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TRAVELLING WAVES FOR THE POPULATION GENETICS MODEL WITH DELAY

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Abstract

Under the assumptions that the spatial variable is one dimensional and the distributed delay kernel is the general Gamma distributed delay kernel, when the average delay is small, the existence of travelling wave solutions for the population genetics model with distributed delay is obtained by using the linear chain trick and geometric singular perturbation theory. On the other hand, for the population genetics model with small discrete delay, the existence of travelling wave solutions is obtained by employing a technique which is based on a result concerning the existence of the inertial manifold for small discrete delay equations.

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1. Introduction

One of the cornerstones of mathematical biology is the population genetics model

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u(1-u)[(\tau_1 - \tau_2)(1-u) - (\tau_3 - \tau_2)u], \tag{1.1}$$

where $u \in \mathbb{R}$, $x \in \mathbb{R}$, $t > 0$. It is well known that this model was first formulated by Fisher [8] and that it is an important reaction-diffusion equation for modelling travelling fronts in population dynamics. For detailed biological backgrounds, see [1, 2, 8, 17].

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Generally, it is assumed that $\tau_1 \geq \tau_3$ and the range of the solution $u(t, x)$ is contained in [0, 1]. Therefore, there are three cases

$$(1) \quad \tau_3 \leq \tau_2 < \tau_1, \quad (2) \quad \tau_2 < \tau_3 \leq \tau_1 \quad \text{and} \quad (3) \quad \tau_3 \leq \tau_1 < \tau_2. \tag{1.2}$$

Aronson and Weinberger [1, 2] discussed the stability properties of the equilibrium states and the existence of the travelling wave solutions connecting these equilibria in detail for Equation (1.2) under the above three different cases.

Recently, considerable interest has focused on the improvement of this model by including temporal delay and spatial averaging acting on the nonlinear reaction term, see [4, 11, 12].

Under the assumption that the distributed delay is a weak kernel, Ashwin *et al.* [3] studied the existence of travelling wave fronts for the population genetics model with distributed delay by using geometrical singular perturbation theory. Meanwhile, Wu and Zou [20] discussed the existence of travelling wave fronts for the population genetics model with discrete delay by employing the monotone iteration and upper and lower solution methods. However, the equations considered in the papers [3] and [20] only correspond to the delayed population genetics model (1.1) with the above case (1), that is, when the parameters τ_1, τ_2 and τ_3 satisfy $\tau_3 \leq \tau_2 < \tau_1$.

In this paper, we consider the delayed population genetics model (1.1) with case (3) above, that is, we assume that the parameters τ_1, τ_2 and τ_3 satisfy $\tau_3 < \tau_1 < \tau_2$. In this case, the reaction term function $f(u) = u(1-u)[(\tau_1 - \tau_2)(1-u) - (\tau_3 - \tau_2)u]$ has the following properties.

For some $\beta \in (0, 1)$, $f(u) < 0$ in $(0, \beta)$, $f(u) > 0$ in $(\beta, 1)$, and $f'(0) < 0$, $f'(1) < 0$, $\int_0^1 f(u)\, du > 0$.

These properties imply that there exists some $\alpha \in (0, 1/2)$ such that

$$\alpha = \frac{\tau_2 - \tau_1}{2\tau_2 - \tau_1 - \tau_3}$$

and $f(u) = (2\tau_2 - \tau_1 - \tau_3)u(1-u)(u-\alpha)$.

Because we discuss the problem on the infinite one-dimensional spatial domain $x \in \mathbb{R}$, it is possible and convenient to express Equation (1.1) in dimensionless variables and parameters. Taking $t^* = (2\tau_2 - \tau_1 - \tau_3)t$, $x^* = x\sqrt{2\tau_2 - \tau_1 - \tau_3}$ and dropping the asterisks for notational simplicity, we obtain

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u(1-u)(u-\alpha). \tag{1.3}$$

For convenience, we directly consider the existence of travelling wave fronts for the following population genetics model with distributed delay:

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u(1 - gk ** u)(u - \alpha), \tag{1.4}$$

where the convolution $gk ** u$ is denoted by

$$gk ** u(x,t) = \int_{-\infty}^{\infty}\int_{-\infty}^{t} g(x-y,t-s)k(t-s)u(s,y)dsdy,$$

and the following population genetics model with discrete delay:

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u[1-u(t-\tau,x)](u-\alpha), \tag{1.5}$$

where $\tau > 0$ is a small delay. We assume that

$$g(x,t) = \frac{1}{2\sqrt{\pi t}} e^{-x^2/4t} \quad \text{and} \quad \int_0^{\infty} k(t)\,dt = 1, \quad tk(t) \in L^1((0,\infty);\mathbb{R}).$$

The derivation of this kind of kernel can be found in [4]. The average delay for the distributed delay kernel $k(t)$ is defined as

$$\tau = \int_0^{\infty} tk(t)\,dt.$$

Usually we use the Gamma distribution delay kernel

$$k(t) = \frac{\alpha^n t^{n-1} e^{-\alpha t}}{(n-1)!}, \quad n = 1, 2, \ldots, \tag{1.6}$$

where $\alpha > 0$ is a constant, n is an integer, with average delay $\tau = n/\alpha$. Two special cases $k(t) = \alpha e^{-\alpha t}$ $(n = 1)$ and $k(t) = \alpha^2 t e^{-\alpha t}$ $(n = 2)$, are called the weak delay kernel and the strong delay kernel respectively [18].

Mathematically, the convolution $gk ** u$ in Equation (1.4) which depends on both the temporal delay and spatial averaging is called spatiotemporal delay or nonlocal delay. A reasonable and detailed discussion on introducing nonlocal delay into the biological model is presented in the articles [4, 11, 12].

Under the assumption that the distributed delay kernel $k(t)$ is the general Gamma distributed delay kernel (1.6) and by using the linear chain trick, the population genetics model (1.4) with distributed delay can be transformed into a non-delay $2n+2$ dimensional ordinary differential system. When the average delay τ is sufficiently small, the $2n + 2$ dimensional ordinary differential system is a standard singularly perturbed system. By using geometric singular perturbation theory [7, 15], we will prove in this paper that there exists a travelling wave solution for Equation (1.4) connecting the equilibria $u_1 = 0$ and $u_3 = 1$ for a particular wave speed.

However, for the population genetics model with discrete delay (1.5), there is no way to recast Equation (1.5) into a non-delay finite-dimensional ordinary differential system. Therefore, the linear chain trick and geometric singular perturbation theory

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[7, 15] cannot be applied to show the existence of a travelling wave solution for Equation (1.5). From the viewpoint of dynamical systems, travelling wave equations (1.5) are infinite dimensional and thus the search for travelling wave solutions is a much deeper and more difficult problem. In this paper, we will employ a technique from the papers [5] and [6] to deal with the existence of the travelling wave solution for the population genetics model with discrete delay (1.5). This technique is based on a result concerning the existence of the inertial manifold for delay equations with small discrete delays.

There are many papers [3, 10, 13, 14, 19] in which the existence of travelling wave solutions for a single-species biological model with distributed (or nonlocal) delay is obtained by geometric singular perturbation theory. However, it is always assumed in these papers that the distributed delay kernel $k(t)$ is a weak or strong kernel. In this paper, we assume that the distributed delay kernel $k(t)$ is the general Gamma distributed delay kernel (1.6). Moreover, these models in [3, 10, 13, 14, 19] only possess two equilibria and the travelling waves of these models are Fisher waves. In this paper, the model under consideration has exactly three equilibria and the travelling wave of the model is a bistable travelling wave.

Recently, geometric singular perturbation theory has also been used to justify the existence of a periodic solution for differential equations with distributed delay [16].

This paper is organised as follows. In Section 2, the existence of a travelling wave for the population genetics model with distributed delay is justified by employing the linear chain trick and geometric singular perturbation theory. Section 3 presents some preliminaries, while Section 4 deals with the existence of a travelling wave for the population genetics model with discrete delay.

2. Existence of a travelling wave for the population genetics model with distributed delay

For convenience, we present some results from the papers [1] and [2] which will be employed in the proof of our theorem.

Making the travelling wave transformation $u(t,x) = u(z)$, $z = x - ct$, where $c > 0$ is the wave speed, and substituting $u(t,x) = u(z)$ into Equation (1.3), we obtain

$$u'' + cu' + u(1-u)(u-\alpha) = 0. \tag{2.1}$$

Let $u' = v$. Equation (2.1) is equivalent to the following system:

$$\begin{aligned} u' &= v, \\ v' &= -cv - u(1-u)(u-\alpha). \end{aligned} \tag{2.2}$$

Obviously, system (2.2) has three equilibria, $E_1 = (0, 0)$, $E_2 = (\alpha, 0)$ and $E_3 = (1, 0)$, which correspond to the three equilibria $u_1 = 0$, $u_2 = \alpha$ and $u_3 = 1$ of Equation (1.3) respectively.

The following results can be found in the papers [1] and [2].

LEMMA 2.1. *There exists a unique wave speed $c = c_* > 0$ such that system* (2.2) *possesses a heteroclinic orbit $\eta_0(z)$ connecting the critical points $E_1 = (0, 0)$ and $E_3 = (1, 0)$. Moreover, the travelling wave $u(z)$ is strictly monotonically decreasing.*

In this section, we will prove the following theorem.

THEOREM 2.2. *Assume that the distributed delay kernel $k(t)$ is the general Gamma distributed delay kernel* (1.6). *Then for sufficiently small average delay τ,* (1.4) *possesses a travelling wave solution $\eta_\tau(z)$ connecting the equilibria $u_1 = 0$ and $u_3 = 1$ for a particular value $c = c(\tau)$ with $c(0) = c_*$.*

PROOF. When the distributed delay kernel $k(t)$ is the general Gamma distributed delay kernel, we define

$$w_n(t, x) = \int_{-\infty}^{\infty}\int_{-\infty}^{t} \frac{e^{-(x-y)^2/4(t-s)}}{2\sqrt{\pi(t-s)}} \left(\frac{n}{\tau}\right)^n \frac{(t-s)^{n-1}e^{-n(t-s)/\tau}}{(n-1)!} u(s, y)\, ds\, dy,$$

$$\vdots$$

$$w_1(t, x) = \int_{-\infty}^{\infty}\int_{-\infty}^{t} \frac{e^{-(x-y)^2/4(t-s)}}{2\sqrt{\pi(t-s)}} \left(\frac{n}{\tau}\right) e^{-n(t-s)/\tau} u(s, y)\, ds\, dy.$$

By computation, it is easy to see that Equation (1.4) is transformed to

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u(1 - w_n)(u - \alpha),$$

$$\frac{\partial w_i}{\partial t} = \begin{cases} \dfrac{\partial^2 w_i}{\partial x^2} + \dfrac{n}{\tau} w_{i-1} - \dfrac{n}{\tau} w_i, & i = n, \dots, 2; \\ \dfrac{\partial^2 w_1}{\partial x^2} + \dfrac{n}{\tau} u - \dfrac{n}{\tau} w_1, & i = 1. \end{cases}$$

Making the travelling wave transformation $u(t, x) = u(z)$, $z = x - ct$, where $c > 0$ is the wave speed, and similarly for the other state variables, yields

$$-cu' = u'' + u(1 - w_n)(u - \alpha),$$

$$-cw_i' = \begin{cases} w_n'' + \dfrac{n}{\tau} w_{i-1} - \dfrac{n}{\tau} w_i, & i = n, \dots, 2; \\ w_1'' + \dfrac{n}{\tau} u - \dfrac{n}{\tau} w_1, & i = 1, \end{cases} \tag{2.3}$$

where $'$ denotes differentiation with respect to z. Let us introduce $v = u'$ and $v_i = w_i'$, $i = 1, \dots, n$. Because we are interested in the situation in which the delay is small, we can replace τ with $\varepsilon^2\tau$, where ε is a small parameter. Then system (2.3) becomes

$$\begin{aligned}
u' &= v, & v' &= -cv - u(1-w_n)(u-\alpha),\\
w_n' &= v_n, & \varepsilon^2 v_n' &= -\varepsilon^2 c v_n - \frac{n}{\tau}w_{n-1} + \frac{n}{\tau}w_n,\\
&\cdots\cdots & &\cdots\cdots\\
w_1' &= v_1, & \varepsilon^2 v_1' &= -\varepsilon^2 c v_1 - \frac{n}{\tau}u + \frac{n}{\tau}w_1.
\end{aligned}$$

If we introduce the new state variables

$$\widetilde{u} = u, \quad \widetilde{v} = v, \quad \widetilde{w}_n = w_n, \quad \widetilde{v}_n = \varepsilon v_n, \quad \dots, \quad \widetilde{w}_1 = w_1, \quad \widetilde{v}_1 = \varepsilon v_1,$$

and then drop the tildes, we have

$$\begin{aligned}
u' &= v, & v' &= -cv - u(1-w_n)(u-\alpha),\\
\varepsilon w_n' &= v_n, & \varepsilon v_n' &= -\varepsilon c v_n - \frac{n}{\tau}w_{n-1} + \frac{n}{\tau}w_n,\\
&\cdots\cdots & &\cdots\cdots\\
\varepsilon w_1' &= v_1, & \varepsilon v_1' &= -\varepsilon c v_1 - \frac{n}{\tau}u + \frac{n}{\tau}w_1.
\end{aligned} \tag{2.4}$$

Note that when ε is a small parameter, system (2.4) is a standard singularly perturbed system. By introducing a new independent variable η defined by $z = \varepsilon\eta$, system (2.4) transforms into

$$\begin{aligned}
\dot{u} &= \varepsilon v, & v' &= \varepsilon[-cv - u(1-w_n)(u-\alpha)],\\
\dot{w}_n &= v_n, & \dot{v}_n &= -\varepsilon c v_n - \frac{n}{\tau}w_{n-1} + \frac{n}{\tau}w_n,\\
&\cdots\cdots & &\cdots\cdots\\
\dot{w}_1 &= v_1, & \dot{v}_1 &= -\varepsilon c v_1 - \frac{n}{\tau}u + \frac{n}{\tau}w_1,
\end{aligned} \tag{2.5}$$

where $\dot{}$ denotes differentiation with respect to η. The singularly perturbed systems (2.4) and (2.5) are called the slow and the fast systems respectively. The two systems are equivalent when $\varepsilon > 0$.

Note that the system (2.4) has two equilibria denoted by $\overline{E}_1$ and $\overline{E}_3$,

$$\overline{E}_1 = (0, 0, \dots, 0, 0) \quad \text{and} \quad \overline{E}_3 = (1, 0, \dots, 1, 0).$$

Therefore, when $\varepsilon > 0$ (that is, when the delay is present), the existence of a travelling wave solution of Equation (1.4) connecting the equilibria $u_1 = 0$ and $u_3 = 1$ is equivalent to the existence of a heteroclinic connection between the equilibrium points $\overline{E}_1$ and $\overline{E}_3$ of the $(2n+2)$-dimensional system (2.4) that correspond to the equilibria $u_1 = 0$ and $u_3 = 1$ of Equation (1.4).

It is obvious that the critical manifold M_0 can be taken as any compact subset of the following set

$$\left\{(u, v, w_n, v_n, \dots, w_1, v_1) \in \mathbb{R}^{2n+2} : v_n = \cdots = v_1 = 0, w_n = \cdots = w_1 = u\right\},$$

and the critical manifold M_0 should be chosen to be large enough to contain the heteroclinic orbit $\eta_0(z)$. By the geometric singular perturbation theorem in [7, 15], we know that if M_0 is normally hyperbolic, then for sufficiently small $\varepsilon > 0$, there exists an invariant slow manifold M_ε for the system (2.4), which implies the persistence of the slow manifold M_0. Furthermore, by analysing system (2.4) restricted to the slow manifold M_ε, which is a two-dimensional submanifold of $\mathbb{R}^{2n+2}$, the existence of the heteroclinic connection we are seeking can be established.

To verify normal hyperbolicity, it is necessary to verify that when $\varepsilon = 0$, the matrix of the linearisation of the fast system (2.5) at any point of the critical manifold M_0 has exactly two $(= \dim M_0)$ eigenvalues on the imaginary axis and the remainder with nonzero real part. The matrix of the linearisation of the fast system (2.5), when $\varepsilon = 0$, is the following $(2n+2) \times (2n+2)$ matrix:

$$\begin{pmatrix}
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \cdots & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \cdots & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & \cdots & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & n/\tau & 0 & -n/\tau & 0 & 0 & 0 & \cdots & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & \cdots & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & n/\tau & 0 & -n/\tau & 0 & \cdots & 0 & 0 & 0 & 0 & 0 \\
\vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \cdots & \vdots & \vdots & \vdots & \vdots & \vdots \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \cdots & 0 & 0 & 1 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \cdots & 0 & n/\tau & 0 & -n/\tau & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \cdots & 0 & 0 & 0 & 0 & 1 \\
-n/\tau & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \cdots & 0 & 0 & 0 & n/\tau & 0
\end{pmatrix}$$

which has eigenvalues

$$\left\{0,\ 0,\ \sqrt{n}/\sqrt{\tau}, \dots,\ \sqrt{n}/\sqrt{\tau},\ -\sqrt{n}/\sqrt{\tau}, \dots,\ -\sqrt{n}/\sqrt{\tau}\right\}.$$

Thus, normal hyperbolicity is verified. Therefore, the geometric singular perturbation theorem [7, 15] implies that there exists an invariant manifold M_ε, close to M_0, for the singularly perturbed system (2.4) when $\varepsilon > 0$ is sufficiently small. Moreover, M_ε can be expressed in the following form:

$$M_\varepsilon = \left\{ (u, v, w_n, v_n, \dots, w_1, v_1) \in \mathbb{R}^{2n+2} \;\middle|\; \begin{array}{ll} w_i = u + h_i(u, v, \varepsilon), & i = n, \dots, 1, \\ v_i = k_i(u, v, \varepsilon), & i = n, \dots, 1 \end{array} \right\},$$

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with $h_i(u, v, 0) = 0$, $k_i(u, v, 0) = 0$ for $i = 1, \ldots, n$. The functions h_i and k_i can be computed by substitution into system (2.4).

Indeed, straightforward calculations, utilising the fact that M_ε is an invariant manifold for system (2.4), yield that the functions h_i and k_i respectively satisfy

$$\begin{aligned} \varepsilon c k_n - n(h_{n-1} - h_n) &= \varepsilon \left[\frac{\partial k_n}{\partial u} v + \frac{\partial k_n}{\partial v} [-c - u(1 - u - h_n)(u - \alpha)] \right], \\ &\vdots \\ \varepsilon c k_1 - n(-h_1) &= \varepsilon \left[\frac{\partial k_1}{\partial u} v + \frac{\partial k_1}{\partial v} [-c - u(1 - u - h_n)(u - \alpha)] \right], \end{aligned} \tag{2.6}$$

and

$$k_i = \varepsilon \left[v + \frac{\partial h_i}{\partial u} v + \frac{\partial h_i}{\partial v} [-c - u(1 - u - h_n)(u - \alpha)] \right], \quad i = n, \ldots, 1. \tag{2.7}$$

Since $h_i(u, v, 0) = 0$ and $k_i(u, v, 0) = 0$ for $i = 1, \ldots, n$, we denote

$$\begin{aligned} h_i(u, v, \varepsilon) &= \varepsilon h_i^{(1)}(u, v) + \varepsilon^2 h_i^{(2)}(u, v) + \cdots, \\ k_i(u, v, \varepsilon) &= \varepsilon k_i^{(1)}(u, v) + \varepsilon^2 k_i^{(2)}(u, v) + \cdots. \end{aligned}$$

Substituting $h_i(u, v, \varepsilon)$ and $k_i(u, v, \varepsilon)$ for $i = 1, \ldots, n$ into Equations (2.6) and (2.7), and equalising the coefficients of the same order power of ε in both sides of Equations (2.6) and (2.7), we obtain

$$\begin{aligned} &h_1^{(1)} = \cdots = h_n^{(1)} = 0, & &k_1^{(1)} = \cdots = k_n^{(1)} = v, \\ &h_i^{(2)} = -\frac{i}{n} u(1 - u)(u - \alpha), \ i = 1, \ldots, n, & &k_1^{(2)} = \cdots = k_n^{(2)} = 0. \end{aligned}$$

In this way, we can determine the coefficients of ε^m in the functions h_i and k_i, $i = 1, \ldots, n$ for an arbitrary natural number m.

Therefore the slow system (2.4) restricted to the manifold M_ε becomes

$$\begin{aligned} u' &= v, \\ v' &= -cv - u(1 - u - h_n)(u - \alpha), \end{aligned}$$

that is,

$$\begin{aligned} u' &= v, \\ v' &= -cv - u(1 - u)(u - \alpha) + O(\varepsilon). \end{aligned} \tag{2.8}$$

Note that the equilibria $\overline{E}_1$ and $\overline{E}_3$ are critical points for the full slow system (2.4) for arbitrary ε. Therefore, for $\varepsilon > 0$ sufficiently small, the system (2.8) still possesses the equilibria $E_1 = (0, 0)$ and $E_3 = (1, 0)$.

In the following, we employ a technique from [10] and [19] to prove that system (2.8) has a heteroclinic orbit $\eta_\varepsilon(z)$ connecting the equilibria $E_1 = (0, 0)$ and $E_3 = (1, 0)$, when the parameter $\varepsilon > 0$ is sufficiently small.

We may now rewrite system (2.8) as

$$\begin{aligned} u' &= v, \\ v' &= \Phi(u, v, c, \varepsilon), \end{aligned} \tag{2.9}$$

where $\Phi(u, v, c, 0) = -cv - u(1-u)(u-\alpha)$. We know that when $\varepsilon = 0$ the travelling wave solution $u(z)$ for system (2.2) is strictly monotone if the wave speed $c = c_* > 0$. Therefore, in the (u, v) phase plane, it can be characterised as the graph of some function, that is, $v = w(u, c_*)$. By the stable manifold theorem, for sufficiently small ε we can also characterise the unstable manifold at the point $(1, 0)$ as the graph of some function $v = w_1(u, c_*, \varepsilon)$, where $w_1(1, c_*, \varepsilon) = 0$. Furthermore, by continuous dependence of the solutions on parameters, this manifold must cross the line $u = 1/2$ somewhere if ε is sufficiently small.

Similarly, let $v = w_2(u, c_*, \varepsilon)$ be the equation for the stable manifold at the origin. Clearly, $w_2(0, c_*, \varepsilon) = 0$ and it also crosses the line $u = 1/2$ somewhere if ε is sufficiently small. Thus, we have $w_1(u, c_*, 0) = w_2(u, c_*, 0) = w(u, c_*)$. For $\varepsilon = 0$ and $c = c_*$, the equation of the corresponding wave in the (u, v) phase plane is $v = w(u, c_*)$. To show that there is a heteroclinic connection when $\varepsilon > 0$ and is sufficiently small, we want to show that there exists a unique value of $c = c(\varepsilon)$, satisfying $c(0) = c_*$, such that the manifolds w_1 and w_2 cross the line $u = 1/2$ at the same point. Define $G(c, \varepsilon) = w_1(1/2, c, \varepsilon) - w_2(1/2, c, \varepsilon)$. Note that both $v = w_1(u, c, \varepsilon)$ and $v = w_2(u, c, \varepsilon)$ satisfy the equation

$$\frac{dv}{du} = \frac{\Phi(u, v, c, \varepsilon)}{v}.$$

We have

$$\begin{aligned} \frac{d}{du}\left(\frac{\partial w_1}{\partial c}(u, c_*, 0)\right) &= \frac{\partial}{\partial c}\left(\frac{dw_1}{du}(u, c, 0)\right)\bigg|_{c=c_*} \\ &= \frac{\partial}{\partial c}\left(\frac{\Phi(u, w_1(u, c, 0), c, 0)}{w_1(u, c, 0)}\right)\bigg|_{c=c_*} \\ &= \frac{\partial}{\partial c}\left(\frac{-cw_1(u, c, 0) - u(1-u)(u-\alpha)}{w_1(u, c, 0)}\right)\bigg|_{c=c_*} \\ &= \frac{\partial}{\partial c}\left(-c - \frac{u(1-u)(u-\alpha)}{w_1(u, c, 0)}\right)\bigg|_{c=c_*} \\ &= -1 + \frac{u(1-u)(u-\alpha)}{w(u, c_*)^2}\frac{\partial w_1}{\partial c}(u, c_*, 0). \end{aligned}$$

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Therefore

$$\frac{d}{du}\left(\frac{\partial w_1}{\partial c}(u, c_*, 0)\exp\left[-\int_{1/2}^{u}\frac{\xi(1-\xi)(\xi-\alpha)}{w(\xi, c_*)^2}\,d\xi\right]\right)$$
$$= -\exp\left[-\int_{1/2}^{u}\frac{\xi(1-\xi)(\xi-\alpha)}{w(\xi, c_*)^2}\,d\xi\right]. \tag{2.10}$$

Integrating from $1/2$ to 1, we get

$$\frac{\partial w_1}{\partial c}(1/2, c_*, 0) = \int_{1/2}^{1}\exp\left[-\int_{1/2}^{s}\frac{\xi(1-\xi)(\xi-\alpha)}{w(\xi, c_*)^2}\,d\xi\right]ds. \tag{2.11}$$

Similarly, we can obtain

$$\frac{\partial w_2}{\partial c}(1/2, c_*, 0) = -\int_{0}^{1/2}\exp\left[-\int_{1/2}^{s}\frac{\xi(1-\xi)(\xi-\alpha)}{w(\xi, c_*)^2}\,d\xi\right]ds. \tag{2.12}$$

Combining Equations (2.11) and (2.12), we have

$$\frac{\partial G}{\partial c}(c_*, 0) = \frac{\partial w_1}{\partial c}(1/2, c_*, 0) - \frac{\partial w_2}{\partial c}(1/2, c_*, 0)$$
$$= \int_{0}^{1}\exp\left[-\int_{1/2}^{s}\frac{\xi(1-\xi)(\xi-\alpha)}{w(\xi, c_*)^2}\,d\xi\right]ds > 0.$$

Thus, by the implicit function theorem, for sufficiently small ε, $G(c, \varepsilon) = 0$ has a unique root $c = c(\varepsilon)$ in some neighbourhood c_*, satisfying $c(0) = c_*$. This implies that the manifolds w_1 and w_2 cross the line $u = 1/2$ at the same point. This indicates that system (2.9) possesses a heteroclinic orbit $\eta_\varepsilon(z)$ connecting the equilibria $E_1 = (0, 0)$ and $E_3 = (1, 0)$, when the parameter $\varepsilon > 0$ is sufficiently small. Therefore, the proof of Theorem 2.2 is complete. □

REMARK 2.3. In fact, the existence of travelling wave solutions for system (2.8) is also established in the paper [9] by another technique (see also [15]).

3. Preliminaries

In this section, we present some known results from the papers [5] and [6] which will be employed in the proof of our theorem.

Consider the delay equations with small discrete delays

$$\dot{x} = f(x(t), x(t-\tau)), \tag{3.1}$$

where $x \in \mathbb{R}^n$ and τ is a small delay.

LEMMA 3.1. *Suppose $f : \mathbb{R}^n \times \mathbb{R}^n \to \mathbb{R}^n$ is C^∞ and globally Lipschitz. Then for sufficiently small $\tau > 0$, the delay equations* (3.1) *have an n-dimensional smooth inertial manifold U_τ in its infinite-dimensional phase space $C([-\tau, 0], \mathbb{R}^n)$, that is, the inertial manifold U_τ is an invariant, finite dimensional and smooth manifold that attracts all other solutions exponentially fast. Moreover, the inertial manifold U_τ consists of the special flow $\eta(t, \xi, \tau)$.*

REMARK 3.2. A solution $\eta(t)$ of the delay equations (3.1) is called a special solution if $\eta(t)$ is defined on $\mathbb{R}$ and satisfies $\sup_{t\in\mathbb{R}} e^{-|t|/\tau}|\eta(t)| < +\infty$.

Suppose that $\eta : \mathbb{R} \times \mathbb{R}^n \to \mathbb{R}^n$ is a continuous function such that for each $\xi \in \mathbb{R}^n$ the function $t \mapsto \eta(t, \xi)$ is a special solution of the delay equations (3.1). Then $\eta(t, \xi)$ is called a special flow for the delay equations (3.1) if

$$\eta(t, \eta(s, \xi)) = \eta(t + s, \xi), \quad \eta(0, \xi) = \xi,$$

whenever $t, s \in \mathbb{R}$ and $\xi \in \mathbb{R}^n$.

It is easily seen that the special flow $\eta(t, \xi, \tau)$ for the delay equations (3.1) satisfies

$$\dot\eta(t, \xi, \tau) = f(\eta(t, \xi, \tau), \eta(t - \tau, \xi, \tau)), \quad \eta(0, \xi, \tau) = \xi,$$

where $\xi \in \mathbb{R}^n$.

It should be noted that the inertial manifold U_τ for delay equations (3.1) is parametrised by $\mathbb{R}^n$ in the following way: for each vector $\xi \in \mathbb{R}^n$, the inertial manifold contains a unique special solution $t \mapsto \eta(t, \xi, \tau)$ of the delay equations (3.1) which satisfies the initial condition $\eta(0, \xi, \tau) = \xi$. Then we identify this special solution $t \mapsto \eta(t, \xi, \tau)$ with the vector $\xi \in \mathbb{R}^n$.

Restricted to the inertial manifold U_τ, the delay equations (3.1) reduce to the following smooth and finite-dimensional vector $X(\xi, \tau)$:

$$X(\xi, \tau) := \frac{\partial \eta}{\partial t}(0, \xi, \tau) = f(\xi, \eta(-\tau, \xi, \tau)),$$

which is called a family of inertial vector fields. Therefore, the inertial vector fields $X(\xi, \tau)$ determine the long-term behaviour of the delay equations (3.1).

The expansion of the family of inertial vector fields $X(\xi, \tau) = f(\xi, \eta(-\tau, \xi, \tau))$ with respect to τ at $\tau = 0$ is

$$\begin{aligned} X(\xi, \tau) = {} & f(\xi, \xi) - \tau D_2 f(\xi, \xi) f(\xi, \xi) \\ & + \frac{\tau^2}{2!}\{D_2^2 f(\xi, \xi)(f(\xi, \xi), f(\xi, \xi)) \\ & + D_2 f(\xi, \xi)(D_1 f(\xi, \xi) + 3D_2 f(\xi, \xi)) f(\xi, \xi)\} + O(\tau^3). \end{aligned} \tag{3.2}$$

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4. Existence of a travelling wave for the population genetics model with discrete delay

To establish the existence of the travelling wave solution for the population genetics model with discrete delay (1.5), we make the following travelling wave transformation $u(t, x) = u(z)$, $z = x + ct$, where z is the travelling wave variable and $c > 0$ is the wave speed. Substituting $u(t, x) = u(z)$ into Equation (1.5), we obtain the travelling wave equation

$$u'' - cu' + u[1 - u(z - c\tau)](u - \alpha) = 0.$$

Let $u' = v_1$, we obtain the equivalent system of first-order equations

$$\begin{aligned} u' &= v_1, \\ v_1' &= cv_1 - u[1 - u(z - c\tau)](u - \alpha). \end{aligned} \tag{4.1}$$

When there is no delay in system (4.1), we obtain

$$\begin{aligned} u' &= v_1, \\ v_1' &= cv_1 - u(1 - u)(u - \alpha). \end{aligned} \tag{4.2}$$

Similar to the proof of Lemma 2.1 of Section 2, we can obtain the following result.

LEMMA 4.1. *There exists a unique wave speed $c = c^* > 0$ such that system* (4.2) *possesses a heteroclinic orbit $\gamma_0(z)$ connecting the critical points $E_1 = (0, 0)$ and $E_3 = (1, 0)$. Moreover, the travelling wave $u(z)$ is strictly monotonically increasing.*

We will now prove the following theorem.

THEOREM 4.2. *For sufficiently small delay τ, Equation* (1.5) *possesses a travelling wave solution connecting the equilibria $u_1 = 0$ and $u_3 = 1$ for a particular value $c = c(\tau)$ with $c(0) = c^* > 0$.*

PROOF. In $\mathbb{R}^2$, take a large enough open ball B_r centred at the origin to contain the heteroclinic orbit $\gamma_0(z)$ for the system (4.2). Fix the open ball B_r in $\mathbb{R}^2 \times \mathbb{R}^2$, take a large enough open ball S_a to contain $B_r \times B_r$. Meanwhile, in $\mathbb{R}^2 \times \mathbb{R}^2$, take a larger open ball S_b, where $b > a$.

Let $V = [u(z), v_1(z)]^T$ and $F = (F_1, F_2)^T = [v_1, \; cv_1 - u[1 - u(z - c\tau)](u - \alpha)]^T$, where T denotes transpose. Then the system (4.1) can be rewritten in the following form:

$$V'(z) = F(V(z), V(z - c\tau)). \tag{4.3}$$

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It is obvious that the function $F : \mathbb{R}^2 \times \mathbb{R}^2 \to \mathbb{R}^2$ is not globally Lipschitz on $\mathbb{R}^2 \times \mathbb{R}^2$. By using a smooth cut-off function defined on $\mathbb{R}^2 \times \mathbb{R}^2$, we can construct a new function $\overline{F}$ such that the new function $\overline{F}$ equals the original function F on the open ball S_a and equals a constant in the complement of the larger open ball S_b. That is, we construct the following new system:

$$V'(z) = \overline{F}(V(z), V(z - c\tau)), \tag{4.4}$$

which agrees with the original system (4.3) on the open ball S_a and is constant in the complement of the larger open ball S_b. Then it is easily checked that the new system (4.4) is C^∞ and globally Lipschitz on $\mathbb{R}^2 \times \mathbb{R}^2$.

By Lemma 3.1, we know that for the wave speed $c = c^*$, the new system (4.4) has an inertial manifold U_τ as long as the delay τ is sufficiently small. Note that the new system (4.4) reduces to system (4.3) on the open ball S_a. Since the delay τ does not change the equilibria, then system (4.3) still has the two equilibria $E_1 = (0, 0)$ and $E_3 = (1, 0)$, which are contained in the open ball S_a. Therefore, the new system (4.4) also has $E_1 = (0, 0)$ and $E_3 = (1, 0)$ as equilibrium points for the arbitrary delay τ.

By employing the expansion (3.2) of the family of inertial vector fields $X(\xi, \tau)$, it can be seen that for sufficiently small τ, the new system (4.4) restricted to the inertial manifold U_τ reduces to the following system:

$$\xi'(z) = \overline{F}(\xi(z), \xi(z)) + O(\tau), \tag{4.5}$$

which still has $E_1 = (0, 0)$ and $E_3 = (1, 0)$ as equilibrium points.

From the above construction of $\overline{F}$, we know that when $\xi = (\xi_1, \xi_2)^T \in B_r$, system (4.5) becomes

$$\xi'(z) = F(\xi(z), \xi(z)) + O(\tau), \tag{4.6}$$

which also possesses $E_1 = (0, 0)$ and $E_3 = (1, 0)$ as equilibrium points.

Thus, rewriting system (4.6), we have

$$\begin{aligned} \xi_1'(z) &= \xi_2, \\ \xi_2'(z) &= c\xi_2 - \xi_1(1 - \xi_1)(\xi_1 - \alpha) + O(\tau), \end{aligned} \tag{4.7}$$

which has $E_1 = (0, 0)$ and $E_3 = (1, 0)$ as equilibrium points.

By employing the expansion (3.2) and further expanding up to second order with respect to the delay τ in the right-hand side of system (4.7), we can obtain

$$\begin{aligned} \xi_1'(z) &= \xi_2, \\ \xi_2'(z) &= c\xi_2 - \xi_1(1 - \xi_1)(\xi_1 - \alpha) - \tau[c\xi_2\xi_1(\xi_1 - \alpha)] \\ &\quad + \tau^2[\xi_1(\xi_1 - \alpha)(c\xi_2 - \xi_1(1 - \xi_1)(\xi_1 - \alpha))]c^2/2 + O(\tau^3). \end{aligned} \tag{4.8}$$

When the delay τ is sufficiently small, system (4.7) possesses $E_1 = (0,0)$ and $E_3 = (1,0)$ as equilibrium points. By Lemma 4.1 and similar phase plane arguments for the existence of a travelling wave solution for system (2.8), we can show that when the delay τ is sufficiently small, system (4.7) still possesses a heteroclinic orbit $\eta(z,\xi,\tau)$ connecting the critical points $E_1 = (0,0)$ and $E_3 = (1,0)$. Moreover, this heteroclinic orbit $\eta(z,\xi,\tau)$ lies in some small neighbourhood of the heteroclinic orbit $\gamma_0(z)$. Therefore the heteroclinic orbit $\eta(z,\xi,\tau)$ also lies in the open ball B_r. This indicates that for the wave speed $c = c^* > 0$, when the delay τ is sufficiently small, there exists some initial condition $\xi \in B_r$ such that the new system (4.4) possesses a special solution $\eta(z,\xi,\tau)$. Meanwhile, this special solution $\eta(z,\xi,\tau)$ satisfies

$$\dot{\eta}(z,\xi,\tau) = \overline{F}(\eta(z,\xi,\tau), \eta(z-\tau,\xi,\tau)), \quad \eta(0,\xi,\tau) = \xi. \tag{4.9}$$

Since this special solution $\eta(z,\xi,\tau)$ lies in the open ball B_r, system (4.9) becomes

$$\dot{\eta}(z,\xi,\tau) = F(\eta(z,\xi,\tau), \eta(z-\tau,\xi,\tau)).$$

Therefore this special solution $\eta(z,\xi,\tau)$ is also a solution for the original system (4.3). That is, for the wave speed $c = c^* > 0$, when the delay τ is sufficiently small, the original system (4.3) (or system (4.1)) possesses a heteroclinic orbit $\eta(z,\xi,\tau)$ connecting the critical points $E_1 = (0,0)$ and $E_3 = (1,0)$. Thus Equation (1.5) possesses a travelling wave solution connecting the equilibria $u_1 = 0$ and $u_3 = 1$. This establishes the proof of Theorem 4.2. □

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References

[1] D. Aronson and H. Weinberger, "Nonlinear diffusion in population genetics, combustion and nerve propagation", in *Partial Differential Equations and Related Topics*, Lecture Notes in Mathematics 446, (Springer, New York, 1975) 5–49.

[2] D. Aronson and H. Weinberger, "Multidimensional nonlinear diffusion arising in population genetics", *Adv. Math.* **30** (1978) 33–76.

[3] P. Ashwin, M. Bartuccelli, T. Bridges and S. Gourley, "Travelling fronts for the KPP equation with spatial-temporal delay", *Z. Angew. Math. Phys.* **53** (2002) 103–122.

[4] N. Britton, "Spatial structures and periodic travelling waves in an integrodifferential reaction-diffusion population model", *SIAM J. Appl. Math.* **50** (1990) 1663–1688.

[5] C. Chicone, "Inertial and slow manifolds for delay equations with small delays", *J. Differential Equations* **190** (2003) 364–406.
[6] C. Chicone, "Inertial flows, slow flows, and combinatorial identities for delay equations", *J. Dynam. Differential Equations* **16** (2004) 805–831.
[7] N. Fenichel, "Geometric singular perturbation theory for ordinary differential equations", *J. Differential Equations* **31** (1979) 53–98.
[8] R. A. Fisher, "The advance of advantageous genes", *Ann. Eugenics* **7** (1937) 355–369.
[9] R. A. Gardner and C. K. R. T. Jones, "Travelling waves of a perturbed diffusion equation arising in a phase field model", *Indiana Univ. Math. J.* **38** (1989) 1197–1222.
[10] S. Gourley, "Travelling fronts in the diffusive Nicholson's blowflies equation with distributed delays", *Math. Comput. Modelling* **32** (2000) 843–853.
[11] S. Gourley and N. Britton, "Instability of travelling wave solutions of a population model with nonlocal effects", *IMA J. Appl. Math.* **51** (1993) 299–310.
[12] S. Gourley and N. Britton, "A predator prey reaction diffusion system with nonlocal effects", *J. Math. Biol.* **34** (1996) 297–333.
[13] S. A. Gourley and M. A. J. Chaplain, "Travelling fronts in a food-limited population model with time delay", *Proc. Roy. Soc. Edinburgh Sect. A* **132** (2002) 75–89.
[14] S. A. Gourley and J. W.-H. So, "Extinction and wavefront propagation in a reaction-diffusion model of a structured population with distributed maturation delay", *Proc. Roy. Soc. Edinburgh Sect. A* **133** (2003) 527–548.
[15] C. K. R. T. Jones, "Geometric singular perturbation theory", in *Dynamical Systems*, Lecture Notes in Mathematics 1609, (Springer, New York, 1995) 44–120.
[16] G. Lin and R. Yuan, "Periodic solution for a predator-prey system with distributed delay", *Math. Comput. Modelling* **42** (2005) 959–966.
[17] J. D. Murray, *Mathematical Biology* (Springer, Berlin, 1989).
[18] S. Ruan, "Delay differential equations in single species dynamics", in *Delay Differential Equations with Applications* (eds. E. Ait Dads, O. Arino and M. Hbid), (Springer, Berlin, 2005) 31–70.
[19] S. Ruan and D. Xiao, "Stability of steady states and existence of travelling waves in a vector disease model", *Proc. Roy. Soc. Edinburgh Sect. A* **134** (2004) 991–1011.
[20] J. Wu and X. Zou, "Travelling wave fronts of reaction-diffusion systems with delay", *J. Dynam. Differential Equations* **13** (2001) 651–687.