alpha, \tau) &:= D_2 u^* \lambda_n e^{-\tau\alpha} \sqrt{1 - p_n^2(\alpha, \tau)}. \end{aligned} \tag{3.35}$$

Moreover for fixed $n \in \mathbb{N}$, *the set of all real-valued eigenvalues of* (3.1) *is an analytic curve*

$$\Sigma_{r,n} = \{(\tau, \mu) : 0 \le \tau \le \tau_n^*, \mu \in \sigma_n(\tau)\} = \{(F_n(\mu), \mu) : \mu \le \bar{\mu}_n\}, \tag{3.36}$$

and the set of all complex-valued eigenvalues of (3.1) *can be represented by a union of denumerable analytic curves* $\Sigma_{c,n} = \bigcup_{k=0}^{\infty} \Sigma_{c,n,k}$ *where*

$$\begin{aligned} \Sigma_{c,n,k} &= \{(\tau, \alpha) : \tau > 0, \alpha \pm i\beta_n(\alpha, \tau) \in \sigma_n(\tau)\} \\ &= \{(\tau, \alpha) : \tau > 0, D_2 u^* \lambda_n \tau = q_{n,k}(\alpha, \tau)\}. \end{aligned} \tag{3.37}$$

Proof It is easy to see that $\sigma_0(\tau) = \{g'(u^*)\}$ for any $\tau \ge 0$. So from now on, we assume that $n \in \mathbb{N}$ is fixed. When $\tau = 0$, $\mu = g'(u^*) - (D_1 + D_2 u^*)\lambda_n$ is the only eigenvalue in $\sigma_n(0)$. Then in the following we assume that $\tau > 0$. First we determine the real-valued eigenvalues of (3.1) when $\tau > 0$ and $n \in \mathbb{N}$ is fixed. If $\mu \in \mathbb{R}$ is an eigenvalue of (3.1), then from (3.24) and solving $E(n, \tau, \mu) = 0$, we obtain that $\tau = F_n(\mu)$ where $F_n(\mu)$ is defined in (3.32). Since $\tau > 0$, it is necessary that $\mu < g'(u^*) - (D_1 + D_2 u)\lambda_n := \bar{\mu}_n$. Hence (τ, μ) lies on the curve $\Sigma_{r,n}$ defined as in (3.36). It is easy to see that $F_n(\bar{\mu}_n) = 0$ and $\lim_{\mu \to -\infty} F_n(\mu) = 0$. We show that there exists a unique $\mu_n^* \in (-\infty, \bar{\mu}_n)$ such that

$$F_n'(\mu) > 0, \;\; \mu \in (-\infty, \mu_n^*), \;\; F_n'(\mu) < 0, \;\; \mu \in (\mu_n^*, \bar{\mu}_n). \tag{3.38}$$

Let

$$G_{1,n}(\mu) = \frac{-\mu}{g'(u^*) - D_1\lambda_n - \mu}, \quad \text{and} \quad G_{2,n}(\mu) = \ln \frac{g'(u^*) - D_1\lambda_n - \mu}{D_2 u^* \lambda_n}.$$

It is straightforward to show that $G_{1,n}'(\mu) > 0$ and $G_{2,n}'(\mu) < 0$ for $\mu \in (-\infty, \bar{\mu}_n)$, $\lim_{\mu \to -\infty} G_{1,n}(\mu) = 1$, $G_{1,n}(\bar{\mu}_n) > 1$, $\lim_{\mu \to -\infty} G_{2,n}(\mu) = \infty$ and $G_{2,n}(\bar{\mu}_n) = 0$. Therefore $G_{1,n}(\mu) = G_{2,n}(\mu)$ has a unique root for $\mu \in (-\infty, \bar{\mu}_n)$, and so does

$$F_n'(\mu) = -\left[\frac{-\mu}{g'(u^*) - D_1\lambda_n - \mu} - \ln \frac{g'(u^*) - D_1\lambda_n - \mu}{D_2 u^* \lambda_n}\right] / \mu^2 = 0$$

This implies that $F_n(\mu)$ attains its maximum $\tau_n^* > 0$ at some $\mu_n^* \in (-\infty, \bar{\mu}_n)$, and (3.38) holds. In particular, (3.38) implies that for $\tau \in (0, \tau_n^*)$, there exist exactly two $\mu \in (-\infty, \bar{\mu}_n)$

(called $\mu_{1,n}$ and $\mu_{2,n}$ with $\mu_{2,n} < \mu_{1,n}$) such that $\tau = F_n(\mu)$, and for $\tau > \tau_n^*$, there is no $\mu > 0$ such that $\tau = F_n(\mu)$. When $\tau = \tau_n^*$, the only root of $\tau = F_n(\mu)$ is $\mu = \mu_n^* = \mu_{1,n}$. This completes the proof for real-valued eigenvalues (part 1–3 and $\Sigma_{r,n}$).

Next we consider the complex-valued eigenvalues of (3.1) when $\tau > 0$ and $n \in \mathbb{N}$ is fixed. Suppose that $\mu = \alpha + i\beta$ ($\beta > 0$) is a root of (3.24). That is, $E(n, \tau, \alpha + i\beta) = 0$. Then, separating the real and imaginary parts of (3.24), we have

$$\begin{aligned} &\alpha + D_1\lambda_n - g'(u^*) + D_2u^*\lambda_n e^{-\tau\alpha}\cos\beta\tau = 0,\\ &\beta - D_2u^*\lambda_n e^{-\tau\alpha}\sin\beta\tau = 0, \end{aligned} \tag{3.39}$$

which yields

$$(\alpha + D_1\lambda_n - g'(u^*))^2 + \beta^2 = D_2^2(u^*)^2\lambda_n^2 e^{-2\tau\alpha}. \tag{3.40}$$

Hence $\beta = \beta_n(\alpha, \tau)$, where $p_n(\alpha, \tau)$ and $\beta_n(\alpha, \tau)$ are defined by (3.35), and it follows from the first equation of (3.39) that (α, τ) satisfies

$$\cos(D_2u^*\lambda_n e^{-\tau\alpha}\tau\sqrt{1 - p_n^2(\alpha, \tau)}) = p_n(\alpha, \tau), \tag{3.41}$$

or equivalently (3.34).

We show that the solution set of (3.34) for any fixed $\tau > 0$ is not empty. Let $\tilde{\alpha}_n = g'(u^*) - D_1\lambda_n - \tau^{-1}$. Then it is easy to see that

$$\lim_{\alpha\to-\infty} p_n(\alpha, \tau) = 0, \quad \lim_{\alpha\to\infty} p_n(\alpha, \tau) = -\infty,$$

and $p_n(\alpha, \tau)$ is strictly decreasing in α for $\alpha \in (\tilde{\alpha}_n, \infty)$, and is strictly increasing in α for $\alpha \in (-\infty, \tilde{\alpha}_n)$. It then follows that there exists $\hat{\alpha}_n > \tilde{\alpha}_n$ such that $p_n(\hat{\alpha}_n, \tau) = -1$. If $p_n(\tilde{\alpha}_n, \tau) = \dfrac{e^{\tau\tilde{\alpha}_n}}{D_2\lambda_n\tau} > 1$, then there exists $\alpha_n^*, \alpha_n^{**} \in \mathbb{R}$ such that $\alpha_n^* < \tilde{\alpha}_n < \alpha_n^{**} < \hat{\alpha}_n$ and $p_n(\alpha_n^*, \tau) = p_n(\alpha_n^{**}, \tau) = 1$. Therefore, the admissible domain for $q_{n,k}(\alpha, \tau)$ is either $I_n^1 := (-\infty, \hat{\alpha}_n)$ or $I_n^2 := (-\infty, \alpha_n^*) \cup (\alpha_n^{**}, \hat{\alpha}_n)$. Since $\lim_{\alpha\to-\infty} q_{n,k}(\alpha, \tau) = 0$, and $\lim_{\alpha\to\hat{\alpha}_n-} q_{n,k}(\alpha, \tau) = \lim_{\alpha\to\alpha_n^*-} q_{n,k}(\alpha, \tau) = \infty$, the Eq. (3.34) $q_{n,k}(\alpha, \tau) = D_2u^*\lambda_n\tau$ always have roots in either I_n^1 or $(-\infty, \alpha_n^*)$. We denote such root by $\alpha_{n,k}(\tau)$, then $\alpha_{n,k}(\tau) \pm i\beta_n(\alpha_{n,k}, \tau) \in \sigma_n(\tau)$. Therefore for any $\tau > 0$, there exists complex eigenvalue $\alpha_{n,k}(\tau) \pm i\beta_n(\alpha_{n,k}, \tau)$ where $\alpha_{n,k}(\tau)$ satisfies (3.34). □

Note that $\alpha_{n,k}(\tau)$ is not necessarily unique, and it is not clear whether the set $\Sigma_{c,n,k}$ is connected. Figure 1 shows the distribution of eigenvalues of (3.24) for varying τ and $D_1, D_2 > 0$.

We also have the following asymptotic behavior of $\alpha_{n,k}(\tau)$.

Proposition 3.7 *Suppose that $D_1, D_2 > 0$, $\alpha_{n,k}(\tau)$ is a root of (3.34) for $n \in \mathbb{N}$, $k \in \mathbb{N}_0$ and $\tau > 0$. Then*

1. *For fixed $\tau > 0$ and $n \in \mathbb{N}$, $\lim_{k\to\infty} \alpha_{n,k}(\tau) = -\infty$.*
2. *For fixed $\tau > 0$ and $k \in \mathbb{N}$, $\lim_{n\to\infty} \alpha_{n,k}(\tau) = \dfrac{\ln(D_2u^*/D_1)}{\tau}$.*

Proof For fixed $\tau > 0$ and $n \in \mathbb{N}$, from (3.34), the root $\alpha_{n,k}(\tau)$ satisfies

$$D_2u^*\lambda_n\tau\sqrt{1 - p_n^2(\alpha, \tau)} = e^{\tau\alpha}[\cos^{-1}(p_n(\alpha, \tau)) + 2k\pi]. \tag{3.42}$$

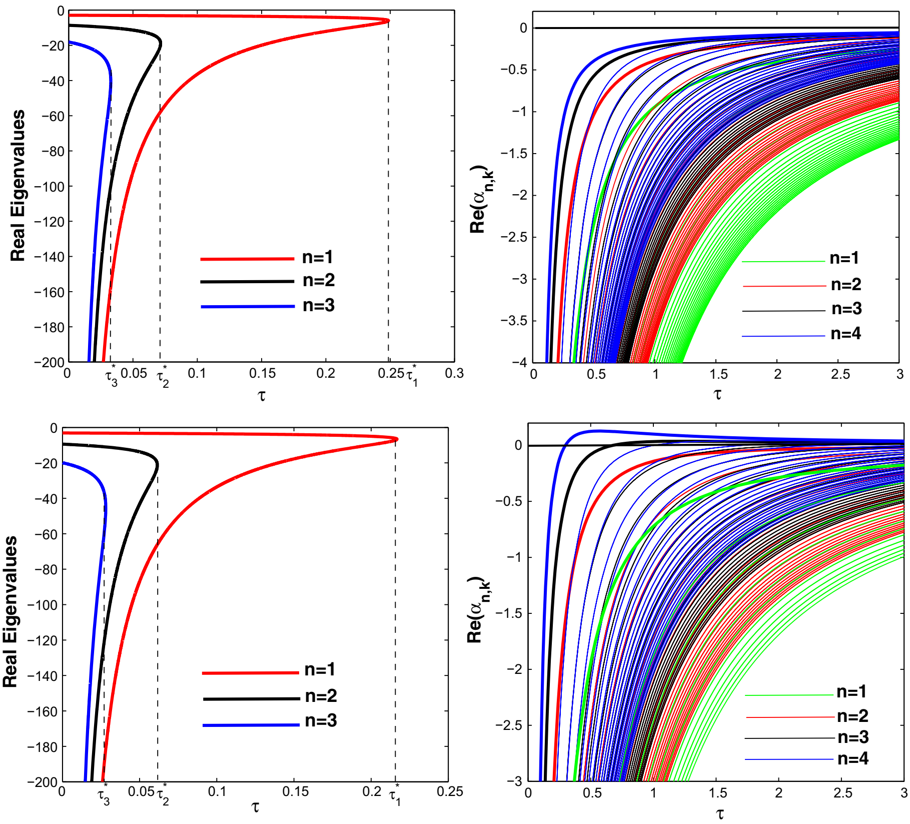

Fig. 1 Distribution of eigenvalues of (3.24) for varying time delay τ for different diffusion coefficients with all the parameters are the same ($u^* = 1$, $g'(u^*) = -1$): $D_1 = 1$ and $D_2 = 0.9$ for top two panels; and $D_1 = 1$ and $D_2 = 1.1$ for bottom ones. Real-valued eigenvalues of (3.24) for $n = 1, 2, 3$ are shown in left two panels, and the real parts $\alpha_{n,k}$ of complex eigenvalues of (3.24), for $n = 1, 2, 3, 4$ and $k = 1, \ldots, 20$, are plotted in the right two panels

When $k \to \infty$, $\cos^{-1}(p_n(\alpha, \tau)) + 2k\pi \to \infty$ but the left hand side of (3.42) is bounded. Hence $e^{\tau\alpha} \to 0$ which implies that $\alpha_{n,k}(\tau) \to -\infty$ as $k \to \infty$. This proves part 1.

For part 2, we fix $\tau > 0$ and $k \in \mathbb{N}$. Substituting $\alpha = \dfrac{\ln(D_2 u^*/D_1)}{\tau} + \delta$ into (3.39) for some $\delta \in \mathbb{R}$ and $\beta > 0$, then (3.39) becomes

$$
\begin{aligned}
&\frac{\ln(D_2 u^*/D_1)}{\tau} + \delta - g'(u^*) + D_1\lambda_n(1 + e^{-\tau\delta}\cos\beta\tau) = 0,\\
&\beta - D_1\lambda_n e^{-\tau\delta}\sin\beta\tau = 0.
\end{aligned}
\tag{3.43}
$$

From the second equation of (3.43), we know $\delta = \dfrac{1}{\tau}\ln\dfrac{D_1\lambda_n\sin\beta\tau}{\beta}$. It then follows from the first equation of (3.43) that

$$
G_n(\beta) := \frac{\ln(D_2/D_1)}{\tau} + \frac{1}{\tau}\ln\frac{D_1\lambda_n\sin\beta\tau}{\beta} - g'(u^*) + D_1\lambda_n + \frac{\beta\cos\beta\tau}{\sin\beta\tau} = 0.
$$

The function $G_n(\beta)$ is well-defined and continuous on the interval $\left(\frac{2k\pi}{\tau}, \frac{(2k+1)\pi}{\tau}\right)$ for any $k \in \mathbb{N}_0$, and $\lim_{\beta\to\frac{(2k+1)\pi}{\tau}-} G_n(\beta) = -\infty$ for any $n \in \mathbb{N}$. Note the fact that $\lim_{\beta\to\frac{2k\pi}{\tau}+} \frac{\sin\beta\tau}{\beta} = 0$ for $k \in \mathbb{N}$, and $\lim_{x\to 0+}\left[\frac{1}{\tau}\ln(D_1\lambda_n x) + \frac{1}{x}\right] = \infty$ for any $n \in \mathbb{N}$. Therefore $\lim_{\beta\to\frac{2k\pi}{\tau}+} G_n(\beta) = +\infty$. This implies $G_n(\beta) = 0$ always has a root, denoted by $\beta_{n,k}$, in $\left(\frac{2k\pi}{\tau}, \frac{(2k+1)\pi}{\tau}\right)$ for any $n \in \mathbb{N}$ and $k \in \mathbb{N}$. Note that $\beta\tau \in (2k\pi, (2k+1)\pi)$ implies that (3.34) is satisfied.

Now, for fixed k, we show that $\beta_{n,k} \to \frac{(2k+1)\pi}{\tau}$ as $n \to \infty$. Since

$$G_{n+1}(\beta) - G_n(\beta) = \frac{1}{\tau}\ln\frac{\lambda_{n+1}}{\lambda_n} + D_1(\lambda_{n+1} - \lambda_n) > 0$$

for large n, we know that $\beta_{n,k}$ is strictly increasing in n, and hence converges to some $\bar\beta \le \frac{(2k+1)\pi}{\tau}$. If $\bar\beta < \frac{(2k+1)\pi}{\tau}$, we have

$$\begin{aligned}0 &= \lim_{n\to\infty} G_n(\beta_{n,k})\\ &= \frac{\ln(D_2u^*/D_1)}{\tau} - g'(u^*) + \lim_{n\to\infty}\left[\frac{1}{\tau}\ln\frac{D_1\lambda_n\sin\bar\beta\tau}{\bar\beta} + D_1\lambda_n + \frac{\bar\beta\cos\bar\beta\tau}{\sin\bar\beta\tau}\right] = +\infty,\end{aligned}$$

which is a contradiction. Thus $\bar\beta = \frac{(2k+1)\pi}{\tau}$.

Recall that $\alpha_{n,k} = \frac{\ln(D_2u^*/D_1)}{\tau} + \delta_{n,k}$, where $\delta_{n,k} = \frac{1}{\tau}\ln\frac{D_1\lambda_n\sin\beta_{n,k}\tau}{\beta_{n,k}}$. It remains to prove that $\lim_{n\to\infty}\delta_{n,k} = 0$ for fixed $k \in \mathbb{N}$. Indeed, from (3.43), we have

$$D_1^2\lambda_n^2 e^{-2\tau\delta_{n,k}} = (\beta_{n,k})^2 + \left[\frac{\ln(D_2u^*/D_1)}{\tau} + \delta_{n,k} - g'(u^*) + D_1\lambda_n\right]^2$$

which will not hold for large n if $\delta_{n,k} \nrightarrow 0$ as $n \to \infty$. This completes the proof. □

The spectral sets $\sigma(\tau)$ and $\sigma_n(\tau)$ have similar structure when $D_1 > 0$ and $D_2 < 0$ (see Fig. 2 for the distribution of eigenvalues of (3.24) for varying τ with $D_1 > 0$, $D_2 < 0$).

Theorem 3.8 *Suppose that $D_1 > 0$ and $D_2 < 0$. Let $\sigma_n(\tau)$ be the spectral set of (3.1) defined as in (3.29). Then $\sigma_0(\tau) = \{g'(u^*)\}$ for any $\tau \ge 0$; for any $n \in \mathbb{N}$, let $\bar\mu_n$ and $F_n(\mu)$ be defined as in (3.32) and (3.33). Then*

1. $\sigma_n(0) = \{\bar\mu_n\}$;
2. *for $\tau \in (0,\infty)$, $\sigma_n(\tau) \cap \mathbb{R} = \{\mu_{3,n}\}$ satisfying $F_n(\mu_{3,n}) = \tau$; $\mu_{3,n} < 0$ if $\bar\mu_n < 0$, and $\mu_{3,n} > 0$ if $\bar\mu_n > 0$;*
3. *for $\tau \in (0,\infty)$, $\sigma_n(\tau)\cap(\mathbb{C}-\mathbb{R}) = \bigcup_{k=0}^{\infty}\sigma_{n,k}(\tau)$, and $\sigma_{n,k}(\tau) = \{\alpha_{n,k}(\tau) \pm i\beta_n(\alpha_{n,k},\tau)\}$, where $\alpha_{n,k}(\tau)$ satisfies (3.34) and*

$$\lim_{n\to\infty}\alpha_{n,k}(\tau) = \frac{\ln(-D_2u^*/D_1)}{\tau}.$$

Moreover for fixed $n \in \mathbb{N}$, the set of all real-valued eigenvalues of (3.1) is an analytic curve

$$\Sigma_{r,n} = \{(\tau,\mu) : \tau \ge 0, \mu \in \sigma_n(\tau)\} = \{(F_n(\mu),\mu) : \mu \in (0,\bar\mu_n] \text{ or } [\bar\mu_n, 0)\}, \quad (3.44)$$

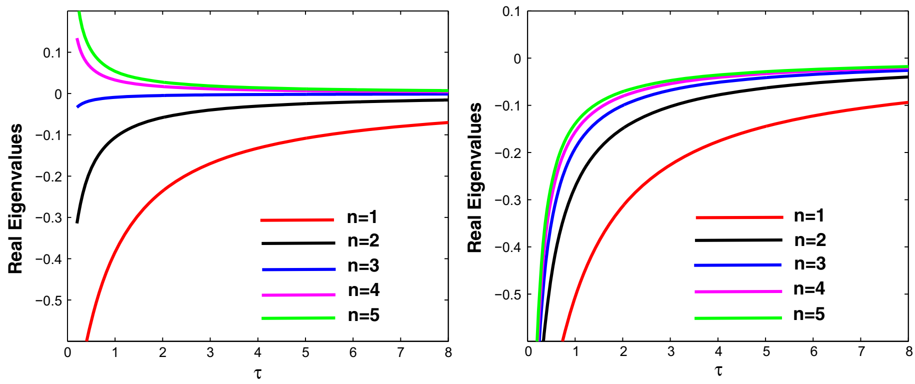

Fig. 2 Distribution of real eigenvalues of (3.24) for $D_2 = -0.9$ and $D_2 = -1.1$ (right)

and the set of all complex-valued eigenvalues of (3.1) *can be represented by a union of denumerable analytic curves* $\Sigma_{c,n} = \bigcup_{k=0}^{\infty} \Sigma_{c,n,k}$ *given as in* (3.37).

Proof The proof is similar to that of Theorem 3.6 and the structure of complex eigenvalues is same as the one with $D_2 > 0$. For real-valued eigenvalues, recall that $\tau = F_n(\mu)$. Since $\tau > 0$, it is necessary that $\bar{\mu}_n < \mu < 0$ when $\bar{\mu}_n < 0$ or $0 < \mu < \bar{\mu}_n$ when $\bar{\mu}_n > 0$, if μ is a real-valued eigenvalue. For $\bar{\mu}_n < 0$, we have $\lim_{\mu\to 0-} F_n(\mu) = +\infty$, $F_n(\bar{\mu}_n) = 0$ and $F_n'(\mu) > 0$. Similarly, for $\bar{\mu}_n < 0$, $\lim_{\mu\to 0+} F_n(\mu) = +\infty$, $F_n(\bar{\mu}_n) = 0$ and $F_n'(\mu) < 0$. Therefore, for any $\tau > 0$, there exists a unique $\tilde{\mu}_n$ between 0 and $\bar{\mu}_n$ such that $F_n(\tilde{\mu}_n) = \tau$ no matter $\bar{\mu}_n > 0$ or $\bar{\mu}_n < 0$. □

In Fig. 3, we plot the distribution of roots of (3.24) for fixed τ. We can observe that the real parts of the roots approach $\ln(|D_2|u^*/D_1)/\tau$ as $n \to \infty$, no matter $D_2 > 0$ or $D_2 < 0$. As a direct consequence of Theorems 3.6 and 3.8, and Proposition 3.7, we have the following stability results of a constant steady state u^* of (2.4).

Corollary 3.9 *Let u^* be a constant steady state of* (2.4).

1. *If $g'(u^*) > 0$, then u^* is unstable for any $D_1 > 0$, $D_2 \in \mathbb{R}$ and $\tau \geq 0$.*
2. *If $g'(u^*) < 0$, then u^* is locally asymptotically stable when $D_1 \geq |D_2|u^*$ and $\tau \geq 0$, and it is unstable when $D_1 < |D_2|u^*$ and $\tau > 0$.*

Proof If $g'(u^*) > 0$, then $\sigma_0(\tau) = \{g'(u^*)\}$ for any $\tau \geq 0$ so u^* is unstable for any $D_1 >$, $D_2 \in \mathbb{R}$ and $\tau \geq 0$.

If $D_2 > 0$ and $g'(u^*) < 0$, then from Theorem 3.6, all real-valued eigenvalues $\mu \leq \bar{\mu}_n < 0$. Assume that $D_1 \geq D_2 u^*$. Suppose that (3.1) has an eigenvalue $\alpha + i\beta$ with $\alpha \leq 0$. Then α satisfies (3.34) with $|p_n(\alpha, \tau)| \leq 1$. But $\alpha \geq 0$ and $D_1 \geq D_2 u^*$ imply that $|p_n(\alpha, \tau)| > 1$, which is a contradiction. Hence when $D_1 \geq D_2 u^*$, any complex-valued eigenvalue of (3.1) has negative real part. Thus u^* is locally asymptotically stable in this case. On the other hand, if $D_1 < D_2 u^*$, then for any $\tau > 0$, from Proposition 3.7 part 2, we have $\alpha_{n,k} > 0$ for sufficiently large $n \in \mathbb{N}$, hence u^* is unstable.

If $D_2 < 0$ and $g'(u^*) < 0$, then all real eigenvalues are negative for $D_1 + D_2 u^* > 0$, and there are infinitely many positive eigenvalue s for $D_1 + D_2 u^* < 0$. Moreover, the complex roots have strictly negative real parts when $D_1 + D_2 u^* > 0$, and infinitely many complex roots will have positive real parts when when $D_1 + D_2 u^* < 0$, since they concentrate on

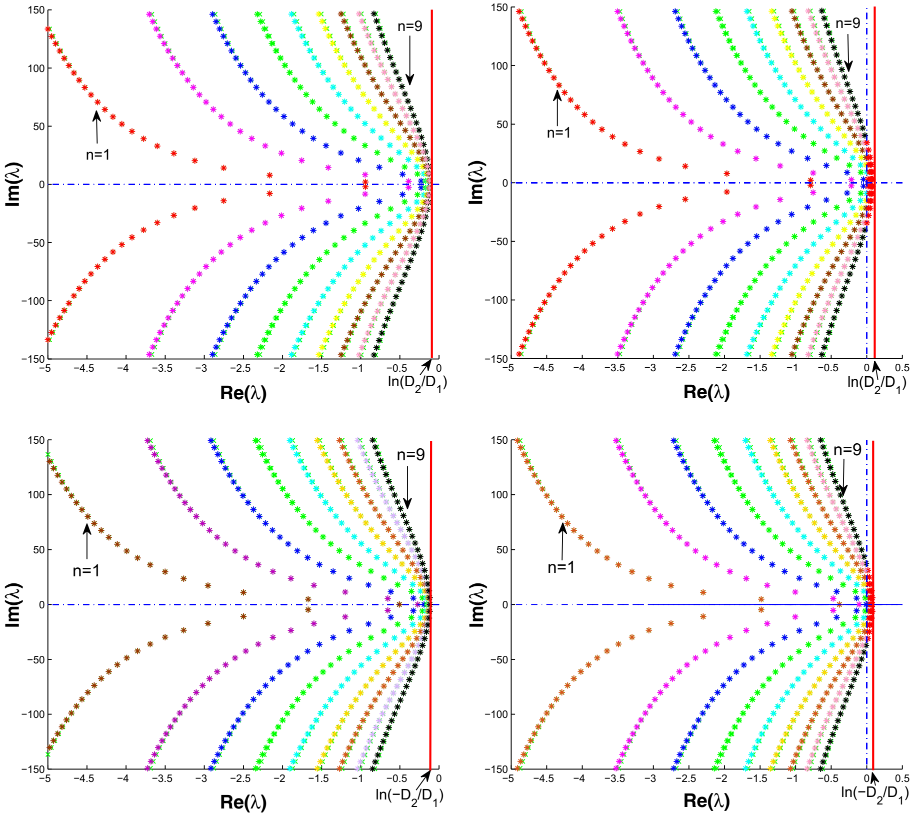

Fig. 3 Distribution of roots of (3.24) for $n = 1, \ldots, 9$ (distinguished by different colors from left to right) with fixed $\tau = 1$. Here, $D_1 = 1$, $D_2 = 0.9$ for the left panel, $D_1 = 1$, $D_2 = 1.1$ for the right one, and all the other parameters are the same ($u^* = 1$ and $g'(u^*) = -1$). For each n, (3.24) is a transcendental equation, and hence it has infinitely many roots. Furthermore, there are only a finite number of roots in any vertical strip in the complex plane. It is observed that there are infinitely many roots, marked by red start in the right panel, with positive real parts when $D_2 > D_1$ (Color figure online)

the vertical line $\{\mu \in \mathbb{C} : \mathrm{Re}\mu = \frac{\ln(-D_2u^*/D_1)}{\tau}\}$ in the complex plane. In summary, when $g'(u^*) < 0$, u^* is linearly stable thus locally asymptotically stable by Theorem 3.4 when $D_1 \geq |D_2|u^*$ and all $\tau \geq 0$, and it is unstable when $D_1 < |D_2|u^*$ and all $\tau > 0$. □

Corollary 3.9 shows that the local stability of u^* completely depends on the ratio $|D_2|u^*/D_1$, but is *independent* of the time delay τ.

Finally we determine the Hopf bifurcation values τ in the case of $D_2u^* > D_1$ and $g'(u^*) < 0$. Note that from Corollary 3.9, in this case, the constant steady state u^* is always unstable for all $\tau > 0$, so there exists no stability switch value $\tau_0 > 0$ which separates stability/instability regimes. But nevertheless such Hopf bifurcation values show that the real part of pairs of complex eigenvalues change from positive to negative. From (3.34) and (3.35), if $\mu = i\beta$ ($\beta > 0$) is an eigenvalue of (3.24), then

$$\tau_{n,k} = \frac{\cos^{-1}(p_n(0,\tau)) + 2k\pi}{\sqrt{1 - p_n^2(0,\tau)}D_2u^*\lambda_n}, \quad \text{where} \quad p_n(0,\tau) = \frac{g'(u^*) - D_1\lambda_n}{D_2u^*\lambda_n}. \tag{3.45}$$

It is clear that $\lim_{n\to\infty} \tau_{n,k} = 0$ for a fixed $k \in \mathbb{N}$, and $\lim_{k\to\infty} \tau_{n,k} = \infty$ for a fixed $n \in \mathbb{N}$. Thus for any $\tau > 0$, there are infinitely many pair of complex eigenvalues with positive real parts when $D_2u^* > D_1$ and $g'(u^*) < 0$.

4 Dynamics with Different Reaction Functions

The local stability of constant steady state solution u^* of (2.4) has been completely classified from results in Sect. 3. In this section we demonstrate global dynamics of (2.4) under under several different assumptions on the nonlinearity of the reaction function $g(u)$: (i) logistic growth; or (ii) strong Allee effect growth.

4.1 Logistic Growth Rate

We assume that g takes the form of logistic type growth rate, defined as follows:

$$\begin{aligned} & g \in C^1([0,\infty), \mathbb{R}),\ \ g(0) = g(1) = 0,\ \ g(u)(u-1) < 0, \quad \text{for } u \in (0,\infty)\backslash\{1\}, \\ & g'(0) = a > 0,\ \ g'(1) = -b < 0, \quad a, b > 0. \end{aligned} \tag{4.1}$$

For the global boundedness of solutions, the following estimate for the total population (L^1 norm) is easy to observe.

Lemma 4.1 *Suppose that the conditions of Proposition 2.1 are satisfied. Then there exists $C_1 > 0$ depending only on g such that*

$$\limsup_{t\to\infty} \int_\Omega u(x,t)dx \le C_1|\Omega|. \tag{4.2}$$

for any solution $u(x,t)$ of (2.4) and (4.1).

Proof Integrating the equation in (2.4), and using the boundary conditions in (2.5) and (4.1), we obtain

$$\frac{d}{dt}\int_\Omega u(x,t)dx = \int_\Omega g(u(x,t))dx. \tag{4.3}$$

From (4.1), there exists $a_1, b_1 > 0$ such that

$$g(u) \le a_1u - b_1u^2, \quad \text{for } \ u \in [0,1]. \tag{4.4}$$

Define

$$U(t) = \int_\Omega u(x,t)dx, \quad t \ge 0.$$

Then from (4.3) and (4.4), we have

$$U'(t) \le a_1U(t) - b_1\int_\Omega u^2(x,t)dx \le a_1U(t) - b_1|\Omega|^{-1}U^2(t), \tag{4.5}$$

which implies (4.2) with $C_1 = a_1/b_1$. □

It is easy to see that the steady-state solutions of the model (2.4) satisfy the following boundary value problem

$$\begin{cases} D_1\Delta u + D_2\mathrm{div}(u\nabla u) + g(u) = 0, & x \in \Omega, \\ \dfrac{\partial u}{\partial n}(x) = 0, & x \in \partial\Omega. \end{cases} \tag{4.6}$$

The non-negative solutions of (4.6) can be classified as follows.

Proposition 4.2 *Suppose that $D_1, D_2 > 0$, and $g(u)$ satisfies the condition (4.1). Then the only non-negative solutions of (4.6) are $u = 0$ and $u = 1$.*

Proof From the strong maximum principle, any non-negative solution $u(x)$ of (4.6) satisfy $0 \le u(x) \le 1$ for $x \in \overline{\Omega}$, and either $u(x) \equiv 0$, or $u(x) \equiv 1$, or $0 < u(x) < 1$ for $x \in \overline{\Omega}$. In the last case, we integrate (4.6) over Ω, and we obtain $\int_\Omega g(u(x))dx = 0$. But on the other hand, $0 < u(x) < 1$ for $x \in \overline{\Omega}$ and $g(u) > 0$ for $u \in (0, 1)$ imply that $\int_\Omega g(u(x))dx > 0$. We obtain a contradiction. Hence $u(x) \equiv 0$ or $u(x) \equiv 1$. □

From Corollary 3.9, we have the following conclusion on the stability of the two non-negative steady state solutions $u = 0$ and $u = 1$.

Proposition 4.3 *Assume that $g(u)$ satisfies the condition (4.1). Then, the trivial steady state $u = 0$ of (2.4) is unstable for any $\tau \ge 0$ and $D_1 > 0$, and the constant positive steady state $u = 1$ is locally asymptotically stable for all $\tau > 0$ and $D_1 \ge |D_2|$, and it is unstable for all $\tau > 0$ when $|D_2| > D_1 > 0$.*

The precise global dynamics of (2.4) is not known. For $D_1 \ge |D_2|$, the positive steady state $u = 1$ appears to be not only locally asymptotically stable but indeed global asymptotically stable. Figures 4 and 5 show numerical simulations in that case of $D_1 > |D_2|$ in which the solution tends to $u = 1$ as $t \to \infty$. On the other hand, when $|D_2| > D_1$, the solution appears to be oscillatory but divergent, see Figs. 4 and 5. When the delay τ increases, the wave length of patterns increases, and the time period also increases. When τ is small, all or more modes are unstable, then patterns are neutralized. When τ is large, some modes are unstable and some are stable, however, unstable ones are more observable.

4.2 Strong Allee Effect

For the growth rate $g(u) = G(u)(u - \beta)$ with strong Allee effect, where $G(u)$ satisfies the condition (4.1) and $\beta \in (0, 1)$, there are constant steady states $u^* = 0, \beta$ or 1 for (2.4). Note that different from logistic case, (2.4) may have other non-constant steady state state solutions but they are unstable even when $\tau = 0$ [18,24]. The characteristic equation of (3.24) at a constant steady state u^* is given by

$$\mu y - D_1\Delta y - D_2u^*e^{-\mu\tau}\Delta y - G'(u^*)(u^* - \beta)y - G(u^*)y = 0, \tag{4.7}$$

where $0 \ne y \in X_{\mathbb{C}}$, which is equivalent to a sequence of following transcendental equations

$$\mu + D_1\lambda_n + D_2u^*\lambda_n e^{-\mu\tau} - G'(u^*)(u^* - \beta) - G(u^*) = 0, \quad n \in \mathbb{N}_0. \tag{4.8}$$

At $u^* = 0$, the roots of (4.8) are given by $\mu = -D_1\lambda_n - a\beta < 0$, indicating that 0 is always stable. For $u^* = \beta$ and $u^* = 1$, we have the following conclusion, via the same logic as the logistic growth case.

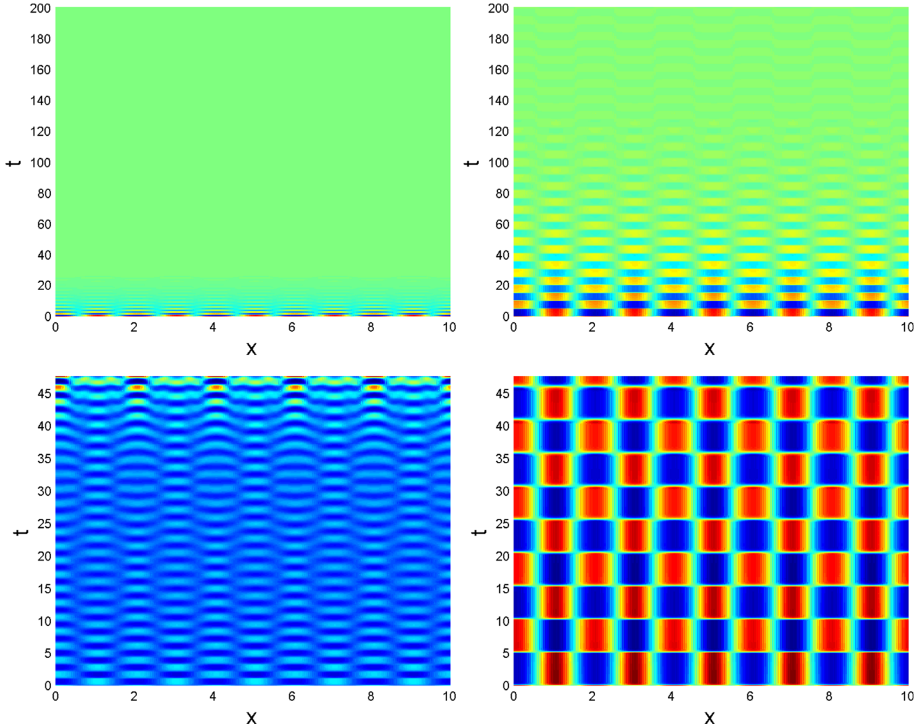

Fig. 4 The solutions of (2.4) and (4.1) in the case of $D_1 = 1$ and $D_2 = 0.9$ for different time delay: $\tau = 1$ for the top-left panel and $\tau = 5$ for the top-right one. Both solutions tend to the constant steady states as $t \to +\infty$, while the convergent speed for large delay is much slower than the one for small delay. Here $\Omega = (0, 10)$, and $g(u) = 0.1u(1-u)$, and the initial value $\phi = 1 + 0.5\cos \pi x$. If D_2 is increased to 1.1 without changing all the other parameters, then the solution, with different time delay $\tau = 1$ (bottom left) and $\tau = 5$ (bottom right), will oscillate both temporally and spatially on a certain interval of time

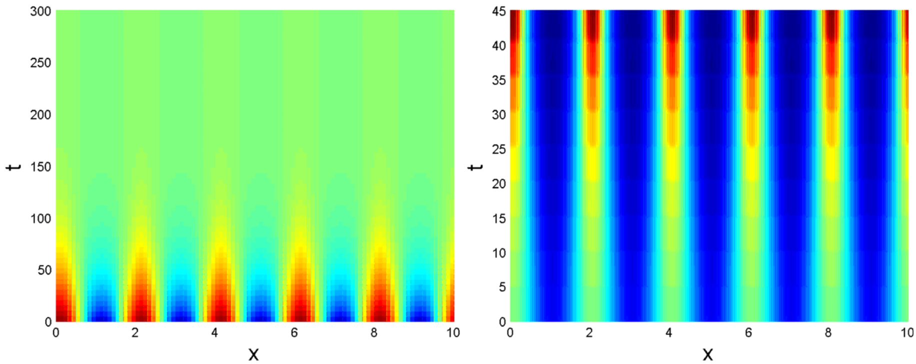

Fig. 5 Numerical simulations of (2.4) and (4.1) for $D = -0.9$ and $D_2 = -1.1$. Here $\tau = 5, \phi = 1+0.1\cos \pi x$ and all the other parameters are the same as Fig. 4

Proposition 4.4 *Assume that $g(u) = G(u)(u - \beta)$ with $G(u)$ satisfying the condition (4.1). The steady states $u = \beta$ is always unstable. If $|D_2| < D_1$, then the constant steady state $u = 1$ is asymptotically stable for all $\tau > 0$; and if $0 < D_1 < |D_2|$, then $u = 1$ is unstable for all $\tau > 0$.*

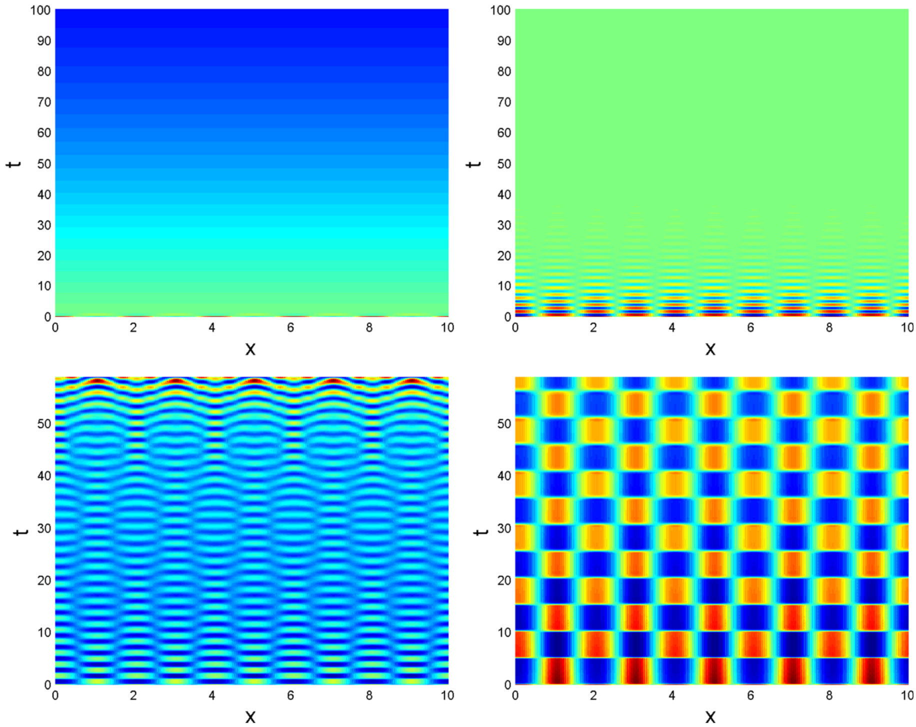

Fig. 6 Choose $D_1 = 1$, $r = 0.1$, $\Omega = (0, 10)$ and Allee effect growth rate with $\beta = 0.2$. If $D_2 = 0.9 < D_1$, then solution tends to the steady states $u = 0$ with small positive initial value $0.1 + 0.1\cos(\pi x)$ (top-left), and to the steady states $u = 1$ with initial value $1 + 0.1\cos(\pi x)$ (top-right). If $D_2 = 1.1 > D_1$, the solution also exhibits oscillation in almost the same manner as in the logistic growth rate: $\tau = 1$ for the bottom-left panel, and $\tau = 5$ for the bottom-right one

We illustrate, by numerical simulations, the stabilities of the steady states $u = 0$ and $u = 1$ under different orders of the two diffusion coefficients D_1 and D_2 (see Fig. 6). When these steady states are both unstable, we obtain almost same patterns as in the logistic growth case (see Figs. 5 and 6).

5 Discussion

In this paper, we propose a novel reaction–diffusion model with spatial memory for "clever" animal movements. The spatial memory is modeled in the form of a delayed diffusion term via a modified Fick's law. We show that the model is well-posed and the stability of a spatially homogeneous steady state only depends on the order of the two diffusion coefficients but is independent of the time delay. We then discuss the model with three different reaction functions.

Open mathematical questions include (1) general results on the global stability of the spatially homogeneous steady state; (2) when the spatially homogeneous steady state is unstable, what is the asymptotic behavior of the solutions? (3) spatiotemporal pattern formation induced by delayed diffusion; (4) the local stability of a spatially non-homogeneous steady state in which the time delay shall play a critical role.

Naturally animals want to escape from high density due to the limitation of resources, in which case $D_2 > 0$. However, some social animals have aggregations, such as starling flocks [1] and insects [3], in the purpose of group defense or group working. To consider this collective animal behavior, we have $D_2 < 0$. The selection of $D_2 > 0$ or $D_2 < 0$ depends on the social behavior of the studied animal species: some always defend and work by individuals, while some always defend and work in groups. Of course, some animals may use optimal mixed strategies of social behavior according to the environmental conditions, for instance, they select to move to higher density this time but select to move to lower density next time. In this case we have the switch between $D_2 > 0$ and $D_2 < 0$ when some environmental conditions change.

The modeling idea of spatial memory behind our proposed model can be extended to multi-species interaction models such as competition models or predator-prey models in the presence of "clever" animal movements. We are in the process of analyzing and simulating some of these extended models. Another extension could be to use a distributed delay instead of a discrete delay for memory waning.

The spatial memory included in our mathematical model is a specific type of episodic-like memory [6], such as footprint judgment within the observable area. Other memory-based movements include, but not limited to, cognitive map (like a GPS navigation system) [10], path integration [25], cultural transmission [5], genetic memory [9], and natal homing [23]. It is theoretically feasible and extremely important to construct mechanistic animal movement models in the incorporation of these different types of memory and cognition.

Acknowledgements The authors thank the anonymous reviewer and the editor for helpful suggestions which improved the initial version of the manuscript. The first author's research is partially supported by NSF Grants DMS-1313243 and DMS-1715651. The second author's research is partially supported by Chinese NSF Grants 11671110 and 11201097. The third author's research is partially supported by an NSERC grant. The fourth author's research is partially supported by a Chinese NSF grant 61763024 and Foundation of a Hundred Youth Talents Training Program of Lanzhou Jiaotong University 152022.

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