PERSISTENCE AND FAILURE OF COMPLETE SPREADING IN DELAYED REACTION-DIFFUSION EQUATIONS

GUO LIN AND SHIGUI RUAN

(Communicated by Yingfei Yi)

ABSTRACT. This paper deals with the long time behavior in terms of complete spreading for a population model described by a reaction-diffusion equation with delay, of which the corresponding reaction equation is bistable. When a complete spreading occurs in the corresponding undelayed equation with initial value admitting compact support, it is proved that the invasion can also be successful in the delayed equation if the time delay is small. To spur on a complete spreading, the choice of the initial value would be very technical due to the combination of delay and Allee effects. In addition, we show the possible failure of complete spreading in a quasimonotone delayed equation to illustrate the complexity of the problem.

1. INTRODUCTION

In this paper, we consider the asymptotic spreading of the following delayed reaction-diffusion equation arising in population dynamics

$$(1.1) \qquad \begin{cases} \frac{\partial u(x,t)}{\partial t} = \triangle u(x,t) - du(x,t) + b(u(x,t-\tau)), \\ u(x,s) = \phi(x,s), s \in [-\tau, 0], \end{cases}$$

where $u(x,t) \in \mathbb{R}$ represents the population density of a species in location $x \in \mathbb{R}$ at time $t > 0$, $d > 0$ is a constant accounting for the death rate, $b : \mathbb{R}^+ \to \mathbb{R}^+$ denotes the birth function, and $\tau > 0$ formulates the maturation period for the population. Notice that the diffusion coefficient has been scaled to be equal to the unity. For some biological backgrounds and mathematical results on this model, we refer to So et al. [21], So and Yang [22], Yi and Zou [29, 30], and references cited therein.

To characterize the asymptotic spreading, we introduce the following definition (see Berestycki et al. [3]).

Definition 1.1. Assume that $u(x,t)$ is a nonnegative function for all $x \in \mathbb{R}$, $t > 0$. We say that *complete spreading occurs* if there is a function $t \to r(t) > 0$ such that $r(t) \to \infty$ as $t \to \infty$ and $u(x,t)$ satisfies

$$\liminf_{t\to\infty} \left\{ \inf_{|x|<r(t)} u(x,t) \right\} > 0.$$

1

Notice that the last inequality is equivalent to $\liminf_{t\to\infty} u(x,t) > 0$ locally uniformly in $x \in \mathbb{R}$; it corresponds to the natural notion of uniform spreading from the origin of $\mathbb{R}$.

We first recall some results on the asymptotic spreading of the delayed reaction-diffusion equation (1.1). If the corresponding ordinary differential equation of (1.1) is monostable, e.g., $b(u) = pue^{-u}$ with $p > d$ (see Gurney et al. [8] and Nicholson et al. [17, 18]), then the asymptotic spreading characterized by the asymptotic speed of spreading has been well studied, e.g., Liang and Zhao [13], Thieme and Zhao [23], and Zhao [31]. Moreover, traveling wave solutions of (1.1), which is also a useful tool describing the spatial propagation, have been extensively considered; we refer to Gourley and So [7], Li et al. [12], Liang and Zhao [13], Ma [14], So et al. [21], Thieme and Zhao [23], and Zhao [31].

In population dynamics, besides the monostable evolutionary models, bistable models are also very important and universal since these models can describe the well-known Allee effect (Du and Shi [4], Hopf and Hopf [9], Wang and Kot [24], and Wang et al. [25]). In particular, Ma and Wu [15], Smith and Zhao [20], and Wang et al. [26, 27] investigated the existence, stability, and uniqueness of traveling wave solutions in (1.1) under the following assumptions:

(A1) $b(0) = 0$ and $dK = b(K)$ with $K > 0$;

(A2) there exists $k \in (0, K)$ such that $b(u) < du, u \in (0, k)$ while $b(u) > du, u \in (k, K)$;

(A3) $b'(u) > 0, u \in [0, K]$, and $d > \max\{b'(0), b'(K)\}$.

Evidently, (A3) implies quasimonotonicity so that the comparison principle appealing to monotone semiflows can be applied. A typical example is (see Ma and Wu [15])

$$b(u) = pu^2 e^{-u},$$

if $d = pue^{-u}$ has two roots for $u \in (0, 2]$. However, if $d = pue^{-u}$ has only one root for $u \in (0, 2]$ and $2pe^{-2} > d$, then this system does not satisfy the quasimonotone condition (A3) so that the theory of classical monotone dynamical systems fails.

In this paper, we shall investigate the long time behavior of (1.1) from the viewpoint of complete spreading. Our main assumptions are first listed as follows:

(B1) $b(0) = 0, dK = b(K)$ with $K > 0$, and $b : \mathbb{R}^+ \to \mathbb{R}^+$ is C^1;

(B2) there exists $k \in (0, K)$ such that $b(u) < du, u \in (0, k)$, while $b(u) > du, u \in (k, K)$;

(B3) there exists $\delta \in (0, k)$ such that $b'(u) > 0, u \in [0, \delta)$;

(B4) $\max\{b'(0), b'(K)\} < d$ and $b'(k) > d$;

(B5) $b(u) \geq 0, u \geq 0, du > b(u), u > K$, and there exists $\overline{K}$ such that $\sup_{u>0} b(u) = \overline{K}$;

(B6) $\int_0^K [b(u) - du] du > 0$.

It should be noted that we do not require $b(u)$ to be nondecreasing for $u \in [0, K]$, so it includes $b(u) = pu^2 e^{-u}$ as an example if $d = pue^{-u}$ has two distinct roots and (B6) holds. Thus, it is possible that (1.1) does not generate a monotone semiflow (see Smith [19]) even if $0 \leq \phi(x, s) \leq K$ for all $(x, s) \in \mathbb{R} \times [-\tau, 0]$, which implies that the comparison principle may fail. To address this issue, we shall introduce a proper undelayed system with bistable nonlinearity if the delay τ is small, which admits comparison principle if the nonlinearity is locally Lipschitz continuous. Using the theory developed by Aronson and Weinberger [1], we shall obtain some sufficient

conditions to ensure that complete spreading occurs in (1.1) even if $\phi(x, \cdot) = 0$ for x outside a bounded nonempty interval. Thus, the complete spreading can be persistent with respect to small time delay even if the birth function is not monotone. Moreover, using the results on complete spreading, we also show that the sign of the wave speed of bistable wavefronts persists if the time delay is small and $b(u), u \in [0, K]$, is monotone.

In particular, to spur on a complete spreading, the choice of the initial value seems to be very technical and the time delay must be small, which is significantly different from the case when $u' = -du + b(u)$ is monostable. However, these conditions on the initial value and time delay are required in some cases, and we show the necessity by investigating the asymptotic spreading of a delayed system with quasimonotonicity.

The rest of this paper is organized as follows. In Section 2, we shall investigate the initial value problem (1.1) and recall some results from Aronson and Weinberger [1]. In Section 3, we shall construct an undelayed bistable system which can be studied by the techniques and results in Aronson and Weinberger [1] and obtain some sufficient conditions on initial values such that a complete spreading occurs. Subsequently, in Section 4, the finite upper bound of the speed of asymptotic spreading is established. In Section 5, we give some comparisons on the complete spreading between monostable and bistable delayed equations. In the last section, a brief discussion on the time delay and Allee effect is presented.

2. INITIAL VALUE PROBLEM

For the sake of convenience, we first introduce some notation. Let

$$X = \{u(x) : u : \mathbb{R} \to \mathbb{R} \text{ is bounded and uniformly continuous}\}.$$

Then X is a Banach space with respect to the supremum norm $|\cdot|$. Denote

$$X^+ = \{u : u \in X \text{ and } u(x) \geq 0 \text{ for all } x \in \mathbb{R}\}.$$

If $a < b$, then

$$X_{[a,b]} = \{u : a \leq u(x) \leq b \text{ for all } x \in \mathbb{R}\}.$$

At the same time, we define

$$\mathcal{C} : [-\tau, 0] \to X$$

as a continuous map with the supremum norm. Similarly, the mappings

$$\mathcal{C}^+ : [-\tau, 0] \to X^+, \ \mathcal{C}_{[a,b]} : [-\tau, 0] \to X_{[a,b]}$$

are continuous. Moreover, $u(t) \in X$ will be interpreted as

$$u(t) =: (u(t))(x) = u(x, t).$$

For $t > 0$, we define $T(t) : X \to X$ as follows:

$$T(t)u(x) = \frac{1}{\sqrt{4\pi t}} \int_{\mathbb{R}} e^{-\frac{(x-y)^2}{4t}} u(y) dy, \ u(x) \in X.$$

Then $T(t) : X \to X$ is an analytic positive semigroup. To use the theory of abstract functional differential equations in Martin and Smith [16], similar to those in Smith and Zhao [20] and Wang et al. [26], if $u(s) \in X$, we denote

$$T(t)u(s) =: T(t)u(x, s) = \frac{1}{\sqrt{4\pi t}} \int_{\mathbb{R}} e^{-\frac{(x-y)^2}{4t}} u(y, s) dy.$$

In Smith and Zhao [20], it was proved that the abstract results in Martin and Smith [16] can be applied to (1.1). Similar to that in [20, Theorem 2.2], we first give the following existence and uniqueness of the mild solution of (1.1).

Lemma 2.1. *Assume that* $\phi \in \mathcal{C}$. *Then there exists* $\sigma \in (0, \infty]$ *such that (1.1) has a unique mild solution* $u : [-\tau, \sigma) \to X$, *which can also be formulated by the integral equation*

$$(2.1) \qquad u(t) = T(t)\phi(0) + \int_0^t T(t-s)F(u_s)ds,$$

with

$$F(u_s) = -du(s) + b(u(s-\tau)), \; u(s) \in X.$$

If $t > \tau$, *then (2.1) defines a classical solution satisfying differential equation (1.1). Moreover, if* σ *is bounded, then* $|u(t)| \to \infty$ *if* $t \to \sigma-$.

Now, we recall some conclusions on reaction-diffusion equations (see Aronson and Weinberger [1], Smith and Zhao [20], Ye et al. [28]).

Lemma 2.2. *Consider the initial value problem*

$$(2.2) \qquad \begin{cases} \dfrac{\partial w(x,t)}{\partial t} = \Delta w(x,t) + f(w(x,t)), \\ w(x,0) = \varphi(x) \in X, \end{cases}$$

in which $f : \mathbb{R} \to \mathbb{R}$ *is locally Lipschitz continuous.*

(S1) *If* $z(\cdot, t) \in X$ *with* $t \in [0, \sigma)$ *satisfies*

$$\begin{cases} \dfrac{\partial z(x,t)}{\partial t} \geq (\leq)\Delta z(x,t) + f(z(x,t)), \\ z(x,0) \geq (\leq)\varphi(x), \end{cases}$$

then $z(x,t) \geq (\leq)w(x,t)$ *for all* $x \in \mathbb{R}, t \in [0, \sigma)$.

(S2) *Assume that* $z(x,t) =: z(t) \in X$ *with* $t \in [0, \sigma)$ *satisfies*

$$z(t) \geq (\leq)T(t-s)z(s) + \int_s^t T(t-\theta)f(z(\theta))d\theta$$

for all $0 \leq s \leq t < \sigma$. *Then* $z(x,t) \geq (\leq)w(x,t)$ *for all* $x \in \mathbb{R}, t \in [0, \sigma)$.

In particular, we also formulate the following long time behavior of two equations without proof.

Lemma 2.3. (i) *Consider the initial value problem*

$$(2.3) \qquad \begin{cases} \dfrac{\partial w(x,t)}{\partial t} = \Delta w(x,t) - dw(x,t), \\ w(x,0) = \varphi(x) \in X^+. \end{cases}$$

Then $w(\cdot, t) \in X^+$ *and* $\lim_{t\to\infty} |w(\cdot, t)| = 0$.

(ii) *Consider the initial value problem*

$$(2.4) \qquad \begin{cases} \dfrac{\partial w(x,t)}{\partial t} = \Delta w(x,t) - dw(x,t) + \overline{K}, \\ w(x,0) = \varphi(x) \in X^+. \end{cases}$$

If $\varphi \in X_{[0, \overline{K}/d]}$, *then* $w(\cdot, t) \in X_{[0, \overline{K}/d]}$ *for all* $t \geq 0$. *Moreover,*

$$\lim_{t\to\infty} |w(\cdot, t) - \overline{K}/d| = 0.$$

The following result was established by Aronson and Weinberger [1, Theorem 3.3], which gives sufficient conditions for the occurrence of a complete spreading in reaction-diffusion equations.

Lemma 2.4. *Consider the initial value problem*

(2.5)
$$\begin{cases} \frac{\partial u(x,t)}{\partial t} = \triangle u(x,t) - du(x,t) + b(u(x,t)), \\ u(x,0) = \phi(x), \end{cases}$$

in which $b(u)$ satisfies (B1), (B2), (B4), *and* (B6).

(i) *There exists $\overline{k} > k$ such that $\int_0^{\overline{k}}[b(u) - du]du = 0$.*

(ii) *Let $\beta \in (\overline{k}, K)$ and define*

$$b_\beta = 2\int_0^\beta \frac{1}{\sqrt{2\int_0^\beta[b(u) - du]du - 2\int_0^s[b(u) - du]du}}ds;$$

then b_β is bounded.

(iii) *Let $c^* > 0$ be the unique wave speed of a bistable wave solution of* (2.5). *If $\phi(x) \in X_{[0,K]}$ and for some $\beta \in (\overline{k}, K), x_0 \in \mathbb{R}$,*

$$\phi(x) \geq \beta, x \in (x_0, x_0 + b_\beta),$$

then $\lim_{t\to\infty} u(r(t), t) = K$, where $|r(t)| < ct$ with $c \in (0, c^*)$. Namely, a complete spreading occurs.

Remark 2.5. Lemma 2.4 only presents partial results of [1, Theorem 3.3].

We now give the boundedness and global existence of a mild solution.

Lemma 2.6. *Assume that $\phi \in \mathcal{C}_{[0,\overline{K}/d]}$. Then* (1.1) *has a unique mild solution $u : [-\tau, \infty) \to X$ such that $u(t) \in X_{[0,\overline{K}/d]}$.*

Lemma 2.7. *Assume that τ is fixed. If $\phi \in \mathcal{C}_{[0,\overline{K}/d]}$, then there exists a constant $C > 0$ such that $\sup_{x\in\mathbb{R}} |\frac{\partial u(x,t)}{\partial t}| < C$, provided $t > 3\tau + 1$.*

Remark 2.8. Let $\tau_0 > 0$ be fixed, then we can choose C such that Lemma 2.7 holds for any $\tau \in [0, \tau_0]$ and $t > 3\tau_0 + 1$. Moreover, the essential proof of Lemma 2.7 is the same as Wang et al. [27, Proposition 4.3] for monotone equations and we omit it here.

3. PERSISTENCE OF COMPLETE SPREADING

In this section, we first construct a bistable equation without delay, which exhibits complete spreading. Then using comparison principle and Lemma 2.4, we will show that complete spreading persists for the delayed reaction-diffusion equation (1.1) under certain conditions. Finally, the sign of wave speed of bistable traveling wave solutions will be considered.

Lemma 3.1. *Let $\epsilon > 0$ be small. Then there exists $F(u)$ such that*

$$F(u) \leq -du + b(v)$$

if $|u - v| < \epsilon, u \geq 0, v \geq 0$, where $F(u)$ satisfies the following assumptions:

(F1) *there exists $\underline{K} \leq K$ such that $F(\underline{K}) = d\underline{K}$ and $\underline{K} \to K$ if $\epsilon \to 0$;*

(F2) *there exists k_1 such that $F(k_1) = 0$ and $F(u) < (>)0$ if $u \in (0, k_1)(u \in (k_1, \underline{K}))$;*

(F3) $\int_0^{\underline{K}} F(u)du > 0$.

Proof. If $u < \epsilon$, we define

$$F(u(x,t)) = -du(x,t).$$

If $u > 4\epsilon$, then we define

$$F(u) = -du + \underline{b}(u),$$

with

$$\min_{e \in [u-\epsilon, u+\epsilon]} b(e) \geq \underline{b}(u) \geq \min_{e \in [u-2\epsilon, u+2\epsilon]} b(e).$$

Due to the smoothness of $b(u)$, if $\epsilon > 0$ is small, then $\underline{b}(u)$ satisfies

(b1) $\underline{b}(u)$ is C^1 if $u \in [4\epsilon, K]$;

(b2) $\underline{b}(4\epsilon) < 4d\epsilon$;

(b3) there exists $\underline{K} \leq K$ such that $\underline{b}(\underline{K}) = d\underline{K}$.

If $u(x,t) \in [\epsilon, 4\epsilon]$, let $\underline{b}(u)$ satisfy

(b4) $0 \leq \underline{b}(u) \leq \min_{e \in [u-\epsilon, u+\epsilon]} b(e)$;

(b5) $\underline{b}(u)$ is C^1 if $u \in [0, K]$;

(b6) $\underline{b}(u) = du$ has no root for $u \in [\epsilon, 4\epsilon]$.

By (B3), there exists $\underline{b}(u)$ satisfying (b1)-(b6). Let $F(u) = -du + \underline{b}(u)$; it is clear that (F1)-(F3) hold. The proof is complete. $\qquad\square$

Lemma 3.2. *Assume that $\tau \leq 1/4$ is small enough. If $\phi \in \mathcal{C}_{[0, \overline{K}/d]}$, then*

$$-du(x,t) + b(u(x, t - \tau)) \geq F(u(x,t))$$

for any $t > 2$, in which F satisfies

(F1′) *there exists $\underline{K} \leq K$ such that $F(\underline{K}) = d\underline{K}$ and $\underline{K} \to K$ if $\tau \to 0$;*

(F2′) *there exists k_1 such that $F(k_1) = 0$ and $F(u) < (>)0$ if $u \in (0, k_1)$ $(u \in (k_1, \underline{K}))$;*

(F3′) $\int_0^{\underline{K}} F(u)du > 0$.

Proof. By what we have done, for any $\epsilon > 0$, there exists $\tau_0 \in (0, 1/4)$ such that

$$|u(x,t) - u(x, t - \tau)| < \epsilon$$

for any $t \geq 2$ and $\tau < \tau_0$. Then the result follows from Lemma 3.1. $\qquad\square$

By Lemma 3.2, the following conclusion is clear.

Lemma 3.3. *If $\tau \leq 1/4$ is small enough and $\phi \in \mathcal{C}_{[0, \overline{K}/d]}$ holds, then $u(x,t)$ satisfies*

(3.1) $$\frac{\partial u(x,t)}{\partial t} \geq \triangle u(x,t) + F(u(x,t)), t \geq 2,$$

where F satisfies (F1′)-(F3′) *in Lemma 3.2.*

Now, we are in a position to display the possibility of complete spreading in (1.1) if the initial value admits a nonempty compact support.

Theorem 3.4. *Assume that Lemma 3.3 and $\phi \in \mathcal{C}_{[0,\overline{K}/d]}$ hold. If for all $s \in [-\tau, 0]$ and some $x \in \mathbb{R}$, $|\phi(y,s) - K|$ is small on a large neighborhood of x, then*

$$\liminf_{t\to\infty} u(x,t) \geq \underline{K} \text{ for each } x \in \mathbb{R}.$$

Proof. Consider

$$(3.2) \qquad \begin{cases} \frac{du(t)}{dt} = -du(t) + b(u(t-\tau)), \\ u(s) = K, s \in [-\tau, 0]. \end{cases}$$

Then $u(t) = K$ for all $t > 0$. By the continuous dependence of the initial value, we see that $u(t) - K, t \in [0, 2]$, will be small if $\sup_{s\in[-\tau,0]} |u(s) - K|$ is small.

Moreover, since

$$\frac{1}{\sqrt{4\pi t}} \int_{-N}^{N} e^{-\frac{y^2}{4t}} dy \to 1, N \to \infty,$$

and the convergence is uniform if $t \in (0, 2]$, then $u(x, 2) - K$ can be small on a large interval of $x \in \mathbb{R}$ if $\phi(x, s) - K$ is small on a large interval of $x \in \mathbb{R}$, $s \in [-\tau, 0]$.

By Lemma 2.4, we complete the proof. □

In fact, besides the above case, there are also some other initial value conditions ensuring that a complete spreading occurs. For example, we have the following results.

Proposition 3.5. *Assume that there exists $K_0 \in (K, \overline{K})$ such that $K_0 e^{-2d} \geq Kd$. If $\phi \in \mathcal{C}_{[0,\overline{K}/d]}$ and $\phi(x, s) > K_0$ on a large interval of $x \in \mathbb{R}$ for all $s \in [-\tau, 0]$, then a complete spreading occurs if $\tau > 0$ is small.*

Proof. From Lemma 2.6 and (2.3), we see that $u(x, 2) \geq K$ on a large interval. Using Lemma 2.4, we complete the proof. □

Proposition 3.6. *Assume that there exists $\beta < K$ such that $\int_0^\beta [b(u) - du]du > 0$ and $b(u) > d\beta$ for any $u > \beta$. If $\phi \in \mathcal{C}_{[0,\overline{K}/d]}$ and $\phi(x, s) > \beta$ holds on a large interval of $x \in \mathbb{R}$ for all $s \in [-\tau, 0]$, then a complete spreading occurs for small $\tau > 0$.*

Proof. Consider the functional differential equation

$$\begin{cases} \frac{du(t)}{dt} = -du(t) + b(u(t-\tau)), \\ u(s) > \beta, s \in [-\tau, 0]. \end{cases}$$

Evidently, we have $u(t) > \beta$ for all $t > 0$. Note that

$$\frac{1}{\sqrt{4\pi t}} \int_{-N}^{N} e^{-\frac{y^2}{4t}} dy \to 1, N \to \infty,$$

and the convergence is uniform if $t \in (0, 2]$, then $u(x, 2) > \beta$ holds on a large interval. The proof is complete. □

We now consider the application of complete spreading by investigating the sign of wave speed of traveling wave solutions in

$$(3.3) \qquad \frac{\partial u(x,t)}{\partial t} = \triangle u(x,t) - du(x,t) + b(u(x,t-\tau))$$

if $b(u)$ is *monotone* for $u \in [0, K]$, which implies that (3.3) satisfies the so-called quasimonotone condition. Herein, a traveling wave solution is a special solution

$u(x,t) = \varrho(x+ct)$, in which $c \in \mathbb{R}$ is the wave speed while $\varrho(\xi) \in C^2(\mathbb{R},\mathbb{R})$ is the wave profile. In Ma and Wu [15], Smith and Zhao [20], and Wang et al. [26], the following result was proved.

Lemma 3.7. *Assume that* (B1)-(B4) *hold and $b(u)$ is monotone for $u \in [0,K]$.*

(i) *There exists a unique $c \in \mathbb{R}$ such that* (3.3) *has a unique traveling wave solution satisfying*

$$\lim_{\xi \to -\infty} \varrho(\xi) = 0, \; \lim_{\xi \to \infty} \varrho(\xi) = K,$$

and $\varrho(\xi)$ is strictly monotone in $\xi \in \mathbb{R}$. Such a traveling wave solution is called a bistable wavefront.

(ii) *Assume that $\phi \in \mathcal{C}_{[0,K]}$ such that*

$$\limsup_{x \to -\infty} \phi(x,s) < k, \; \liminf_{x \to \infty} \phi(x,s) > k \text{ for all } s \in [-\tau, 0].$$

Let $u(x,t)$ be the unique mild solution to (1.1). *Then there exists $\xi^+ \in \mathbb{R}$ such that*

$$\lim_{t \to \infty} \sup_{x \in \mathbb{R}} |\varrho(x+ct+\xi^+) - u(x,t)| = 0.$$

We have the following result on the positivity of the wave speed c.

Theorem 3.8. *Assume that* (B1)-(B4) *and* (B6) *hold and $b(u)$ is monotone for $u \in [0,K]$. If $\tau > 0$ is small enough, then the wave speed $c > 0$.*

Proof. Let $\phi(x,s) = \varrho(x+cs)$, then $\lim_{\xi \to \infty} \varrho(\xi) = K$ implies that Theorem 3.4 holds such that a complete spreading can occur. Thus $c > 0$ by Lemma 3.7. The proof is complete. $\square$

4. Finite speed of geographic expansion

In this section, we shall prove that if the initial value $\mathcal{C}_{[0,\overline{K}/b]} \ni \phi = 0$ outside a bounded nonempty interval of $x \in \mathbb{R}$, then $u(x,t)$ has a rough upper bound of spreading speed at which the geographic range of the individual expands. Consider the initial value problem

$$(4.1) \qquad \begin{cases} \dfrac{\partial w(x,t)}{\partial t} = \Delta w(x,t) - dw(x,t) + f(w(x,t-\tau)), \\ w(x,s) = \varphi(x,s), s \in [-\tau, 0], \end{cases}$$

where f satisfies the following assumptions:

(f1) $f(0) = 0, f(M) = dM$ with $M > 0$;
(f2) $f(u) > du, u \in (0,M)$;
(f3) f is C^1 and $f'(u) \geq 0, f(u) \leq f'(0)u, u \in [0,M]$.

By the results in Smith and Zhao [20], we have the following lemma.

Lemma 4.1. *Assume that $\varphi \in \mathcal{C}_{[0,M]}$.*

(1) (4.1) *has a unique mild solution $w(t) \in X_{[0,M]}$.*
(2) *If $\underline{w}(t) : [-\tau, \infty) \to X_{[0,M]}$ such that*

$$\underline{w}(t) \leq T(t-s)\underline{w}(s) + \int_s^t T(t-\theta)[-d\underline{w}(\theta) + f(\underline{w}_\theta)]d\theta$$

for any $0 \leq s < t < \infty$, then $\underline{w}(t) \leq w(t), t > 0$.

To formulate our result, for $\lambda > 0, c > 0$, we define

$$\Delta(\lambda, c) = \lambda^2 - c\lambda - d + f'(0)e^{-\lambda c\tau}.$$

Lemma 4.2. *There exists a constant $c^* > 0$ such that $\Delta(\lambda, c) = 0$ has no real root if $c < c^*$ and two real roots if $c > c^*$.*

We first recall a conclusion from Thieme and Zhao [23].

Lemma 4.3. *If (f1)-(f3) hold and $\varphi \in \mathcal{C}_{[0,M]}$ with $\varphi(x, \cdot) = 0$ for x outside a bounded interval, then*

$$\lim_{t \to \infty} \sup_{|x| > ct} w(x, t) = 0$$

for any $c > c^*$. Moreover, if $\varphi(x, s) > 0$ for some x and s, and $c < c^*$, then

$$\lim_{t \to \infty} \inf_{|x| < ct} w(x, t) = \lim_{t \to \infty} \sup_{|x| < ct} w(x, t) = M.$$

Now we present a result on the bound of the wave speed.

Theorem 4.4. *Assume that $\phi \in \mathcal{C}_{[0, \overline{K}/b]}$ with $\varphi(x, \cdot) = 0$ for x outside a bounded interval. Then*

$$\lim_{t \to \infty} \sup_{|x| > ct} u(x, t) = 0$$

for any $c > c^*$ by letting $f'(0) = \sup_{u \in [0, \overline{K}/d]} b'(u)$ in Lemma 4.2.

Proof. Let $\sup_{u \in [0, \overline{K}/d]} b'(u) = b^+$. If $b^+u < k/2$, define

$$\overline{b}(u) = b^+u.$$

Otherwise, let $\overline{b}(u)$ satisfy

(c1) $\overline{b}(u) \leq b^+u, u > 0$;
(c2) $\overline{b}(u) = du$ has only one positive root $\overline{K}/d$;
(c3) $\overline{b}(u) = \overline{K}$ if $u > \overline{K}/d$;
(c4) $\overline{b}(u)$ is monotone if $u \in [0, \overline{K}/d]$.

Clearly, such a $\overline{b}(u)$ is admissible and satisfies (f1)-(f3). Moreover, by the proof of Lemma 2.6, we have

$$
\begin{aligned}
u(t) &= T(t-s)u(s) + \int_s^t T(t-\theta)F(u_\theta)d\theta \\
&\leq T(t-s)u(s) + \int_s^t T(t-\theta)[-du(\theta) + \overline{b}(u_\theta)]d\theta
\end{aligned}
$$

for any $0 \leq s < t < \infty$. Using Lemmas 4.1-4.3, we complete the proof. $\square$

5. Failure of complete spreading

In this section, we shall show some differences between monostable and bistable equations when complete spreading is concerned. For the sake of comparison, we first recall the complete spreading of a monostable equation. Then we demonstrate that complete spreading may fail to occur in a quasimonotone equation of which the corresponding reaction equation is bistable, which also demonstrates the necessity of requirements on the initial value and time delay for the occurrence of complete spreading in delayed reaction-diffusion equations.

5.1. **A monostable equation.** We first list some results on the complete spreading of a monostable equation

(5.1)
$$\begin{cases} \dfrac{\partial w(x,t)}{\partial t} = \Delta w(x,t) - dw(x,t) + f(w(x,t-\tau)), \\ w(x,s) = \varphi(x,s), s \in [-\tau, 0], \end{cases}$$

where f satisfies the following assumptions:

(A1) $f(0) = 0$ and there is an $M > 0$ such that $f(M) = dM$;
(A2) $f(w) > dw, w \in (0, M)$;
(A3) f is C^1 and $f(w) \leq f'(0)w$;
(A4) $f(w) > 0$ is bounded for all $w > 0$.

Differing from those in Section 4, we do not require monotonicity of the birth function.

Lemma 5.1. *Assume that $\varphi \in \mathcal{C}^+$. Then $w(t) \in X^+$ is bounded and*

$$\limsup_{t\to\infty} |w(t)| \leq \sup_{u\geq 0} f(u)/d,$$

where $w(t)$ is the unique mild solution to (5.1).

By Fang and Zhao [6] (also see Hsu and Zhao [10] and Li et al. [11]), we have the following conclusion.

Theorem 5.2. *Assume that $\varphi \in \mathcal{C}^+$ with $\varphi(x,s) > 0$ for some x and s. Then*

$$\liminf_{t\to\infty} \inf_{|x|<ct} u(x,t) > 0$$

for any $c < c^*$, where c^* is defined by Lemma 4.2.

5.2. **A bistable equation.** In this subsection, we show the necessity of requirements on the initial value and time delay for the occurrence of complete spreading in a delayed equation. Clearly, if τ is small enough, it is not difficult to extend our conclusion to the equation

(5.2)
$$\begin{cases} \frac{\partial u(x,t)}{\partial t} = \triangle u(x,t) + F(u(x,t), u(x,t-\tau)), \\ u(x,s) = \phi(x,s), s \in [-\tau, 0], \end{cases}$$

in which $F : \mathbb{R}^2 \to \mathbb{R}$ such that

(5.3)
$$\frac{du(t)}{dt} = F(u,u)$$

is a bistable equation with $F(0,0) = F(k,k) = F(K,K), 0 < k < K$.

In particular, let $r > 0, a \in (0, 1/2)$ and

$$F(u,v) = ru(1-u)(v-a), u,v \in [0,1].$$

Then (5.2) satisfies conditions in Smith and Zhao [20] and Wang et al. [26] so that its traveling wave solutions can be investigated. From the viewpoint of asymptotic spreading, the invasion process from an unbounded domain to an unbounded domain can be successful by the stability of traveling wave solutions if the wave speed is positive. However, if the initial value is far away from the traveling wave solutions, whether a complete spreading can occur remains open. We now give an example to illustrate the possible failure of complete spreading.

The following comparison principle was established by Smith and Zhao [20].

Lemma 5.3. *Assume that* $F(u,v) = ru(1-u)(v-a)$ *and* $\phi(s) \in \mathcal{C}_{[0,1]}$. *Then* $u(t) \in X_{[0,1]}$ *for all* $t > 0$. *Moreover, if* $\overline{u} \in X_{[0,1]}$ *satisfies*

$$(5.4) \qquad \begin{cases} \frac{\partial \overline{u}(x,t)}{\partial t} \geq (\leq)\triangle\overline{u}(x,t) + F(\overline{u}(x,t),\overline{u}(x,t-\tau)), \\ \overline{u}(x,s) \geq (\leq)\phi(x,s), s \in [-\tau,0], \end{cases}$$

then $\overline{u}(x,t) \geq (\leq)u(x,t)$.

Assume that $\tau > 2$. For $x \in \mathbb{R}$, we define

$$(5.5) \qquad \phi(x,s) = \begin{cases} \beta, s \in [-1,0], \\ \psi(s), s \in [-2,-1], \\ 0, s \in [-\tau,-2], \end{cases}$$

where $\beta \in (a,1)$ and $\int_0^\beta ru[1-u][u-a]du > 0$, $\psi(-2) = 0, \phi(-1) = \beta$ and $\psi(s)$ is monotone and continuous. Thus, the solution of (5.2) is spatially homogeneous and is the same as the following functional differential equation

$$(5.6) \qquad \begin{cases} \frac{du(t)}{dt} = ru(t)(1-u(t))(u(t-\tau)-a), \\ u(s) = \phi(x,s), s \in [-\tau,0] \text{ for any } x \in \mathbb{R}. \end{cases}$$

It is easy to check that

$$u(t) < a, t \in [\tau,2\tau]$$

if $\tau > 2$ is large enough. Thus, we obtain

$$u(x,t) < a, t \in [\tau,2\tau], x \in \mathbb{R}.$$

Therefore, we can choose $\lambda > 0$ small enough such that

$$u(x,t) \leq ae^{-\lambda t} =: \overline{u}(t), \ t \in [\tau,2\tau],$$

and

$$\frac{d\overline{u}(t)}{dt} \geq r\overline{u}(t)(1-\overline{u}(t))(\overline{u}(t-\tau)-a), \ t > 2\tau.$$

Since the quasimonotone condition holds, the comparison principle implies that

$$0 \leq u(x,t) \leq ae^{-\lambda t}, \ t > 2\tau,$$

and we have $\lim_{t\to\infty} \sup_{x\in\mathbb{R}} u(x,t) = 0$.

Remark 5.4. By Lemma 5.3, we further see that the complete spreading will be a failure if its initial value in $\mathcal{C}_{[0,1]}$ is smaller than that in (5.5). Namely, the complete spreading will be a failure if its initial value does not satisfy proper requirements and the delay is large.

6. Discussion

In ecological communities, there are factors that can lead to the so-called phenomenon of Allee effect, for example, the need of a minimal group size necessary to successfully raise offspring, produce seeds, and forage. These facts play crucial roles in the persistence of higher living organisms. Generally a small group size often leads to the decline of genes such that the species may go extinct. Therefore, there is a positive threshold of the population density that must be surpassed if a community admitting Allee effect would persist. In population dynamics, the Allee effect is often modeled by an equation with bistable nonlinearity.

Moreover, if the period of hatching or duration of gestation is considered, then we need to include time delay in the evolutionary system. For many higher living organisms, not only the number of individuals is required, but also the structure of community should be considered since the shortage of mates could lead to the Allee effect. An easy but extreme example is the evolution of a community in which the individuals are of the same sex. Clearly, the community will go extinct if the species is sexually reproductive. Therefore, if a group with Allee effect that arises from the shortage of mates would persist, then proper gender ratio is needed. The requirements on both the population number and the population structure imply that proper initial value should be equipped in order to obtain a successful complete spreading in a bistable evolutionary system with time delay. In this paper, we have shown that if the initial value does not satisfy proper constraints in the whole delay interval, then complete spreading cannot be successful even if the initial value can surpass the threshold for all $x \in \mathbb{R}$ at some point of the delayed interval.

To formulate the spatial propagation of evolutionary systems, a useful tool is the traveling wave solution. In particular, the existence of a stable traveling wave solution can be used to explain the spatial invasion process from an unbounded domain to the whole $\mathbb{R}$ (mathematically, we can see the second item of Lemma 3.7). However, to characterize the invasion direction, we need to know the sign of wave speed. To our knowledge, the sign of wave speed of bistable traveling wave solutions in delayed diffusion systems remains open. Therefore, it is not an easy work to formulate the invasion direction of a bistable equation with time delay. However, if the delay is small enough in a scalar equation with quasimonotonicity, then we have proved that the sign of wave speed does not change.

For undelayed systems, for example, reaction-diffusion systems, the hair trigger effect can formulate the success/failure of propagation of perturbation of the unpopulated state, see Aronson and Weinberger [1, 2]. In particular, if the corresponding reaction system is monostable and the unpopulated state is unstable, it was proved the hair trigger effect could exist. Furthermore, for delayed models (5.1), we can also say that the hair trigger effect still holds since the phase space is $\mathcal{C}$ and $\mathcal{C}^+ \ni \varphi(x, \cdot) = 0$ outside a bounded nonempty interval of $x \in \mathbb{R}$ can be regarded as a perturbation of $0 \in \mathcal{C}$; see Theorem 5.2. However, if the corresponding reaction system is bistable, then the success of complete spreading may encounter some difficulties and we gave an example in Section 5. Therefore, the hair trigger effect can be false in the delayed diffusion system of which the corresponding reaction system is bistable, which implies that the combination of Allee effect and time delay may lead to very plentiful and complex dynamics in evolutionary systems.

References

[1] D. G. Aronson and H. F. Weinberger, *Nonlinear diffusion in population genetics, combustion, and nerve pulse propagation*, Partial differential equations and related topics (Program, Tulane Univ., New Orleans, La., 1974), Springer, Berlin, 1975, pp. 5–49. Lecture Notes in Math., Vol. 446. MR0427837 (55 #867)

[2] D. G. Aronson and H. F. Weinberger, *Multidimensional nonlinear diffusion arising in population genetics*, Adv. in Math. **30** (1978), no. 1, 33–76, DOI 10.1016/0001-8708(78)90130-5. MR511740 (80a:35013)

[3] Henri Berestycki, François Hamel, and Grégoire Nadin, *Asymptotic spreading in heterogeneous diffusive excitable media*, J. Funct. Anal. **255** (2008), no. 9, 2146–2189, DOI 10.1016/j.jfa.2008.06.030. MR2473253 (2009k:35136)

[4] Yihong Du and Junping Shi, *Allee effect and bistability in a spatially heterogeneous predator-prey model*, Trans. Amer. Math. Soc. **359** (2007), no. 9, 4557–4593, DOI 10.1090/S0002-9947-07-04262-6. MR2309198 (2008h:35138)

[5] Lawrence C. Evans, *Partial differential equations*, Graduate Studies in Mathematics, vol. 19, American Mathematical Society, Providence, RI, 1998. MR1625845 (99e:35001)

[6] Jian Fang and Xiao-Qiang Zhao, *Existence and uniqueness of traveling waves for non-monotone integral equations with applications*, J. Differential Equations **248** (2010), no. 9, 2199–2226, DOI 10.1016/j.jde.2010.01.009. MR2595719 (2011a:45019)

[7] 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), no. 3, 527–548, DOI 10.1017/S0308210500002523. MR1983685 (2004d:35129)

[8] W.S.C. Gurney, S.P. Blythe and R.M. Nisbet, *Nicholson's blowflies revisited*, Nature **287** (1990), 17-21.

[9] F. A. Hopf and F. W. Hopf, *The role of the Allee effect in species packing*, Theoret. Population Biol. **27** (1985), no. 1, 27–50, DOI 10.1016/0040-5809(85)90014-0. MR787223

[10] Sze-Bi Hsu and Xiao-Qiang Zhao, *Spreading speeds and traveling waves for nonmonotone integrodifference equations*, SIAM J. Math. Anal. **40** (2008), no. 2, 776–789, DOI 10.1137/070703016. MR2438786 (2009e:39008)

[11] Bingtuan Li, Mark A. Lewis, and Hans F. Weinberger, *Existence of traveling waves for integral recursions with nonmonotone growth functions*, J. Math. Biol. **58** (2009), no. 3, 323–338, DOI 10.1007/s00285-008-0175-1. MR2470192 (2010b:92095)

[12] W.-T. Li, S. Ruan, and Z.-C. Wang, *On the diffusive Nicholson's blowflies equation with nonlocal delay*, J. Nonlinear Sci. **17** (2007), no. 6, 505–525, DOI 10.1007/s00332-007-9003-9. MR2371145 (2009a:35134)

[13] Xing Liang and Xiao-Qiang Zhao, *Asymptotic speeds of spread and traveling waves for monotone semiflows with applications*, Comm. Pure Appl. Math. **60** (2007), no. 1, 1–40, DOI 10.1002/cpa.20154. MR2270161 (2007i:37144)

[14] Shiwang Ma, *Traveling waves for non-local delayed diffusion equations via auxiliary equations*, J. Differential Equations **237** (2007), no. 2, 259–277, DOI 10.1016/j.jde.2007.03.014. MR2330948 (2008f:35205)

[15] Shiwang Ma and Jianhong Wu, *Existence, uniqueness and asymptotic stability of traveling wavefronts in a non-local delayed diffusion equation*, J. Dynam. Differential Equations **19** (2007), no. 2, 391–436, DOI 10.1007/s10884-006-9065-7. MR2333414 (2008f:35206)

[16] R. H. Martin Jr. and H. L. Smith, *Abstract functional-differential equations and reaction-diffusion systems*, Trans. Amer. Math. Soc. **321** (1990), no. 1, 1–44, DOI 10.2307/2001590. MR967316 (90m:35194)

[17] A.J. Nicholson, *Compensatory reactions of populations to stresses, and their evolutionary significance*, Aust. J. Zool. **2** (1954), 1-8.

[18] A.J. Nicholson, *An outline of the dynamics of animal populations*, Aust. J. Zool. **2** (1954), 9-65.

[19] Hal L. Smith, *Monotone dynamical systems*, Mathematical Surveys and Monographs, vol. 41, American Mathematical Society, Providence, RI, 1995. An introduction to the theory of competitive and cooperative systems. MR1319817 (96c:34002)

[20] Hal L. Smith and Xiao-Qiang Zhao, *Global asymptotic stability of traveling waves in delayed reaction-diffusion equations*, SIAM J. Math. Anal. **31** (2000), no. 3, 514–534, DOI 10.1137/S0036141098346785. MR1740724 (2001c:35239)

[21] Joseph W.-H. So, Jianhong Wu, and Xingfu Zou, *A reaction-diffusion model for a single species with age structure. I. Travelling wavefronts on unbounded domains*, R. Soc. Lond. Proc. Ser. A Math. Phys. Eng. Sci. **457** (2001), no. 2012, 1841–1853, DOI 10.1098/rspa.2001.0789. MR1852431 (2002g:92022)

[22] Joseph W.-H. So and Yuanjie Yang, *Dirichlet problem for the diffusive Nicholson's blowflies equation*, J. Differential Equations **150** (1998), no. 2, 317–348, DOI 10.1006/jdeq.1998.3489. MR1658605 (99m:35255)

[23] Horst R. Thieme and Xiao-Qiang Zhao, *Asymptotic speeds of spread and traveling waves for integral equations and delayed reaction-diffusion models*, J. Differential Equations **195** (2003), no. 2, 430–470, DOI 10.1016/S0022-0396(03)00175-X. MR2016819 (2004h:45007)

[24] Mei-Hui Wang and Mark Kot, *Speeds of invasion in a model with strong or weak Allee effects*, Math. Biosci. **171** (2001), no. 1, 83–97, DOI 10.1016/S0025-5564(01)00048-7. MR1839210 (2002f:92031)

[25] Mei-Hui Wang, Mark Kot, and Michael G. Neubert, *Integrodifference equations, Allee effects, and invasions*, J. Math. Biol. **44** (2002), no. 2, 150–168, DOI 10.1007/s002850100116. MR1889908 (2003a:92026)

[26] Zhi-Cheng Wang, Wan-Tong Li, and Shigui Ruan, *Existence and stability of traveling wave fronts in reaction advection diffusion equations with nonlocal delay*, J. Differential Equations **238** (2007), no. 1, 153–200, DOI 10.1016/j.jde.2007.03.025. MR2334595 (2008f:35212)

[27] Zhi-Cheng Wang, Wan-Tong Li, and Shigui Ruan, *Entire solutions in bistable reaction-diffusion equations with nonlocal delayed nonlinearity*, Trans. Amer. Math. Soc. **361** (2009), no. 4, 2047–2084, DOI 10.1090/S0002-9947-08-04694-1. MR2465829 (2009j:35193)

[28] Q. Ye, Z. Li, M. Wang, and Y. Wu, *Introduction to Reaction Diffusion Equations* (The Second Edition), Science Press, Beijing, 2011.

[29] Taishan Yi and Xingfu Zou, *Global attractivity of the diffusive Nicholson blowflies equation with Neumann boundary condition: a non-monotone case*, J. Differential Equations **245** (2008), no. 11, 3376–3388, DOI 10.1016/j.jde.2008.03.007. MR2460028 (2010b:35037)

[30] Taishan Yi and Xingfu Zou, *Global dynamics of a delay differential equation with spatial non-locality in an unbounded domain*, J. Differential Equations **251** (2011), no. 9, 2598–2611, DOI 10.1016/j.jde.2011.04.027. MR2825342 (2012h:35359)

[31] Xiao-Qiang Zhao, *Spatial dynamics of some evolution systems in biology*, Recent progress on reaction-diffusion systems and viscosity solutions, World Sci. Publ., Hackensack, NJ, 2009, pp. 332–363, DOI 10.1142/9789812834744_0015. MR2532932 (2010k:35255)

School of Mathematics and Statistics, Lanzhou University, Lanzhou, Gansu 730000, People's Republic of China
E-mail address: ling@lzu.edu.cn

Department of Mathematics, University of Miami, P.O. Box 249085, Coral Gables, Florida 33124-4250
E-mail address: ruan@math.miami.edu