SPREADING SPEEDS AND TRAVELING WAVE SOLUTIONS IN
COOPERATIVE INTEGRAL-DIFFERENTIAL SYSTEMS

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Abstract. We study a cooperative system of integro-differential equations. It is shown that the system in general has multiple spreading speeds, and when the linear determinacy conditions are satisfied all the spreading speeds are the same and equal to the spreading speed of the linearized system. The existence of traveling wave solutions is established via integral systems. It is shown that when the linear determinacy conditions are satisfied, if the unique spreading speed is not zero then it may be characterized as the slowest speed of a class of traveling wave solutions. Some examples are presented to illustrate the theoretical results.

1. Introduction. Integro-differential equations have been used to study growth and spread of populations with long distance dispersal in continuous time and space, and many interesting findings have come out of this field. The simplest scalar integro-differential equation is given by

$$\frac{\partial u}{\partial t} = d \int_{-\infty}^{\infty} k(x - y)u(t, y)dy - du + f(u(t, x)).$$  (1)
In this equation \( u(t, x) \) represents the density of a population at time \( t \) and position \( x \), \( d \) is the jumping rate, \( k \) is the dispersal kernel, and \( f \) describes the population growth. Medlock and Kot [13] used this model to investigate the disease spread in a population. Lutscher et al. [10] employed it to examine the spread of a population in a stream. Similar models were also discussed by Fedotov [1] and Méndez [11].

The spreading speed of a population describes the asymptotic rate at which the population expands its spatial range. A traveling wave is a special solution that maintains a fixed shape and fixed speed. Spreading speeds and traveling waves provide important insight about spatial dynamics of an invading species. Medlock and Kot derived the minimal traveling wave speed for (1) with a specific \( f \) by using the idea of linear determinacy given in [14]. Lutscher et al. used the same idea to obtain the minimal wave speed and showed it coincides with the spreading speed in some sense under certain conditions. For more work on traveling wave solutions for (1) and related results, see Su et al. [16] and the papers cited therein. Jin and Zhao [2] studied the case where \( d \) and \( f \) are periodic functions in \( t \).

Most ecological models involve interactions of multiple species. It is therefore important to investigate the spatial dynamics of multi-species systems in the form

\[
\frac{\partial u}{\partial t} = D \int_{-\infty}^{\infty} K(x-y)u(t,y)dy - Du + f(u(t,x)),
\]

(2)

In this system the vector-valued function \( u(t, x) = (u_1(t, x), u_2(t, x), ..., u_m(t, x)) \) represents densities of the populations of \( m \) species or classes at time \( t \) and position \( x \), \( D = \text{diag}(d_1, ..., d_m) \) with each \( d_i \) nonnegative, \( K = \text{diag}(k_1, ..., k_m) \) with each \( k_i \) a probability density function, and \( f(u) = (f_1, f_2, ..., f_m) \) independent of \( x \) and \( t \). We shall assume that the origin is an unstable equilibrium. We are interested in the dynamics about the spatial transitions from the origin to an equilibrium with positive components.

The mathematical theory regarding spreading speeds for cooperative discrete-time recursions was developed by Lui [9] and Weinberger, Lewis and Li [17, 3, 4, 18]. This theory has been applied to integro-difference equations and reaction-diffusion equations. We shall demonstrate that the theory can be also used to study (2). We particularly show that in general (2) has multiple spreading speeds with the well defined fastest spreading speed and slowest spreading speed. We also show that when the linear determinacy conditions are satisfied all the species spread at the same spreading speed that can be computed through linearization.

Traveling wave solutions for general cooperative systems have been studied by several authors; see for example Li et al. [4], Liang and Zhao [7, 8], and Li and Zhang [6]. However the results obtained in these papers require some compactness or weak compactness assumptions that are not satisfied by (2). We shall establish the existence of traveling wave solutions via compact integral operators, which has been proven useful in the study of existence of traveling wave solutions for partially degenerate reaction-diffusion systems (see Li [5]). We show that when the linear determinacy conditions are satisfied, if the unique spreading speed of system (2) is not zero then it represents the slowest speed of a class of traveling wave solutions.

This paper is arranged as follows. In Section 2 we provide spreading speed results. The existence of traveling wave solutions is discussed in Section 3. Applications to some particular population models are presented in Section 4. The proofs about the existence and properties of the solutions for (2) are given in the Appendix.
2. Hypotheses and spreading speeds. We first introduce some notations. We shall use boldface Roman symbols like \( u(x) \) to denote \( m \)-vector-valued functions of \( x \), and boldface Greek letters like \( \alpha \) to stand for \( m \)-vectors, which may be thought of as constant vector-valued functions. We define \( u(x) \geq v(x) \) to mean that \( u_i(x) \geq v_i(x) \) for all \( i \) and \( x \), and \( u(x) > v(x) \) to mean that \( u_i(x) > v_i(x) \) for all \( i \) and \( x \). We also define \( \max\{u(x), v(x)\} \) (\( \min\{u(x), v(x)\} \)) to mean the vector-valued function whose \( i \)th component at \( x \) is \( \max\{u_i(x), v_i(x)\} \) (\( \min\{u_i(x), v_i(x)\} \)). We use \( |\cdot| \) to denote the Euclidean norm. We use the notation \( \mathbf{0} \) for the constant vector all of whose components are 0. We shall also use the notation \[ C_\alpha := \{u : u(x) \text{ is continuous, and } 0 \leq u(x) \leq \alpha \text{ for all } x\} \]

We shall make the following hypotheses about the system (2).

**Hypotheses 2.1.**

i. \( f(0) = 0 \), there is a constant \( \beta >> 0 \) such that \( f(\beta) = 0 \) which is minimal in the sense that there are no constant \( \nu \) other than \( \beta \) such that \( f(\nu) = 0 \) and \( 0 << \nu \leq \beta \), and the equation \( f(\alpha) = 0 \) has a finite number of constant roots.

ii. The system is cooperative; i.e., \( f_i(\alpha) \) is nondecreasing in all components of \( \alpha \) with the possible exception of the \( i \)th one.

iii. \( f(\alpha) \) is uniformly Lipschitz continuous in \( \alpha \) so that there is \( \rho > 0 \) such that for any \( \alpha_1, \alpha_2 \geq 0, i = 1, 2, |f(\alpha_1) - f(\alpha_2)| \leq \rho(\alpha_1 - \alpha_2) \).

iv. \( f \) has the Jacobian \( f'(0) \) at \( 0 \) with the property that \( f'(0) \) has a positive eigenvalue whose eigenvector has positive components.

v. \( d_i \geq 0 \) for all \( i \).

vi. Each \( k_i \) is a nonnegative continuous probability function or a Dirac delta function with \( \int_{-\infty}^{\infty} k_i(x)dx = 1 \), and each \( k_i(\mu) = \int_{-\infty}^{\infty} k_i(x)e^{\mu x}dx \) converges for one positive value and one negative value of \( \mu \).

We shall study the spreading speeds and traveling wave solutions for (2) under Hypotheses 2.1. It should be noted that Hypotheses 2.1 vi does not require the dispersal kernels \( k_i \) to be symmetric. The non-symmetry of dispersal kernels will be emphasized in the application examples given in Section 4.

Our first theorem is about the existence and basic properties of solutions for (2).

**Theorem 2.1.** Assume that Hypotheses 2.1 are satisfied. Then the initial value problem consisting of (2) and \( u(0, x) = u_0(x) \in C_\mathcal{B} \) has a unique solution \( u(x,t) \).

Let \( Q_t \) denote the time-\( t \) solution map for (2). \( Q_t \) has the following properties

i. \( Q_t \) is order-preserving on nonnegative functions; i.e., if \( u \geq v \geq 0 \), then \( Q_t[u] \geq Q_t[v] \geq 0 \).

ii. \( Q_t \) is translation invariant; i.e., \( Q_t[T_y[v]] = T_y[Q_t[v]] \) for all \( y \) where \( T_y[v](x) = v(x - y) \).

iii. \( Q_t \) is continuous in the topology of uniform convergence on bounded sets; i.e., if the uniformly bounded sequence \( v_n(x) \) converges to \( v(x) \), uniformly on every bounded set, then \( Q_t[v_n] \) converges to \( Q_t[v] \), uniformly on every bounded set.

iv. The family \( \{Q_t, t > 0\} \) represents a semigroup.

v. For any fixed \( t > 0 \), let \( M_t \) be the linearization of \( Q_t \) with respect to the initial data \( u_0 \) for system (2). Then there is a family \( M_t^{(\kappa)} \) of bounded linear order-preserving operators on \( m \)-vector-valued functions with the properties that

a. for every sufficiently large positive integer \( \kappa \) there is a constant vector \( \omega >> 0 \) such that

\[ Q_t[v] \geq M_t^{(\kappa)}[v], \text{ when } 0 \leq v \leq \omega; \]
i.e., in a neighborhood of the zero equilibrium, one can bound the nonlinear operator below by a sequence of linear operators.

b. For every $\mu > 0$ the matrices $B_{t,\mu}$ and $B_{\nu,\mu}^{(n)}$ are defined as follows

$$B_{t,\mu} \alpha := M_{1} e^{-\mu x} \alpha |_{x=0}, \quad B_{\nu,\mu}^{(n)} \alpha := M_{1} e^{-\nu x} \alpha |_{x=0}.$$

Then $B_{\nu,\mu}^{(n)}$ converge to $B_{t,\mu}$ as $\kappa \to \infty$ uniformly on $t$ in a bounded interval.

Since the proof of this theorem deviates from the major theme of present study on spreading speeds and traveling waves of system (2), we postpone it into the Appendix. We now recall the framework developed in Weinberger et al. [17] in establishing spreading speeds for (2). Let $Q$ denote the time one solution map of (2). Define the sequence $a_{n}(c; x)$ by the recursion

$$a_{n+1}(c; x) = \max \{ \phi(x), Q[a_{n}(c; \cdot)](x + c) \},$$

where $a_{0}(c; x) = \phi(x)$, and $\phi(x)$ is any nonincreasing continuous function with $\phi(x) = 0$ for $x \geq 0$ and $0 < \phi(-\infty) < \beta$. By definition $a_{0} \leq a_{1}$, and an induction argument shows that for all $n$, $a_{n} \leq a_{n+1} \leq \beta$, and $a_{n}(c; x)$ is nonincreasing in $c$ and $x$. Thus the sequence $a_{n}$ increases to a limit function $a(c; x)$ that is again nondecreasing in $c$ and $x$ and bounded by $\beta$. The results from Lui [9] show that $a(c; -\infty) = \beta$, and that the constant vector $a(c; \infty)$ is a fixed point of $Q$, which is nondecreasing in $c$ and independent of the choice of $\phi$. Define

$$c^{*} := \sup \{ c; a(c; \infty) = \beta \},$$

and

$$c_{+}^{*} := \sup \{ c; a(c; \infty) \neq 0 \}.$$

Clearly $c_{+}^{*} \geq c^{*}$. It was shown in [17] that $c^{*}$ is the slowest spreading speed and $c_{+}^{*}$ is an upper bound for all the spreading speeds for (2). In the case that there are only two equilibria $0$ and $\beta$, $c_{+}^{*} = c^{*}$ so that all the components spread at the same speed $c^{*}$. In Li et al. [4] a fastest spreading speed $c_{+}^{*}$ was defined as follows. Let $b_{n}(x)$ be the solution of the recursion define by $Q$ with $b_{0}(x) = \phi(x)$. We define the function

$$B(c; x) = \limsup_{n \to \infty} b_{n}(x + nc).$$

As in the case of the function $a(c, x)$ we can show that $B(c, \infty)$ is independent of the choice of initial function $\phi$. We define the fastest spreading speed $c_{+}^{*}$ by the formula

$$c_{+}^{*} := \sup \{ c; B(c; \infty) \neq 0 \}.$$

It was shown in [4] that $c^{*} \leq c_{+}^{*} \leq c_{+}^{*}$.

It was shown in [17, 4] that $c^{*}$ is the slowest speed while $c_{+}^{*}$ the fastest speed for $Q$. One can then extend the results to the integro-differential system (2) by using the semigroup property of $Q_{t}$ given in Theorem 3.1. The proof is essentially the same as that of Theorem 4.1 in Liang and Zhao [7], and is omitted. The following two theorems on spreading speeds follow directly from Theorem 2.1 and Theorem 2.2 in [4] and the semigroup property of the solution operators of (2).

**Theorem 2.2.** There is an index $j$ for which the following statement is true: Suppose that the initial function $u_{0}(x)$ is $0$ for all sufficiently large $x$, and that there are positive constants $0 < \rho \leq \sigma < 1$ such that $0 \leq u_{0} \leq \sigma \beta$ for all $x$ and $u_{0} \geq \rho \beta$
for all sufficiently negative $x$. Then for any positive $\varepsilon$, the solution $u(t, x)$ of system (2) has the properties
\[
\lim_{t \to \infty} \left[ \sup_{x \geq t(c^* + \varepsilon)} u_j(t, x) \right] = 0,
\]
and
\[
\lim_{t \to \infty} \left[ \sup_{x \leq t(c^* - \varepsilon)} \{\beta - u(t, x)\} \right] = 0.
\]
That is, the $j$th component spreads at a speed no higher than $c^*$, and no component spreads at a lower speed.

**Theorem 2.3.** There is an index $j$ for which the following statement is true: Suppose that the initial function $u_0(x)$ is 0 for all sufficiently large $x$, and that there are positive constants $0 < \rho \leq \sigma < 1$ such that $0 \leq u_0 \leq \sigma \beta$ for all $x$ and $u_0 \geq \rho \beta$ for all sufficiently negative $x$. Then for any positive $\varepsilon$, the solution $u(t, x)$ of system (2) has the properties
\[
\lim_{t \to \infty} \left[ \inf_{x \leq t(c_j - \varepsilon)} u_j(t, x) \right] > 0,
\]
and
\[
\lim_{t \to \infty} \left[ \sup_{x \geq t(c_j + \varepsilon)} u_j(t, x)(x) \right] = 0.
\]
That is, the $i$th component spreads at a speed no less than $c_j^*$, and no component spreads at a higher speed.

The linearized system of (2) around 0 is given by
\[
\frac{\partial u}{\partial t} = D \int_{-\infty}^{\infty} K(x - y)u(t, y)dy - Du + f'(0)u(t, x).
\]
(4)

One can find that the moment generating matrix of the time one solution map of (4) is given by $e^{C_\mu}$, where
\[
C_\mu = D \int_{-\infty}^{\infty} K(x)e^{\mu x}dx - D + f'(0).
\]
The proof of this formula is the same as the first part of the proof of Lemma 5.6 given in the Appendix (see (6) with $\kappa \to \infty$).

We assume that the matrix $f'(0)$ is in Frobenius normal form with the diagonal blocks irreducible, so that the same is true of $C_\mu$. The blocks are ordered starting at the uppermost block. Let $\gamma_\sigma(\mu)$ be the principal eigenvalue of the $\sigma$th irreducible diagonal block of $C_\mu$. Define
\[
\bar{c} := \inf_{\mu > 0} (1/\mu)\gamma_1(\mu).
\]
(5)

We shall use $\bar{\mu}$ to denote the smallest extended positive number at which the infimum in (5) is attained. $\bar{\mu}$ is either a finite number or $\infty$. Lemma 6.5 in Liu [9] shows that $(1/\mu)\gamma_1(\mu)$ is nonincreasing for $0 < \mu < \bar{\mu}$.

**Lemma 2.4.** The following two statements are valid.

i. If for some $i$ with the $i$th species associated with the first diagonal block of $C_\mu$, $d_i > 0$ and $k_i(x)$ is positive at some positive number, then $\bar{\mu}$ is finite.

ii. If for every $i$ with the $i$th species associated with the first diagonal block of $C_\mu$, $d_i = 0$ or $k_i(x)$ is zero for all $x > 0$, and if $\bar{\mu} = \infty$, then $\bar{c} = 0$. 
Proof. Since \( \gamma_1(0) > 0 \), \( \lim_{\mu \to 0^+} \frac{\gamma_1(\mu)}{\mu} = \infty \). If \( \gamma_1(\mu) \) is undefined for some \( \mu > 0 \) (i.e., \( \bar{k}_i(\mu) \) is divergent for some \( i \) with the \( i \)th species associated with the first diagonal block of \( C^{(1)}_\mu \)), \( \bar{\mu} \) is clearly finite. To prove the statement (i), it suffices to show that if \( \gamma_1(\mu) \) is defined for all \( \mu > 0 \), then \( \lim_{\mu \to \infty} \frac{\gamma_1(\mu)}{\mu} = \infty \). To this end, let \( C^{(1)}_\mu \) denote the first diagonal block of \( C_\mu \). Assume that for some \( i \) with the \( i \)th species associated with \( C^{(1)}_\mu \), \( d_i > 0 \) and \( k_i(x_0) > 0 \) with \( x_0 > 0 \). If \( k(x) \) is continuous at \( x_0 \), then there is an interval \([a, b] \) containing \( x_0 \) such that \( b > a > 0 \) and \( k_i(x) > 0 \) on \([a, b] \). It follows that \( \bar{k}_i(\mu) = \int_{-\infty}^\infty k_i(x)e^{\mu x}dx \geq re^{\mu \bar{\mu}} \) where \( r = \int_{a}^{b} k_i(x)dx > 0 \). If \( k(x) \) is a Dirac Delta function concentrating at \( x_0 \), \( \bar{k}_i(\mu) = e^{\mu \bar{\mu}} \).

Let \( \xi^{(1)}(\mu) \) denote an eigenvector corresponding to \( \gamma_1(\mu) \) for \( C^{(1)}_\mu \). The \( i \)th equation of \( C^{(1)}_\mu \) \( \xi^{(1)}(\mu) = \gamma_1(\mu)\xi^{(1)}(\mu) \) shows
\[
\gamma_1(\mu) = d_i \bar{k}_i(\mu) - d_i + f'_{i}(0) + (1/\xi_1^{(1)}(\mu)) \sum_{j \neq i} c^{(1)}_{ij}(\mu) \xi_1^{(1)}(\mu)
\]
where \( c^{(1)}_{ij}(\mu) \geq 0 \) is the \( i \)th row \( j \)th column entry of \( C^{(1)}_\mu \) and \( \xi_1^{(1)}(\mu) > 0 \) is the \( j \)th component of \( \xi^{(1)}(\mu) \). It follows that
\[
\gamma_1(\mu) \geq d_i e^{\mu \bar{\mu}} - d_i + f'_{i}(0), \text{ or } \gamma_1(\mu) \geq d_i e^{\mu \bar{\mu}} - d_i + f'_{i}(0).
\]
This shows that if \( \gamma_1(\mu) \) is defined for all \( \mu > 0 \) then \( \lim_{\mu \to \infty} \frac{\gamma_1(\mu)}{\mu} = \infty \), so that \( \bar{\mu} \) is finite. This proves the statement (i).

Assume that for every \( i \) with the \( i \)th species associated with \( C^{(1)}_\mu \), \( d_i = 0 \) or \( k_i(x) \) is zero for all \( x > 0 \). Then simple calculations show for \( \mu > 0 \), \( d_i \bar{k}_i(\mu) \leq d_i \) for some positive constant \( d_i \). Therefore if \( C^{(1)}_\mu \) with \( \mu > 0 \) is bounded above by a constant matrix, and thus \( \gamma_1(\mu) \) with \( \mu > 0 \) is bounded above by a constant. It follows that if \( \bar{\mu} = \infty \) then \( \bar{c} = 0 \). The proof is complete.

If \( C_\mu \) is well defined at \( \mu > 0 \), we use \( \xi(\mu) \) to denote an eigenvector corresponding to \( \gamma_1(\mu) \) for matrix \( C_\mu \).

The following hypotheses describe the linear determinacy conditions for (2).

**Hypotheses 2.2.**

i. There is a positive entry to the left of each of the irreducible diagonal blocks other than the first (uppermost) one in \( f'(0) \).

ii. a. \( \gamma_1(0) > 0 \); and
   b. \( \gamma_1(0) > \gamma_\sigma(0) \) for all \( \sigma > 0 \).

iii. Either
   a. \( \bar{\mu} \) is finite, \( C_{\bar{\mu}} \) is well defined,
   \[
   \gamma_1(\bar{\mu}) > \gamma_\sigma(\bar{\mu}),
   \]
   and
   \[
   f(\min\{\tau \xi(\bar{\mu}), \beta\}) - f'(0)\tau \xi(\bar{\mu}) \leq 0
   \]
   for all positive \( \tau \);
   or
   b. for all \( \sigma > 1 \), \( C_\mu \) is well defined for all \( \mu > 0 \), and there is a sequence \( \mu_\nu \nearrow \bar{\mu} \) such that for each \( \nu \) the inequalities (6) and (7) with \( \bar{\mu} \) replaced by \( \mu_\nu \) are valid.

Note that (6) implies that \( \xi(\bar{\mu}) \gg 0 \).
The following theorem follows from Theorem 3.1 in [17]. Note that we have dropped the hypothesis that the time one solution operator \( Q \) of (2) is reflection invariant (i.e., all \( k_i(x) \) are symmetric). In [17] the reflection invariance was assumed, but it was not used in the proof of Theorem 3.1. Consequently Theorem 3.1 in [17] is still valid without the reflection invariance assumption, and it works for the integral differential system (2).

**Theorem 2.5.** Under the Hypotheses 2.1 and 2.2,

\[ c_+^* = c^* = \bar{c}, \]

so that (2) has a single speed and is linearly determinate.

**Remark 1.** The results on spreading speeds in [17] require that every \( \bar{k}_i(\mu) \) in Hypothesis 2.1 vi is convergent for all real number \( \mu \). This is unnecessary. If for some \( i, \bar{k}_i(\mu) \) converges in an interval that is not \( (-\infty, \infty) \), a proof similar to the second half of the proof of Theorem 4.1 in [12] shows that Theorem 2.5 still holds.

3. **Existence of traveling wave solutions.** We use \( w(x-ct) \) to denote a nonincreasing traveling wave solution of (2) with speed \( c \) connecting two different constant equilibria \( \nu_1 \) and \( \nu_2 \) with \( \nu_1 \geq \nu_2 \). It satisfies

\[ -cw'(x) = D \int_{-\infty}^{\infty} K(x-y)w(y)dy - Dw(x) + f(w(x)), \quad (1) \]

and \( w(-\infty) = \nu_1, \ w(\infty) = \nu_2. \)

An important observation from (1) is that for \( c \neq 0 \)

\[ \lim_{x \to \infty} w'(x) = \lim_{x \to -\infty} w'(x) = 0. \]

This can be easily shown by taking \( x \to \infty \) and \( x \to -\infty \) on both sides of (1).

Choose \( \kappa > \rho + d \) where \( d = \max\{d_1, ..., d_m\} \) and \( \rho \) is given in Hypothesis 2.1 iv.

Define

\[ R[u](x) := D \int_{-\infty}^{\infty} K(x-y)u(y)dy - Du(x) + f(u(x)), \]

and

\[ H(u)(x) = [R[u](x) + \kappa u]/\kappa. \]

Clearly \( R(\alpha) = 0 \) if and only if \( H(\alpha) = \alpha. \) It follows from Hypothesis 2.1 iv that for \( 0 \leq v \leq u \leq \beta. \)

\[ \kappa(H(u) - H(v)) = D \int_{-\infty}^{\infty} K(x-y)[u(y) - v(y)]dy + (\kappa - D)(u(x) - v(x)) + f(u(x)) - f(v(x)) \geq D \int_{-\infty}^{\infty} K(x-y)[u(y) - v(y)]dy + (\kappa - \rho - d)(u(x) - v(x)) \geq 0. \]

If \( c > 0, \) define

\[ (m_c)_i(x) = \begin{cases} 0 & \text{when } x > 0, \\ \frac{\kappa}{c} e^{\frac{\kappa}{c} x} & \text{when } x \leq 0. \end{cases} \]

and if \( c < 0, \) define

\[ (m_c)_i(x) = \begin{cases} \frac{\kappa}{-c} e^{\frac{\kappa}{-c} x} & \text{when } x \geq 0, \\ 0 & \text{when } x < 0. \end{cases} \]
One can further verify that each \( m_i^c(x) \) defined above has the properties that 
\( m_i^c(x) \geq 0 \), \( m_i^c(x) \) is bounded, and 
\( \int_{-\infty}^{+\infty} m_i^c(x)dx = 1 \), so that \( m_i^c \) represents a 
probability density function. Let 
\[ m_c(x) = \text{diag}((m_c)_1(x),\ldots,(m_c)_k(x)). \]

We have that 
\[ \int_{-\infty}^{+\infty} m_c(x)dx = 1. \]

Define 
\[ \tilde{Q}_c[u](x) = \int_{-\infty}^{+\infty} m_c(x-y)H(u)(y)dy. \]

The operator \( \tilde{Q}_c \) is a cooperative convolution operator. It is continuous and compact 
with respect to the topology of uniform convergence on bounded intervals.

We first have the following result.

**Lemma 3.1.** Assume Hypotheses 2.1 are satisfied. Let \( c \neq 0 \). Then \( w(x-ct) \) is a 
nonincreasing traveling wave solution of \( (2) \) connecting two different constant equilibria \( \nu_1 \) and \( \nu_2 \) if and only if \( w \) is a continuous nonincreasing function satisfying 
\[ w(x) = \tilde{Q}_c[w](x) \]
and connecting \( \nu_1 \) and \( \nu_2 \).

The proof of this lemma is essentially the same as the first part of the proof of 
Theorem 3.1 in Li [5]. We shall omit it here. This lemma shows that \( w(x-ct) \) is a 
nonincreasing traveling wave solution of \( (2) \) if and only if \( w \) is a fixed point of \( \tilde{Q}_c \), 
or a traveling wave with speed zero for \( \tilde{Q}_c \).

One can define a function sequence \( \tilde{a}_n(\tilde{c},c;x) \) by \( (3) \) with \( Q \) by \( \tilde{Q}_c \)
\[ \tilde{a}_{n+1}(\tilde{c},c;x) = \max\{\phi(x),\tilde{Q}_c[\tilde{a}_n(\tilde{c},c;\cdot)](x+\tilde{c})\}. \]
Let \( \tilde{a}(\tilde{c},c;x) \) denote the limit of \( \tilde{a}_n(\tilde{c},c;x) \) as \( n \to \infty \). Define 
\[ \tilde{c}^*(c) := \sup\{\tilde{c};\tilde{a}(\tilde{c},c;\infty) = \beta\}, \]
and 
\[ \tilde{c}^*_+(c) := \sup\{\tilde{c};\tilde{a}(\tilde{c},c;\infty) \neq 0\}. \]

The next two lemmas follow from Theorem 4.2 in [4] and Theorem 4.1 [6], respectively.

**Lemma 3.2.** If Hypotheses 2.1 are satisfied, then for \( \tilde{c} \geq \tilde{c}^*(c) \), there is a nonincreasing 
traveling wave solution \( \tilde{w}(x-\tilde{c}) \) satisfying 
\[ \tilde{w}(x) = \tilde{Q}_c[\tilde{w}](x+\tilde{c}) \] 
with \( \tilde{w}(-\infty) = \beta \) and \( \tilde{w}(\infty) \) an equilibrium other than \( \beta \).

**Lemma 3.3.** If Hypotheses 2.1 are satisfied, then for \( \tilde{c} \geq \tilde{c}^*_+(c) \), there is a nonincreasing 
traveling wave solution \( \tilde{w}(x-\tilde{c}) \) satisfying 
\[ \tilde{w}(x) = \tilde{Q}_c[\tilde{w}](x+\tilde{c}) \] 
with \( \tilde{w}(+\infty) = 0 \) and \( \tilde{w}(\infty) \) an equilibrium other than \( 0 \).

The following lemma is about linear determinacy for \( \tilde{Q}_c \).

**Lemma 3.4.** Assume that Hypotheses 2.1 and Hypotheses 2.2 are satisfied. Then 
\[ \tilde{c}^*(c) = \tilde{c}^*_+(c) = \bar{c}(c), \]
where 
\[ \bar{c}(c) = \inf_{\mu > 0} (1/\mu) \ln \frac{\kappa + \gamma_1(\mu)}{\kappa + \epsilon \mu}. \]
Lemma 3.5. If for (2),

It is easily seen that the principal eigenvalue \( \tilde{\lambda}_1(c; \mu) \) of the first diagonal block of \( \tilde{B}_{c,\mu} \) is

\[
\tilde{\lambda}_1(c; \mu) = \frac{\kappa + \gamma_1(\mu)}{\kappa + c\beta}.
\]

If Hypotheses 2.1 and Hypotheses 2.2 are satisfied, the recursion determined by \( \tilde{Q}_c \) is also linearly determinate. According to Theorem 3 in [4], \( \tilde{c}^*(c) = \tilde{c}^*_+(c) = \tilde{c}(c) \), where \( \tilde{c}(c) = \inf_{\mu > 0} (1/\mu) \ln \tilde{\lambda}_1(c; \mu) \). The proof is complete.

The following lemma is useful in establishing existence of traveling wave solutions for (2).

Lemma 3.5. If \( c \geq \tilde{c} \) and \( c \neq 0 \), then for large \( \kappa \), \( \tilde{c}(c) \leq 0 \).

**Proof.** If \( \bar{\mu} = \infty \), by Lemma 2.4, \( \tilde{c} = 0 \). Since \( c \geq \tilde{c} \) and \( c \neq 0 \), \( c > 0 \). It follows that \( \lim_{\mu \to \infty} \tilde{\lambda}_1(c; \mu) = \lim_{\mu \to \infty} \frac{\kappa + \gamma_1(\mu)}{\kappa + c\beta} = \lim_{\mu \to \infty} \frac{\kappa/\mu + \gamma_1(\mu)/\mu}{\kappa/\mu + c} = 0 \). This yields \( \tilde{c}(c) \leq 0 \).

If \( \bar{\mu} \) is finite, choose \( \kappa > 0 \) large such that \( \kappa + c\beta > 0 \). Then

\[
\tilde{\lambda}_1(c; \bar{\mu}) = \frac{\kappa + \gamma_1(\bar{\mu})}{\kappa + \bar{\mu}c} = \frac{\kappa + \bar{\mu}c}{\kappa + \bar{\mu}c} \leq \frac{\kappa + \bar{\mu}c}{\kappa + \bar{\mu}c} = 1,
\]

so that \( \tilde{c}(c) \leq 0 \). The proof is complete.

We are now ready to present the results on the existence of traveling wave solutions for (2).

Theorem 3.6. Assume that Hypotheses 2.1 and Hypotheses 2.2 are satisfied. Then for \( c \geq \tilde{c} \) and \( c \neq 0 \), system (2) has a nonincreasing traveling wave solution \( w(x - ct) \) with \( w(\infty) = 0 \) and \( w(\infty) \) an equilibrium other than 0.

**Proof.** For \( c \geq \tilde{c} \) and \( c \neq 0 \), Lemma 3.5 shows that \( \tilde{c}(c) \leq 0 \). By Lemma 3.3, there is a nonincreasing traveling wave solution \( \tilde{w}(x) \) for \( \tilde{Q}_c \) with speed 0 such that \( \tilde{w}(\infty) = 0 \) and \( \tilde{w}(-\infty) \) an equilibrium other than 0. By Lemma 3.1, \( \tilde{w}(x - ct) \) is a traveling solution of (2). The proof is complete.

Theorem 3.7. Assume that Hypotheses 2.1 and Hypotheses 2.2 are satisfied. Then the following statements are true for system (2):

i. for \( c \geq \tilde{c} \) and \( c \neq 0 \), there is a nonincreasing traveling wave solution \( w(x - ct) \) with \( w(-\infty) = \beta \) and \( w(\infty) \) an equilibrium other than \( \beta \).
ii. if there is a nonincreasing traveling wave \( w(x - ct) \) with \( w(-\infty) = \beta \) and \( w(\infty) \) an equilibrium other than \( \beta \), then \( c \geq \tilde{c} \).

Proof. For \( c \geq \tilde{c} \) and \( c \neq 0 \), Lemma 3.5 shows that \( \tilde{c}(c) \leq 0 \). By Lemma 3.2, there is a nonincreasing traveling wave solution \( \tilde{w}(x) \) for \( \tilde{Q}_c \) with speed 0 such that \( \tilde{w}(-\infty) = \beta \) and \( \tilde{w}(\infty) \) an equilibrium other than \( \beta \). By Lemma 3.1, \( w(x - ct) \) is a traveling solution of (2). This proves the statement (i).

The proof of the statement (ii) is similar to the second part of the proof of Theorem 3.1 in [4] and is omitted here. The proof is complete.

4. Applications. In this section we apply the results obtained in the preceding sections to some particular models.

We first consider the single species model

\[
\frac{\partial u}{\partial t} = d \int_{-\infty}^{\infty} k(x - y)u(t, y)dy - du + ru(1 - u),
\]

where \( d > 0 \), \( r > 0 \), and \( k \) is the dispersal kernel. This model can be used to study the spread of a species with logistic growth. Model (2) is linearly determinate since \( ru(1 - u) \leq ru \) for all \( u \geq 0 \). The results in Section 2 show that the spreading speed of the model is

\[
\tilde{c} = \inf_{\mu > 0} d \int_{-\infty}^{\infty} k(x)e^{\mu x}dx + r - d.
\]

The work in Sun et al. [16] shows that in the case when \( \int_{-\infty}^{\infty} k(x)e^{\mu x}dx \) is convergent for all \( \mu > 0 \), for \( c \geq \tilde{c} \) and \( c \neq 0 \), \( \tilde{c} \) is the slowest speed of nonincreasing traveling wave solutions that connect 0 and 1, and such a traveling wave does not exist if \( c < \tilde{c} \). The results in Section 3 indicate that this statement is still true when \( \int_{-\infty}^{\infty} k(x)e^{\mu x}dx \) is convergent for \( \mu \) in a bounded interval.

Assume that \( k(x) \) is continuous and \( k(x) = 0 \) for all \( x > 0 \). Let \( r > d \). Then for all \( \mu > 0 \)

\[
0 < r - d \leq d \int_{-\infty}^{\infty} k(x)e^{\mu x}dx + r - d \leq r.
\]

This implies that \( \tilde{c} = 0 \). For \( c > \tilde{c} \), (2) has a nonincreasing traveling wave with speed \( c \) that connects 0 and 1. If \( w(x) \) is a continuous nonincreasing traveling wave for (2) with speed \( \tilde{c} = 0 \) that connects 0 and 1, then \( w \) satisfies

\[
d \int_{-\infty}^{\infty} k(x - y)w(y)dy + w(r - d - rw) = 0.
\]

Since \( w(\infty) = 0 \), there is a real number \( x_0 \) such that \( w(x_0) > 0 \) and \( r - d - rw(x_0) > 0 \). On the other hand, the first term in (4) is nonnegative for all \( x \) and particularly for \( x_0 \). It follows that (4) cannot hold at \( x_0 \). We therefore have that (2) has no continuous nonincreasing traveling wave with speed \( \tilde{c} = 0 \) that connects 0 and 1. This example indicates that the assumption \( c \neq 0 \) in the theorems given in Section 3 cannot be dropped in general.

We next consider the two-species Lotka-Volterra competition model

\[
\begin{align*}
\frac{\partial p}{\partial t} &= d_1 \int_{-\infty}^{\infty} k_1(x - y)p(t, y)dy - d_1p + r_1p(1 - p - a_1q), \\
\frac{\partial q}{\partial t} &= d_2 \int_{-\infty}^{\infty} k_2(x - y)q(t, y)dy - d_2q + r_2q(1 - q - a_2p).
\end{align*}
\]

(5)
Here $p$ and $q$ represent the densities of two species, respectively; $r_i > 0$ are the intrinsic growth rates of the species; $a_i > 0$ are the competition coefficients; $d_i ≥ 0$ are jumping rates; and $k_i$ are dispersal kernels and satisfy Hypotheses 2.1 vi. This system has the trivial equilibrium $(0,0)$, and two mono-culture equilibria $(1,0)$ and $(0,1)$. The coexistence equilibrium is given by $(p^*,q^*)$ with

$$p^* = \frac{1 - a_1}{1 - a_1a_2}, \quad q^* = \frac{1 - a_2}{1 - a_1a_2}.$$ 

It is in the first quadrant if and only if $(1 - a_1)(1 - a_2) > 0$.

Standard stability analysis shows that $(1,0)$ is unstable if $a_2 < 1$, $(0,1)$ is unstable if $a_1 < 1$, and $(p^*,q^*)$ is stable when $a_1 < 1$ and $a_2 < 1$ and unstable when $a_1 > 1$ and $a_2 > 1$.

For the case of $a_1 < 1$ and $a_2 < 1$, Yu and Yuan [20] studied the existence of traveling wave solutions connecting $(0,0)$ with $(p^*,q^*)$ when $k_i(x)$, $i = 1,2$, are symmetric and $\int_{-\infty}^{\infty} k_i(x) e^{\mu x} dx$ converge for any real number $\mu$. Zhang and Li [19] studied the same problem for a more general case where $k_i(x)$ may be non-symmetric and $\int_{-\infty}^{\infty} k_i(x) e^{\mu x} dx$ may converge for $\mu$ in a bounded interval. Pan and Lin [15] investigated the existence of traveling waves connecting $(0,1)$ and $(1,0)$ for the case of $a_1 < 1 < a_2$ under the assumption that for $i = 1,2$, $k_i(x)$ are symmetric and $\int_{-\infty}^{\infty} k_i(x) e^{\mu x} dx$ converge for any real number $\mu$. We shall study the spreading speed and traveling waves that describe the spatial transition from $(0,1)$ to $(1,0)$ or $(p^*,q^*)$ for the more general case where $k_i$ are allowed to be non-symmetric and $\int_{-\infty}^{\infty} k_i(x) e^{\mu x} dx$ may converge in a bounded interval. Our conditions for existence of traveling wave solutions are different from those given in [15].

As is well-known, the change of variables

$$u = p, \quad v = 1 - q$$

converts the system (5) into the system

$$\begin{cases}
\frac{\partial u}{\partial t} = d_1 \int_{-\infty}^{\infty} k_1(x - y) u(t,y) dy - d_1 u + r_1 u(1 - a_1 - u + a_1 v), \\
\frac{\partial v}{\partial t} = d_2 \int_{-\infty}^{\infty} k_2(x - y) v(t,y) dy - d_2 v + r_2 (1 - v) q(a_2 u - v),
\end{cases}$$

(6)

which is cooperative in the biologically realistic range $0 \leq u \leq 1$, and $0 \leq v \leq 1$. This change of variables maps $(0,1)$ into the origin $(0,0)$. The target equilibrium $\beta = (\beta_1,\beta_2)$ is given by $\beta_1 = p^*, \beta_2 = 1 - q^*$ if $a_2 < 1$ and $\beta_1 = \beta_2 = 1$ if $a_1 ≥ 1$.

Note that if $a_1 < 1$ and $a_2 ≥ 1$, there is an extra equilibrium $(0,1)$ for (6) which lies on the closed rectangle with vertices $(0,0)$ and $(\beta_1,\beta_2)$.

The matrix $C_\mu$ for (6) is given by

$$C_\mu := \begin{pmatrix}
d_1 \tilde{k}_1(\mu) - d_1 + r_1(1 - a_1) & 0 \\
r_2 a_2 & d_2 \tilde{k}_2(\mu) - d_2 - r_2
\end{pmatrix}.$$ 

We have that

$$\gamma_1(\mu) = d_1 \tilde{k}_1(\mu) - d_1 + r_1(1 - a_1), \quad \gamma_2(\mu) = d_2 \tilde{k}_2(\mu) - d_2 - r_2.$$ 

The spreading speed of the linearized problem is given by $\bar{c} = \inf_{\mu > 0} \mu^{-1} \gamma_1(\mu)$ or equivalently

$$\bar{c} = \inf_{\mu > 0} \mu^{-1} [d_1 \tilde{k}_1(\mu) - d_1 + r_1(1 - a_1)].$$

(7)

We use $\bar{\mu}$ to denote the smallest extended positive number at which the infimum in (7) is attained.
Theorem 4.1. Let $a_1 < 1$. Assume that either
(a) $\bar{\mu}$ is finite and $\bar{k}_2(\bar{\mu})$ is convergent, and
\[ d_1 \bar{k}_1(\bar{\mu}) - d_2 \bar{k}_2(\bar{\mu}) + d_2 - d_1 + r_1(1 - a_1) + r_2 \geq r_2 \max\{a_1 a_2, 1\}. \] (8)
or
(b) $\bar{\mu} = \infty$, $\bar{k}_1(\mu)$ is convergent for all $\mu > 0$, and there is a sequence $\mu_\alpha \to \infty$ such that for each $\sigma$
\[ d_1 \bar{k}_1(\mu_\alpha) - d_2 \bar{k}_2(\mu_\alpha) + d_2 - d_1 + r_1(1 - a_1) + r_2 \geq r_2 \max\{a_1 a_2, 1\}. \]
Then the following statements are valid.

i. (6) has a unique spreading speed $\bar{c}$ given by (7).

ii. If $a_2 \leq 1$, or $a_2 > 1$ and
\[ \bar{c} + \inf_{\mu > 0} \mu^{-1}(d_2 \bar{k}_2(-\mu) - d_2) > 0, \] (9)
for any $c \geq \bar{c}$ and $c \neq 0$, (6) has a nonincreasing traveling wave solution $(u(x \cdot ct), v(x \cdot ct))$ with $(u(-\infty), v(-\infty)) = (\beta_1, \beta_2)$ and $(u(\infty), v(\infty)) = (0, 0)$, and such a traveling wave does not exist if $c < \bar{c}$.

Proof. It is easily seen that Hypotheses 2.1 and Hypotheses 2.2 i-ii are satisfied by (6). An eigenvector of $C_\mu$ which corresponds to $\gamma_1(\mu)$ is $\xi = (\xi_1(\mu), \xi_2(\mu))$ where $\xi_1(\mu) = \gamma_1(\mu) - \gamma_2(\mu)$, $\xi_2(\mu) = r_2 a_2$.

If $\bar{\mu}$ is finite, (7) in Hypothesis 2.2 iii takes the form
\[ r_1 \xi_1(\bar{\mu}) [\xi_1(\bar{\mu}) + a_1 \xi_2(\bar{\mu})] \leq 0, \quad -r_2 \xi_2(\bar{\mu}) [a_2 \xi_1(\bar{\mu}) - \xi_2(\bar{\mu})] \leq 0. \]
These two inequalities are equivalent to
\[ \gamma_1(\bar{\mu}) - \gamma_2(\bar{\mu}) \geq r_2 \max\{a_1 a_2, 1\}, \]
which is (8). Clearly this inequality also implies (6). Theorem 2.5 shows that system (6) has a unique spreading speed given by $\bar{c}$. Thus statement (i) is established if $\bar{\mu}$ is finite. Similarly one can prove the statement if $\bar{\mu} = \infty$.

Observe that if $a_2 \leq 1$, $0$ and $\beta$ are the only two equilibria in $C_\beta$, and if $a_2 > 1$, there is an extra equilibrium $(0, 1)$ in $C_\beta$. In any case, the nonexistence of a nonincreasing traveling wave solution with a speed $c < \bar{c}$ connecting $0$ and $\beta$ in (6) follows from Theorem 3.7 (ii).

If $a_2 \leq 1$, since there are only two equilibria $0$ and $\beta$, Theorem 3.7 (i) shows that for $c \geq \bar{c}$ and $c \neq 0$, (6) has a nonincreasing traveling wave solution with speed $c$ connecting $0$ and $\beta$. If $a_2 > 1$, Theorem 3.6 implies that for $c \geq \bar{c}$ and $c \neq 0$, there exists a nonincreasing traveling wave solutions $(u(x \cdot ct), v(x \cdot ct))$ connecting $(0, 0)$ with $\beta$ or with $(0, 1)$. If it connects $(0, 0)$ with $(0, 1)$ then $u(x \cdot ct) \equiv 0$ so that $v(x \cdot ct)$ satisfies
\[ \frac{\partial v}{\partial t} = d_2 \int_{-\infty}^{\infty} k_2(x - y) v(t, y) dy - d_2 v - r_2 (1 - v) v. \]
Let $w(x \cdot ct) = 1 - v(x \cdot ct)$ then $w(x \cdot ct)$ is a nondecreasing traveling wave with $w(\infty) = 1$ and $w(-\infty) = 0$ for the system
\[ \frac{\partial w}{\partial t} = d_2 \int_{-\infty}^{\infty} k_2(x - y) w(t, y) dy - d_2 w + r_2 (1 - w) w. \]
Since the nonlinear reaction term $r_2(1-w)w$ is dominated by its linearization $r_2w$, Theorem 3.7 implies that the traveling wave speed $c$ must satisfy

$$-c \geq \inf_{\mu > 0} \mu^{-1} (d_2 k_2(-\mu) - d_2 + r_2).$$

This and $c \geq \bar{c}$ yield $\bar{c} + \inf_{\mu > 0} \mu^{-1} (d_2 k_2(-\mu) - d_2 + r_2) \leq 0$, which contradicts (9). This proves the statement (ii). The proof is complete. 

We present some numerical simulations to the model (5) with $a_1 = \sqrt{2}(1 - \ln 2)$, $a_2 = 3\sqrt{2}(1 - \ln 2)$, $r_1 = r_2 = 1$, and $d_1 = 1$, and $k_i(x) = \frac{1}{\sigma_i \sqrt{2\pi}} e^{-\frac{x^2}{2\sigma_i^2}}$. It is easily seen that $\bar{k}_i(\mu) = e^{\frac{1}{2} \mu^2 \sigma_i^2}$ where $i = 1, 2$.

We first choose $\sigma_1 = \sigma_2 = 1$ and $d_2 = 1$. One can verify that the infimum in (7) occurs at $\bar{\mu} = \sqrt{\ln 2}$ and $\bar{c} = \sqrt{\ln 4}$, and (8) and (9) are satisfied. Theorem 4.1 shows that $\bar{c}$ is the unique spreading speed and it is the slowest speed of a class of traveling wave solutions connecting $(0,0)$ with $(1,1)$ for (6). We demonstrate the results numerically for the original system (5); see Figure 1.

We now keep all other parameter values, set $\sigma_2 = 2$, and vary $d_2$ from $2^{-7}$ to $2^{7}$. It is readily seen that for (8) to hold, we should have

$$d_2 \leq \frac{\sqrt{2} \ln 2}{2^{2\sigma_2^2/2} - 1} \approx 0.3268.$$  

We then examine the asymptotic traveling wave speed for the system (5). It appears that for values of $d_2$ up to $2^2 = 4$ the computed spreading speed (for the system (5)) is close to the speed $\bar{c}$ predicted by the linearization even though the sufficient condition (8) is violated when $d_2 > 0.3268$. However the two speeds differ for large $d_2$. See Figure 2.

5. Appendix. In this section we shall present the proof of Theorem 2.1. Essentially we shall establish the well-posedness of the proposed system (2) under Hypotheses 2.1, including existence, uniqueness, and continuity with respect to the initial data in the sense of compact open topology. We also generalize the comparison principle to the cooperative system from [2] to integral differential systems. All these results are required for further study on the spreading speed and the existence of traveling wave solutions for (2). We first present a lemma concerning the linear part in (2).

**Lemma 5.1.** Consider the slightly more general linear part of the system (2):

$$\frac{\partial u}{\partial t} = (Au)(t,x) = D_1 \int_{-\infty}^{\infty} K(x-y)u(t,y)dy - D_2 u(t,x),$$

supplemented with the initial condition $u(0,x) = \psi(x) \in C_{B}$. The semigroup operator $u(t,x) = e^{At} \psi$ is order preserving on each component. Furthermore, we have the following estimate:

$$|e^{At}u_0|_{L^p} \leq e^{-(D_2 - D_1)t} \|\psi\|_{L^p}, \quad \forall t \in \mathbb{R}, p \in [1, \infty].$$  

The group operator $e^{At}$ for any $t$ is uniformly continuous in the compact open topology with respect to the initial data $\psi$, i.e., for any $\varepsilon > 0$, $K > 0, t_0 > 0$, there
A numerical simulation of system (5) with parameters chosen as
\[ d_1 = d_2 = 1, \quad r_1 = r_2 = 1, \quad a_1 = \sqrt{2} (1 - \ln 2), \]
\[ a_2 = 3\sqrt{2} (1 - \ln 2) \] and kernels \( k_1, k_2 \) are both standard normal
distribution with mean and standard deviation equal to 0 and 1.
Initial conditions for \( p, q \) are indicated in panel (e) and (f) using
dashed lines. Panels (a) and (b) describe the three-dimensional
profiles of numerical solutions for \( p \) and \( q \). (c) Individuals of \( p \)
spread in a region initially occupied by \( q \). Replacing individuals of
\( q \) completely, population of \( p \) establish themselves by proceeding
in a traveling wave. (d) At the front of the traveling wave there
are few individuals of \( p \) and a large number of \( q \), while at the rear
end of the traveling wave population of \( p \) take up the space with
individuals of \( q \) retreating. At wavefront the traveling wave has a
speed \( \bar{c} \leq c \geq \bar{c} \). Panels (e) and (f) provide snapshots of profiles for
\( p \) and \( q \) at time interval of 25 time units. Solid curves denote so-
lutions and dashed lines indicate initial conditions. The numerical
simulation uses MATLAB software and built-in ODE solver ode45.

\[
\text{exist } \delta(\varepsilon, K) > 0, M(\varepsilon, K) > 0 \text{ such that if, for } \psi_1, \psi_2 \in C^2 \beta \text{ satisfying } |
\psi_1(x) - \psi_2(x)| < \delta \text{ for } x \in [-K - M, K + M], \text{ then } u_1, u_2 \text{ of solutions associated to the}
\text{initial data } \psi_1, \psi_2 \text{ satisfy that}
\]
\[
|u_1(t,x) - u_2(t,x)| < \varepsilon, \quad \forall t \in [0, t_0], x \in [-K, K].
\]

**Proof:** We first define that \( K(0)(x) = \delta(x) \), the classical Dirac delta function,
then \( K(0) \ast \psi = \psi \). By induction we define \( K^{(n+1)} \ast \psi = K \ast K^{(n)} \ast \psi \) for \( n \geq 0 \).
Later on, we will denote \( K \ast \psi \) by the convolution operator defined as
\[
[K \ast \psi](x) = \int_{\mathbb{R}} K(x-y) \psi(y) dy
\]
Figure 2. Numerical calculation of spreading speed for the system (5). Parameter values are \( \sigma_1 = 1, \sigma_2 = 2, d_1 = 1, r_1 = r_2 = 1, a_1 = \sqrt{2}(1 - \ln 2), \) and \( a_2 = 3\sqrt{2}(1 - \ln 2). \) The parameter \( d_2 \) varies on a log 2 scale. Note that the actual values for \( d_2 \) are used for horizontal axis ticks. The solid line corresponds to \( \bar{c} = \sqrt{\ln 4}. \) The dots represent numerically calculated values for the traveling wave speed. For each case of \( d_2, \) the simulation is run for a sufficiently long time, 1000 time units. Then a contour line of \( p = 0.5 \) is drawn to determine its slope.

for any \( \psi \in L^p, \, 1 \leq p \leq \infty. \) Then solution \( u(t, x) \) of (1) can be written as

\[
u(t, x) = [e^{At}\psi](x) = e^{-D_2t} \sum_{n=0}^{\infty} \frac{(tD_1)^n}{n!} [K^{(n)} \ast \psi](x).
\] (3)

Notice that \( |K \ast \psi|_{L^\infty} \leq |\psi|_{L^\infty} \) by using the fact that \( \int K dx = 1, \) the above series can be claimed to be uniformly convergent in the \( L_x^\infty \) norm for \( t \) in a bounded interval. (3) can be obtained by iterating the equivalent integral equation of (1):

\[
u(t, x) = e^{-D_2t}\psi(x) + \int_0^t e^{-D_2(t-s)} \int_{-\infty}^{\infty} K(x-y)u(s, y)dyds.
\]

It is trivial to notice that \( e^{At} \) is order preserving with respect to its each component by (3). The \( L^p \)-norm estimate (2) can be obtained by using the special case of well-known Young’s inequality

\[
|K \ast u|_{L^p} \leq |K|_{L^1} |u|_{L^p} = |u|_{L^p}.
\]

We now prove that the convolution operator \( K \ast \) is continuous with respect to \( \psi \) in the sense of compact open topology. For any \( \varepsilon > 0 \) and \( K > 0, \) since
\[ \int_{\mathbb{R}} K(y)dy = 1, \text{ there exists a } M_1 > 0 \text{ such that } \int_{|y| \geq M_1} K(y)dy \leq \frac{\varepsilon}{2|\beta|_\infty}. \]

Assume that \( \sup_{s \in [-K-M_1,K+M_1]} \psi(s) \leq \delta \), then we have for \( x \in [-K,K] \),

\[
\begin{align*}
|K \ast \psi|(x) &= \int_{\mathbb{R}} K(y)\psi(x-y)dy \\
&= \int_{-M_1}^{M_1} K(y)\psi(x-y)dy + \int_{|y| \geq M_1} K(y)\psi(x-y)dy \\
&\leq 1 \cdot \max_{y \in [-M_1,M_1]} \psi(x-y) + |\beta|_\infty \int_{|y| \geq M_1} K(y)dy \leq \delta + \frac{\varepsilon}{2}.
\end{align*}
\]

Let \( \delta = \varepsilon/2 \). Under the assumption that \( \psi(s) \leq \delta \) for \( s \in [-K-M_1,K+M_1] \), one has

\[
|K \ast \psi|(x) \leq \varepsilon, \quad \forall x \in [-K,K],
\]

which implies the continuity of \( K \ast \) under the compact open topology with respect to the initial data \( \psi \). In order to discuss the continuity of \( K^{(n)} \) we introduce \( M_n > 0 \) such that \( \int_{|y| \geq M_n} K(y)dy \leq \frac{\varepsilon}{2 n|\beta|_\infty} \). Following (4), it is straightforward to notice that

\[
\max_{x \in [-K,K]} |K \ast \psi|(x) \leq \max_{x \in [-K,K]} \psi(x) + \varepsilon/(2n)
\]

By induction, we have therefore

\[
\max_{x \in [-K,K]} |K^{(n)} \ast \psi|(x) \leq \max_{x \in [-K,K]} (K^{(n-1)} \ast \psi)(x) + \varepsilon/(2n)
\]

\[
= \max_{x \in [-K-M_n,K+M_n]} (K^{(n-1)} \ast \psi)(x) + \varepsilon/(2n)
\]

\[
\leq \cdots
\]

\[
\leq \max_{x \in [-K-nM_n,K+nM_n]} \psi(x) + \varepsilon/2,
\]

which implies that, for any given \( \varepsilon > 0, K > 0 \), if \( \max_{x \in [-K-nM_n,K+nM_n]} \psi(x) < \delta = \varepsilon/2 \), then

\[
\max_{x \in [-K,K]} |K^{(n)} \ast \psi|(x) < \delta + \varepsilon/2 = \varepsilon.
\]

Thus the continuity of \( K^{(n)} \ast \) with respect to compact open topology follows. Finally with the above results, we can show the continuity of \( e^{At} \) for \( t \in [0,t_0] \). For given \( \varepsilon > 0, K > 0 \), we pick up \( N > 0 \) such that

\[
e^{-D_2 t} \sum_{n=1}^{\infty} \frac{(tD_1)^n}{n!} |\beta|_\infty < \frac{\varepsilon}{4}.
\]

Let \( M_N \) be defined such that

\[
\int_{|y| \geq M_N} K(y)dy \leq \frac{\varepsilon}{4n|\beta|_\infty} \min(1,e^{(D_2-D_1)t_0}).
\]

Hence, for \( x \in [-K,K] \)

\[
e^{-D_2 t} \sum_{n=1}^{N} \frac{(tD_1)^n}{n!} K^{(n)} \ast \psi(x) \leq e^{-(D_2-D_1)t} \left( \max_{x \in [-K-NM_N,K+NM_N]} \psi(x) \right) + \frac{\varepsilon}{4}.
\]
We pick up $\delta = \varepsilon \min(1, e^{(D_2 - D_1)\rho_0}) / 2$ to obtain for all $t \in [0, t_0], x \in [-K, K],$

$$u(t, x) = e^{-D_2 t} \sum_{n=0}^{\infty} \frac{(D_1)^n}{n!} K(n) * \psi \leq \varepsilon + \varepsilon + \varepsilon = \varepsilon,$$

under the condition that $\psi(s) < \delta$ for $s \in [-K - NM_N, K + NM_N]$. The proof is complete.

In the following theorem we show the existence of solution $u(t, x)$ to (2) by using the contraction mapping theorem when the initial data $\psi \in C_{\beta}$.

**Theorem 5.2.** For any $u_0 \in C_{\beta}$, the system of differential integral equations (2) admits a unique solution $u(t, x)$ satisfying $u(0, x) = u_0(x)$ and $u \in C([0, \tau], C_{\beta})$.

**Proof.** Introduce $\Lambda > \rho$ such that, for any $u_1, u_2 \in [0, \beta]$, if $u_1 \geq u_2$, we have

$$\Lambda u_1 + f(u_1) - \Lambda u_2 - f(u_2) \geq (\Lambda - \rho)(u_1 - u_2),$$

where we used the monotone property on $f$ in Hypothesis 2.1. We rewrite (2) as

$$\frac{\partial u}{\partial t} = D \int_{-\infty}^{\infty} K(x - y)u(t, y)dy - (D + \Lambda)u + \Lambda u + f(u(t, x)),$$

With $D_1 = D, D_2 = \Lambda + D$ in (1), we write the solution as the integral equation by the variation of parameters:

$$u(t, x) = e^{At}u_0(x) + \int_{0}^{t} e^{A(t-s)}(\Lambda u(s, x) + f(u(s, x)))ds$$

$$= [Fu](t, x).$$

Given the initial condition $u_0 \in C_{\beta}$, solving (2) is equivalent to finding out the fixed point problem of $F$, i.e., $Fu = u$ in $C([0, \tau], C_{\beta})$. First, we notice that the nonlinear operator $F$ is continuous on $C([0, \tau], C_{\beta})$ in the $L_{x,t}^{\infty}$ norm. Then we show that $FC([0, \tau], C_{\beta}) \subset C([0, \tau], C_{\beta})$. For given $u_0 \in C_{\beta}$, we have

$$Fu \leq e^{-\Lambda t}u + \int_{0}^{t} e^{-\Lambda(t-s)}\Lambda ds = \beta,$$

where we used the fact in the Hypotheses 2.1 that $f(\beta) = 0$ and linear estimates (1). We then prove that $F$ is a contraction mapping on $C([0, \tau], C_{\beta})$ for sufficiently small $\tau > 0$. For given $u_1, u_2 \in C([0, \tau], C_{\beta}),$

$$|Fu_1(t, x) - Fu_2(t, x)| \leq \int_{0}^{t} e^{-\Lambda(t-s)}(\Lambda + \rho)|u_1(s, x) - u_2(s, x)|ds$$

$$\leq (\Lambda + \rho)\tau \max_{0 \leq s \leq \tau} |u_1(s, x) - u_2(s, x)|$$

Therefore, for $\tau$ chosen such that $\tau \leq \frac{1}{2(\Lambda + \rho)}$, $|Fu_1 - Fu_2|_{L^\infty_{x,t}} \leq \frac{1}{2}|u_1 - u_2|_{L^\infty_{x,t}}$, $F$ is a contraction mapping on $C([0, \tau], C_{\beta})$, so there exist a unique fixed point $u$ of $F$ on $C([0, \tau], C_{\beta})$, which turns out to be the solution of (2). Also notice that $\tau$ is independent of the initial condition $u_0$, so the solution $u$ of (2) can be extended to the whole half line $R^+$. The proof is complete.

Denote $u(t, x) = Q_t[\psi](x)$ by the solution of (2) with $\psi$ as the initial data. To apply the general theory on spreading speed and traveling wave solutions developed in [17, 3, 4], we need to show that $Q_t$ is order preserving in $C_{\beta}$ in the sense that for $u, v \in C_{\beta}$, if $u \geq v$, then $Q_t[u] \geq Q_t[v]$ for all $t \geq 0$. In order to establish
the monotonicity of $Q_t$, we introduce some concepts of upper and lower solutions of (2).

**Definition 5.3.** A function $\bar{u} \in C(R^+ \times R, R^d)$ is called an upper solution of (2) if $\frac{\partial \bar{u}}{\partial t}$ exists and

\[
\frac{\partial \bar{u}}{\partial t} \geq D \int_{-\infty}^{\infty} K(x-y)\bar{u}(t,y)dy - D\bar{u} + f(\bar{u}(t,x)).
\]

A function $u \in C(R^+ \times R, R^d)$ is called a lower solution of (2) if $\frac{\partial u}{\partial t}$ exists and

\[
\frac{\partial u}{\partial t} \leq D \int_{-\infty}^{\infty} K(x-y)u(t,y)dy - Du + f(u(t,x)).
\]

**Theorem 5.4.** Let $\bar{u}(t,x)$ and $u(t,x)$ be upper and lower solutions of (2), respectively. If $\bar{u}(0,x) \geq u(0,x)$, then $\bar{u}(t,x) \geq u(t,x)$ for all $t \geq 0$.

**Proof:** We need to show that $v(t,x) = \bar{u}(t,x) - u(t,x) \geq 0$ for all $(t,x) \in R^+ \times R^d$. Introduce $w(t) = \inf_{x \in R} v(t,x)$, from Theorem 5.2, $w(t)$ is continuous with respect to $t$ and $w(0) \geq 0$. We prove that $w(t) \geq 0$ for all $t \geq 0$ by contradiction. Assume this is not true, there exists $t_0$, such that, without loss of generality, $w_1(t_0) < 0$, and $w_i(t) \geq 0$ for all $0 \leq t \leq t_0$ and $2 \leq i \leq k$. We take $\delta > \rho$ such that

\[
w_1(t_0)e^{-\delta t_0} = \min_{t \in [0,t_0]} w_1(t)e^{-\delta t} < w_1(\tau)e^{-\delta \tau}, \quad \forall \tau \in [0,t_0).
\]

It is straightforward to choose a sequence of points $\{x_k\}_{k=1}^{\infty}$ such that $v_1(t_0,x_k) < 0$ for all $k \geq 1$, and $\lim_{k \to \infty} v_1(t_0,x_k) = w_1(t_0)$. Let $\{t_k\}_{k=1}^{\infty}$ be a sequence such that

\[
v_1(t_k,x_k)e^{-\delta t_k} = \min_{t \in [0,t_0]} v_1(t,x_k)e^{-\delta t}.
\]

We have the bounds for $v_1(t_k,x_k)e^{-\delta t_k}$:

\[
w_1(t_0)e^{-\delta t_0} < v_1(t_k,x_k)e^{-\delta t_k} \leq v_1(t_k,x_k)e^{-\delta t_k} \leq v_1(t_0,x_k)e^{-\delta t_0}.
\]

Then by usual squeezing theorem, we have the limit $\lim_{k \to \infty} v_1(t_k,x_k)e^{-\delta t_k} = w_1(t_0)e^{-\delta t_0}$,

which together imply the following

\[
\lim_{k \to \infty} v_1(t_k,x_k) = w_1(t_0).
\]

Then from (5), we have

\[
0 \geq \frac{\partial(v_1(t,x_k)e^{-\delta t})}{\partial t} \bigg|_{t=t_k} = e^{-\delta t_k} \left( \frac{\partial v_1(t_k,x_k)}{\partial t} - \delta v_1(t_k,x_k) \right)
\]

and hence $\frac{\partial v_1(t_k,x_k)}{\partial t} \leq \delta v_1(t_k,x_k)$. Back to the equation on $v(t,x)$, we have

\[
\frac{\partial v_1(t_k,x_k)}{\partial t} = \frac{\partial \bar{u}_1(t_k,x_k)}{\partial t} - \frac{\partial u_1(t_k,x_k)}{\partial t} \\
\geq D \int_{-\infty}^{\infty} K(x-y)v_1(t_k,y)dy - Dv_1(t_k,x_k) + f_1(\bar{u}(t_k,x_k)) - f_1(u(t_k,x_k)) \\
\geq D \int_{-\infty}^{\infty} K(x-y)v_1(t_k,y)dy - Dv_1(t_k,x_k) + \rho v_1(t_k,x_k),
\]
where we used the fact that \( f_1 \) is Lipschitz continuity, non-decreasing in all the components \( u_i, i = 2, \cdots, d \), and \( v_1(t_k, x_k) \leq 0 \). Combining the above inequalities, we have

\[
(\delta + D - \rho)v_1(t_k, x_k) \geq D \int_{-\infty}^{\infty} K(x_k - y)v_1(t_k, y)dy \geq Dw_1(t_k).
\]

Taking a limit as \( k \to \infty \) in the above inequality, thinking of the fact that \( w_1(t_0) < 0 \), we obtain \( \delta \leq \rho \), which immediately yields a contradiction against the choice \( \delta > \rho \). So the proof is complete.

In the following theorem we discuss the continuity of \( u(t, x) = Q_1[\psi](x) \) under the compact open topology with respect to the initial data \( \psi \in C_\beta \), which essentially a generalization of Lemma 5.1.

**Theorem 5.5.** For any \( \varepsilon > 0 \), \( K \geq 0 \) and \( t_0 > 0 \), there exists \( \delta = \delta(\varepsilon, K, t_0) > 0 \) and \( M = M(\varepsilon, K, t_0) > 0 \) such that if \( \psi_1, \psi_2 \in C_\beta \) with \( |\psi_1(x) - \psi_2(x)| < \delta \) for all \( x \in [-K - M, K + M] \), then \( u_1(t, z) - u_2(t, z) \leq \varepsilon \) for all \( z \in [-K, K] \).

**Proof:** Here we reduce the proof to the linear case in Lemma 5.1. Let \( w(t, x) = u_1(t, x) - u_2(t, x) \). Then \( w(t, x) \) satisfies

\[
\frac{\partial w(t, x)}{\partial t} = D \int_{-\infty}^{\infty} K(x - y)w(t, y)dy - Dw(t, x) + f(u_1(t, x)) - f(u_2(t, x)).
\]

We first assume that \( \psi_1 \geq \psi_2 \). By Theorem 5.4, \( u_1(t, x) \geq u_2(t, x) \) for all \( t \geq 0 \) and \( x \in R \). Then \( w(t, x) \geq 0 \) and

\[
\frac{\partial w(t, x)}{\partial t} \leq D \int_{-\infty}^{\infty} K(x - y)w(t, y)dy - Dw(t, x) + \rho \sum_{i=1}^{d} w_i(t, x)1,
\]

where \( 1 \) denotes the constant vector all of whose components are 1. Let \( v(t, x) \) be the solution of integral differential equation:

\[
\frac{\partial v(t, x)}{\partial t} = D \int_{-\infty}^{\infty} K(x - y)v(t, y)dy - Dv(t, x) + \rho \sum_{i=1}^{d} v_i(t, x)1,
\]

supplemented with the initial data \( v(0, x) = \psi_1(x) - \psi_2(x) \). By Theorem 5.4, we have \( w(t, x) \leq v(t, x) \) for all \( t \in R^+, x \in R \). Then as a direct application of Lemma 5.1, we can claim the compact open continuity of \( u \) with respect to initial condition \( \psi \). In the case of \( \psi_1 \geq \psi_2 \), we define

\[
\hat{\psi}_1(x) = \max\{\psi_1(x), \psi_2(x)\}, \quad \hat{\psi}_2(x) = \min\{\psi_1(x), \psi_2(x)\}, \quad \forall x \in R,
\]

and let \( \hat{u}_1(t, x) \) and \( \hat{u}_2(t, x) \) be the solutions of (2) through initial functions \( \hat{\psi}_1 \) and \( \hat{\psi}_2 \), respectively. Then \( \hat{\psi}_1(x) - \hat{\psi}_2(x) = |\psi_1(x) - \psi_2(x)| \) and \( \hat{u}_1(t, x) \leq u_1(t, x), u_2(t, x) \leq \hat{u}_2(t, x) \) for all \( (t, x) \in R^+ \times R \). Thus \( |u_1(t, x) - u_2(t, x)| \leq |\hat{u}_1(t, x) - \hat{u}_2(t, x)| \). By the discussion in the case of \( \psi_1(x) \geq \psi_2(x) \), we see that the claim also holds true for \( \psi_1 \) and \( \hat{\psi}_2 \) with \( \hat{\psi}_1 \geq \psi_2 \).

In the following we continue to establish Property \( v \) in Theorem 2.1 if \( f \) satisfies the Hypotheses 2.1. Without loss of generality, we take \( t = 1 \). Let \( Q_1 = Q, M_1 = M, B_{1,\mu} = B_\mu \) and \( B_{1,\mu}^c = B_\mu^c \). We summarize the result into the following lemma.

**Lemma 5.6.** If \( f \) satisfies the Hypotheses 2.1, then there exists a family \( M^{(c)} \) of linear maps which satisfies the Property \( v \) in Theorem 2.1 as \( t = 1 \).
Proof. The proof here is similar to that of Lemma 4.1 for the case of reaction diffusion equation in [17]. We will just sketch the proof. Choose \( \Lambda \geq 0 \) such that the diagonal elements of the matrix \( f'(0) + \Lambda I \) are strictly positive. For any \( \kappa > 1 \), we define \( M^{(\kappa)}[\nu] \) to be the time one map of the linear system

\[
\frac{\partial w(t,x)}{\partial t} = D \int_{-\infty}^{\infty} K(x-y)w(t,y)dy - Dw(t,x) + (1 - \kappa^{-1})f'(0)w - \kappa^{-1}\Lambda w(t,x)
\]

\( w(x,0) = \nu(x) \) \( (5) \)

That is, \( M^{\kappa}[\nu] := w(x,1) \). For the initial data \( \nu(x) = e^{-\mu x} \alpha \), the solution has the separated form \( w = e^{-\mu x} \eta(t) \). Plugging it into (5), we have the ordinary differential equation satisfied by \( \eta(t) \):

\[
\eta'(t) = \left[ D \int_{-\infty}^{\infty} K(x)e^{\mu x}dx - D + (1 - \kappa^{-1})f'(0) \right] \eta(t) - \kappa^{-1}\Lambda \eta(t).
\]

Thus

\[
B^{(\kappa)}_\mu = \exp \left( \left[ D \int_{-\infty}^{\infty} K(x)e^{\mu x}dx - D + (1 - \kappa^{-1})f'(0) \right] - \kappa^{-1}\Lambda \right), \quad (6)
\]

and a standard result on ordinary differential equations show that this matrix converges to the matrix \( B_\mu \), which is obtained by replacing \( \kappa^{-1} \) by 0, as \( \kappa \to \infty \). This is Property (b) of Theorem 2.1 v. In order to establish Property a, we define for each \( i \) the projection

\[
\{ \pi_i[\alpha] \}_j = \begin{cases} 
\alpha_j & \text{if } \{ f'(0) + \Lambda I \}_ij > 0, \\
0 & \text{if } \{ f'(0) + \Lambda I \}_ij = 0.
\end{cases}
\]

Note that by the definition of \( \Lambda \), \( \{ \pi_i[\alpha] \}_i = \alpha_i \), and that \( \pi_i[\alpha] \leq \alpha \) when \( \alpha \geq 0 \). Hypotheses 2.1 then also imply that

\[
f_i(\alpha) \geq f_i(\pi_i[\alpha]).
\]

Moreover,

\[
\pi_i[\alpha] \cdot \nabla f_i(0) = (f'(0)\alpha)_i
\]

for all \( \alpha \). Let \( \sigma \) be a positive lower bound for all the positive entries of the matrix \( f'(0) + \Lambda I \). By triangle inequality

\[
|\pi_i[\alpha]| \leq \sum_{j=1}^{k} \{ \pi_i[\alpha] \}_j \leq \sigma^{-1}\{ \pi_i[\alpha] \cdot \nabla f_i(0) + \Lambda \alpha_i \}
\]

for all \( \alpha \geq 0 \). Let \( \xi(0) \) be the eigenvector of \( B_0 \). The differentiability of \( f_i \) shows that for any \( \kappa \geq 1 \), there is a positive number \( \Lambda_\kappa \) such that if \( 0 \leq \alpha \leq \Lambda_\kappa \xi(0) \), then for all \( i \)

\[
\nabla f_i(0) \cdot \pi_i[\alpha] - f_i(\pi_i[\alpha]) \leq (\sigma/\kappa)|\pi_i[\alpha]|,
\]

which therefore implies that

\[
(1 - \kappa^{-1})f'(0)\alpha - \kappa^{-1}\Lambda \alpha \leq f(\alpha),
\]

when \( 0 \leq \alpha \leq \Lambda_\kappa \xi(0) \). Note that, with initial data \( \nu = \xi(0) \), the time one solution of (5), \( w(x,1) = e^{[1-\kappa^{-1}\gamma_1(0)-\kappa^{-1}\Lambda]t} \xi(0) \). Therefore, if \( 0 \leq \nu \leq \Lambda_\kappa e^{-\gamma_1} \xi(0), \) then \( 0 \leq w(x,1) \leq \Lambda_\kappa \xi(0) \). Finally comparison Theorem 5.4 shows that \( M^{\kappa}[\nu] \leq Q[\nu] \) which is the property \( v \) of Theorem 2.1 with \( \omega = \Lambda_\kappa e^{-\gamma_1} \xi(0) \). The proof is complete. \( \square \)
We conclude this section with a summary of proof of Theorem 2.1. The property i of Theorem 2.1 is justified in Theorem 5.4. The property ii can be seen from the fact that if \( u(t, x) \) solves the system (2), then so does \( u(t, x - y) \) for any fixed \( y \in \mathbb{R} \). The property iii is confirmed in Theorem 5.5. Property iv is a result of Theorem 5.2. The final property v is just proved above. So the proof of Theorem 2.1 is complete.

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