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Spreading speeds and monostable waves in a reaction-diffusion model with nonlinear competition



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ABSTRACT

In this paper the wave propagation dynamics of a Lotka-Volterra type of model with cubic competition is studied. The existence of traveling waves and the uniqueness of spreading speeds are established. It is also shown that the spreading speed is equal to the minimal speed for traveling waves. Furthermore, general conditions for the linear or nonlinear selection of the spreading speed are obtained by using the comparison principle and the decay characteristics for traveling waves. By constructing upper solutions, explicit conditions to determine the linear selection of the spreading speed are derived.

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1. Introduction

The classical Lotka-Volterra models contain quadratic competition terms. It has been shown that the quadratic competition terms cannot accurately model competitive dynamics in all cases. For instance, in [4] the authors tested the Lotka-Volterra model with biological data from experiments with a competitive system of two species of Drosophila. However, an exact fit was not found. By applying a curvilinear regression approach in [4], analytical models of competition were fitted. By using statistical and biological criteria, the best one was chosen in [4] and is nowadays called the Gilpin-Ayala model. This model has a cubic competition term and represents an extension of the classical Lotka-Volterra model of competition. The cubic competition model is also known in the physics literature as the well-known Gross-Pitaevskii model (e.g., [2,11] and references therein), which accurately describes the dynamics of atomic Bose-Einstein condensates. In [10], Perthame dealt with the following Lotka-Volterra type system with cubic nonlinearities

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$$\begin{cases} u_t = d_1 u_{xx} + r_1 u \left(1 - b_1 u - a_1 v^2 \right), & t > 0, \ x \in \mathbb{R}, \\ v_t = d_2 v_{xx} + r_2 v \left(1 - b_2 v - a_2 u^2 \right), & t > 0, \ x \in \mathbb{R} \end{cases}$$
(1.1)

with initial data

$$u(x,0) = u_0^*(x) \ge 0, \ v(x,0) = v_0^*(x) \ge 0,$$
 (1.2)

which was also mentioned in [5], where u(x,t) and v(x,t) represent the densities of two competing species u and v at location x at time t, respectively; d_i , r_i and $1/b_i$, i = 1, 2 are the diffusive rate coefficients, the net growth rate coefficients and the carrying capacity coefficients; a_1 and a_2 are the nonnegative competition coefficients of v and v, respectively. Following [1], by using the scalings

$$\begin{split} \sqrt{\frac{r_1}{d_1}} x \to x, & r_1 t \to t, \\ b_1 u(x,t) \to u(x,t), & b_2 v(x,t) \to v(x,t), \\ d = \frac{d_2}{d_1}, & r = \frac{r_2}{r_1}, & \frac{a_1}{b_2^2} \to a_1, & \frac{a_2}{b_1^2} \to a_2, \end{split}$$

model (1.1) is transformed to an equivalent non-dimensional system

$$\begin{cases} u_t = u_{xx} + u \left(1 - u - a_1 v^2 \right), & t > 0, \ x \in \mathbb{R}, \\ v_t = dv_{xx} + rv \left(1 - v - a_2 u^2 \right), & t > 0, \ x \in \mathbb{R}. \end{cases}$$
(1.3)

Obviously, (1.3) has an invariant region $\mathbb{W} = \{(u, v) | 0 \le u \le 1, 0 \le v \le 1\}$. Through a simple computation, we have in \mathbb{W} that, if the competition coefficients a_1 and a_2 satisfy

$$a_1 > 1, \quad a_2 < \frac{1}{3},$$

then (1.3) has three constant steady states

$$q_1 = (0,0), q_2 = (0,1), q_3 = (1,0),$$

among them, q_2 is stable and q_1, q_3 are unstable. While, if

$$a_1 > 1$$
, $a_2 > 1$,

then (1.3) has four constant steady states

$$q_1 = (0,0), q_2 = (0,1), q_3 = (1,0), q_4 = (u^*, v^*),$$

where (u^*, v^*) is a positive solution of the kinetic system of (1.3)

$$\begin{cases} \frac{du}{dt} = u \left(1 - u - a_1 v^2 \right), \\ \frac{dv}{dt} = rv \left(1 - v - a_2 u^2 \right). \end{cases}$$
(1.4)

Moreover, q_2 , q_3 are stable and q_1 , q_4 are unstable. Usually, the former is called the monostable case while the latter is termed as the bistable case. For the bistable case, in [10], by applying the method of energy functions the author proved that the speed of the traveling wave connecting q_2 to q_3 has the sign of $a_2 - a_1$.

This indicates that both the diffusive rate d and the growth rate r do not influence the propagation direction of the bistable traveling wave, which is completely different from the result for the classical Lotka-Volterra model with linear competition, see [7,8], and definitely shows that the conclusions drawn from the Lotka-Volterra case cannot be generalized that easily. Therefore, in this paper we will study the propagation behaviors for the monostable case. Specifically, we will discuss the existence of the single spreading speed (short for asymptotic speeds of spread) and traveling wave solutions, the relationship between the spreading speed and the minimal speed of the traveling waves as well as the selection mechanism for the minimal wave speed of the traveling waves for system (1.3). Hence, throughout this work we will always assume that the competitive coefficients a_1 and a_2 satisfy

$$a_1 > 1, \quad a_2 < \frac{1}{3}.$$
 (1.5)

The rest of this paper is organized as follows. In section 2, we prove the existence of spreading speeds and traveling waves connecting q_2 to q_3 . Further, the uniqueness of spreading speeds is proved, and it is shown that this speed is equal to the minimal wave speed. In Section 3, the generic conditions for the linear or nonlinear selection of the spreading speed are derived. In Section 4, some explicit conditions to determine the linear selection mechanism of the spreading speed are presented. Finally, in Section 5 some conclusions are drawn, and some open issues will be discussed.

2. Spreading speeds and traveling wave solutions

Let $C = BC(\mathbb{R}, \mathbb{R}^2)$ be the space of all bounded and continuous functions from \mathbb{R} to \mathbb{R}^2 equipped with the compact open topology, that is, a sequence $\{\varphi_n\}$ converges to φ in C if and only if $\{\varphi_n(x)\}$ converges to $\varphi(x)$ in \mathbb{R}^2 uniformly for x in any compact subset of \mathbb{R} . Let $C_+ = \{(\varphi_1, \varphi_2) \in C : \varphi_i(x) \geq 0, \forall x \in \mathbb{R}, i = 1, 2\}$. For any $\varphi_1, \varphi_2 \in C$, we write $\varphi_1 \leq \varphi_2$ if $\varphi_2 - \varphi_1 \in C_+$, $\varphi_1 < \varphi_2$ if $\varphi_2 - \varphi_1 \in C_+ \setminus \{0\}$, and $\varphi_1 \ll \varphi_2$ if $\varphi_2 - \varphi_1 \in Int(C_+)$. For any vectors $c, d \in \mathbb{R}^2$, we write $c \leq d$ if $d - c \in \mathbb{R}^2_+$, c < d if $d - c \in \mathbb{R}^2_+ \setminus \{0\}$, and $c \ll d$ if $d - c \in Int(\mathbb{R}^2_+)$. For $c, d \in \mathbb{R}^2$ with $c \leq d$, we define $C_{c,d} = [c, d]_C = \{\varphi \in C : c \leq \varphi \leq d\}$ and $[c, d]_{\mathbb{R}^2} = \{\varphi \in \mathbb{R}^2 : c \leq \varphi \leq d\}$. Here $Int(\Lambda)$ represents the interior of the function space Λ .

In order to use the theory as developed in [3], we transform (1.3) into a cooperative system by letting $u = 1 - \overline{u}$ and $v = \overline{v}$. For simplicity, we drop out the bar and obtain

$$\begin{cases} u_t = u_{xx} + (1-u) \left(a_1 v^2 - u \right), \\ v_t = dv_{xx} + rv \left(1 - v - a_2 (1-u)^2 \right) \end{cases}$$
 (2.1)

with the nonnegative initial data

$$u(x,0) = 1 - u_0^*(x) \ge 0, \quad v(x,0) = v_0^*(x) \ge 0, \quad x \in \mathbb{R}.$$
 (2.2)

Correspondingly, the equilibrium points q_1, q_2 and q_3 become $\alpha = (1, 0)$, $\beta = (1, 1)$ and $\mathbf{0} = (0, 0)$, respectively. Moreover, β is stable, $\mathbf{0}$ and α are unstable. Let $\{Q\}_{t\geq 0}$ denote the solution semiflow associated with system (2.1)-(2.2). Then, we have

$$Q_t[\psi](x) = W(x, t; \psi), \quad \forall \psi \in BC(\mathbb{R}, \mathbb{R}^2_+), \quad t \ge 0, \tag{2.3}$$

where $W(x,t;\psi) = (u,v)(x,t;\psi)$ is the unique solution of (2.1)-(2.2) satisfying $W(x,0;\psi) = \psi(x) = (u,v)(x,0)$. It is easy to see that $\{Q_t\}_{t\geq 0}$ is a monotone semiflow on $[\mathbf{0},\beta]_{\mathcal{C}}$ and has fixed points $\mathbf{0},\alpha$ and β on $[\mathbf{0},\beta]_{\mathbb{R}^2}$. We now define a translation operator T_y , for any $y\in\mathbb{R}$, on \mathcal{C} by

$$T_y[u](x) = u(x-y), \ \forall x \in \mathbb{R}, \ u \in \mathcal{C}.$$

For any $\overline{\omega} \in \mathbb{R}^2$ satisfying $\mathbf{0} \ll \overline{\omega} \leq \beta$, we take $\psi \in \mathcal{C}$ with the following properties:

- (B1) ψ is a non-increasing function;
- (B2) $\psi(x) = 0$ for all $x \ge 0$;
- (B3) $\psi(-\infty) = \overline{\omega}$.

Let $Q := Q_1$. Then define an operator R_c by

$$R_c[\hat{a}](s) = \max\{\psi(s), T_{-c}Q[\hat{a}](s)\}, \forall \hat{a} \in \mathbb{R}$$

$$(2.4)$$

and a sequence of functions $a_n(c;s)$ by

$$a_0(c;s) = \psi(s), \quad a_{n+1}(c;s) = R_c[a_n(c;\cdot)](s).$$
 (2.5)

By following the theory as presented in [3,12], two numbers are defined:

$$c_{+}^{*} = \sup\{c : a(c, +\infty) = \beta\}, \quad \overline{c}_{+} = \sup\{c : a(c, +\infty) > \mathbf{0}\},$$
 (2.6)

where $a(c, s) = \lim_{n\to\infty} a_n(c, s)$ in \mathbb{R}^2 for each $s \in \mathbb{R}$. It is obvious that $c_+^* \leq \overline{c}_+$. By Remark 3.7 in [3] on spreading speeds, and by using a similar proof as the proof of Theorem 2.17 in [6], we have the following results:

Lemma 2.1. For the monotone semiflow $\{Q_t\}_{t\geq 0}$ on $C_{\mathbf{0},\beta}$ defined in (2.3), the following statements are valid:

(i) If $\psi \in C_{0,\beta}$, $0 \le \psi \ll \beta$, and $\psi(x) = 0$, $\forall x \ge L$, for some $L \in \mathbb{R}$, then

$$\lim_{t \to \infty, x > ct} [Q_t[\psi](x) - \mathbf{0}] = \mathbf{0} \quad \text{for any } c > \overline{c}_+.$$

(ii) If $\psi \in C_{\mathbf{0},\beta}$ and $\psi(x) \geq \sigma$, $\forall x \leq l$, for some $\sigma \gg \mathbf{0}$ and $l \in \mathbb{R}$, then

$$\lim_{t \to \infty} \prod_{x \le ct} [Q_t[\psi](x) - \beta] = \mathbf{0} \quad \text{for any } c < c_+^*.$$

This lemma implies that c_+^* and \overline{c}_+ are the lowest and highest rightward spreading speeds for the system $\{Q_t\}_{t\geq 0}$ on $C_{0,\beta}$. If $\overline{c}_+ = c_+^*$, we say that the system $\{Q_t\}_{t\geq 0}$ admits a single rightward spreading speed.

The following theorem implies that \overline{c}_+ is the minimal wave speed for traveling waves of system (2.1) connecting β to **0**.

Theorem 2.2. For any $c \geq \overline{c}_+$, system (2.1) has a traveling wave W(x-ct) = (U(x-ct), V(x-ct)) connecting β to $\mathbf{0}$, and W(z), z = x - ct is non-increasing in $z \in \mathbb{R}$; while for any $c < \overline{c}_+$, there is no traveling wave connecting β to $\mathbf{0}$.

Proof. It is easy to verify that the continuous-time semiflow $\{Q_t\}_{t\geq 0}$ satisfies (A1), (A3)-(A5) in [3] on $\mathcal{M}_{\beta} = \mathcal{C}_{\mathbf{0},\beta}$. Then, the result holds only by excluding the second possibility (ii) in Theorem 4.2 in [3].

By way of contradiction, suppose that (ii) in Theorem 4.2 in [3] is true. Obviously, α is the unique intermediate equilibrium between $\mathbf{0}$ and β . Hence we first restrict system (2.1) on the order interval $[\mathbf{0}, \alpha]_{\mathcal{C}}$, then it follows that $v \equiv 0$ and

$$u_t = u_{xx} - u(1 - u), (2.7)$$

which admits a non-increasing traveling wave $U_1(x-ct)$ connecting 1 to 0; and if system (2.1) is restricted on the order interval $[\alpha, \beta]_{\mathcal{C}}$, then we have $u \equiv 1$ and

$$v_t = dv_{xx} + rv(1 - v), (2.8)$$

which has a non-increasing traveling wave $V_1(x-ct)$ connecting 1 to 0.

By (2.7), we know that $U_2(x-ct) = 1 - U_1(x-ct)$ is non-decreasing traveling wave connecting 0 to 1 of the system

$$w_t = w_{xx} + w(1 - w). (2.9)$$

It is well-known that systems (2.8) and (2.9) have spreading speeds $c_1^* = 2\sqrt{dr}$ and $c_2^* = 2$ and are equal to the minimal speeds of their traveling waves, respectively. Thus, we have

$$c \ge c_1^* = 2\sqrt{dr} > 0, \quad -c \ge c_2^* = 2 > 0.$$

This is a contradiction. Thus, the proof is complete. \Box

Next we prove that \overline{c}_+ is the single rightward spreading speed for $\{Q_t\}_{t>0}$ on $\mathcal{C}_{0,\beta}$.

Theorem 2.3. The following statements are valid:

(i) If $\psi \in C_{\mathbf{0},\beta}$, $\mathbf{0} \le \psi \ll \beta$, and $\psi(x) = \mathbf{0}$, $\forall x \ge L$, for some $L \in \mathbb{R}$, then

$$\lim_{t\to\infty,x>ct} [Q_t[\psi](x) - \mathbf{0}] = \mathbf{0} \text{ for any } c > \overline{c}_+.$$

(ii) If $\psi \in \mathcal{C}_{\mathbf{0},\beta}$, $\psi(x) \geq \sigma$, $\forall x \leq l$, for some $\sigma \gg \mathbf{0}$ and $l \in \mathbb{R}$, then

$$\lim_{t \to \infty, x \le ct} [Q_t[\psi](x) - \beta] = \mathbf{0} \quad \text{for any} \quad c < \overline{c}_+.$$

Proof. By Lemma 2.1, it suffices to prove that $\overline{c}_+ = c_+^*$. Otherwise, by the definition of \overline{c}_+ and c_+^* , we have $\overline{c}_+ > c_+^*$. Using (1) and (3) of Theorem 4.2 in [3], we know that system (2.1) has a traveling wave solution $(U,V)(x-c_{+}t)$ connecting β to α . Thus, $U\equiv 1$ and V is a traveling wave of (2.8) connecting 1 to 0. Then, $c_+^* \geq c_1^* > 0$, where c_1^* is defined as in the proof of Theorem 2.2. Hence we can choose $c_1 \in (c_+^*, \overline{c}_+)$, and set $\mu(\sigma) = d\sigma^2 + r$. Due to the fact that $c_1 > c_1^* = \inf_{\sigma>0} \frac{\mu(\sigma)}{\sigma}$, then there exists a $\sigma_1 > 0$ such that $c_1 = \frac{\mu(\sigma_1)}{\sigma_1}$. If we let $\mu_1 := \mu(\sigma_1)$, then we have

$$\sigma_1 c_1 - d\sigma_1^2 - r = 0. (2.10)$$

Moreover, let $H(\sigma, c) = \sigma c - \sigma^2$. It is easy to see that $H(0, c_1) = 0$, $\frac{\partial H}{\partial \sigma}(0, c_1) = c_1 > 0$, and then there is a $\sigma_2 \in (0, \sigma_1)$ such that $H(\sigma_2, c_1) > 0$. To proceed, we define two wave-like functions:

$$\overline{u}(x,t) = \min \left\{ a_1 e^{-\sigma_2(x - c_1 t)}, \ 1 \right\}, \quad \overline{v}(x,t) = e^{-\sigma_1(x - c_1 t)}, \quad t \ge 0, \ x \in \mathbb{R}.$$
 (2.11)

We now verify that $(\overline{u}, \overline{v})$ is an upper solution to system (2.1). If $x - c_1 t \leq \frac{\ln a_1}{\sigma_2}$, then $\overline{u} = 1$. From the first equation it follows that

$$\frac{\partial \bar{u}}{\partial t} - \frac{\partial^2 \bar{u}}{\partial x^2} + (1 - \bar{u})(\bar{u} - a_1 \bar{v}^2) = 0,$$

and by (2.10), the second equation leads to

$$\frac{\partial \bar{v}}{\partial t} - d \frac{\partial^2 \bar{v}}{\partial x^2} - r \bar{v} (1 - \bar{v} - a_2 (1 - \bar{u})^2)
\ge \frac{\partial \bar{v}}{\partial t} - d \frac{\partial^2 \bar{v}}{\partial x^2} - r \bar{v} = e^{-\sigma_1 (x - c_1 t)} (\sigma_1 c_1 - d \sigma_1^2 - r) = 0.$$

While for $x - c_1 t > \frac{\ln a_1}{\sigma_2}$, we have $\overline{u} = a_1 e^{-\sigma_2(x - c_1 t)}$. For the second equation, it can be verified as above. For the first equation, we have

$$\begin{split} & \frac{\partial \bar{u}}{\partial t} - \frac{\partial^2 \bar{u}}{\partial x^2} + (1 - \bar{u})(\bar{u} - a_1 \bar{v}^2) \\ & \geq a_1 e^{-\sigma_2(x - c_1 t)} \left[(\sigma_2 c_1 - \sigma_2^2) + (1 - \bar{u}) \left(1 - e^{(\sigma_2 - 2\sigma_1)(x - c_1 t)} \right) \right] \\ & = a_1 e^{-\sigma_2(x - c_1 t)} \left[H(\sigma_2, c_1) + \left(1 - e^{-\sigma_2(x - c_1 t)} \right) \left(1 - e^{(\sigma_2 - 2\sigma_1)(x - c_1 t)} \right) \right] \geq 0. \end{split}$$

Thus, we have shown that $(\overline{u}, \overline{v})$ is an upper solution to system (2.1). For a given function $\psi(x)$ satisfying (B1)-(B3), and by taking a sufficiently large positive constant L, we have

$$\varphi(x) := (\bar{u}, \bar{v})(x - L, 0) \ge \psi(x), \quad \forall x \in \mathbb{R}.$$

The comparison principle leads to

$$Q_t[\psi](x) \le Q_t[\varphi](x) \le (\bar{u}, \bar{v})(x - L, t), \quad x \in \mathbb{R}, \ t \in \mathbb{R},$$

where Q_t is defined in (2.3). By using (2.4) and (2.5), and for $a_0 = \psi \leq \varphi$, we have

$$a_1(c_1, x) = \max\{\psi(x), T_{-c_1}Q[a_0](x)\} \le \max\{\varphi(x), Q[\varphi](x + c_1)\}.$$

From (2.11), it then follows that

$$\begin{cases}
\overline{u}(x-L,0) = \min \left\{ a_1 e^{-\sigma_2(x-L)}, 1 \right\}, \\
\overline{v}(x-L,0) = e^{-\sigma_1(x-L)},
\end{cases} (2.12)$$

and

$$\begin{cases}
\overline{u}(x+c_1-L,1) = \min \left\{ a_1 e^{-\sigma_2(x-L,1)}, 1 \right\}, \\
\overline{v}(x+c_1-L,1) = e^{-\sigma_1(x-L)}.
\end{cases}$$
(2.13)

So we obtain

$$Q_1[\varphi](x+c_1) \le (\bar{u}, \bar{v})(x+c_1-L, 1)$$

= $(\bar{u}, \bar{v})(x-L, 0) = \varphi(x),$

that is, $a_1(c_1, x) \leq \varphi(x), \forall x \in \mathbb{R}$. By induction, we get

$$a_n(c_1, x) < \varphi(x), \ \forall x \in \mathbb{R}, \ n > 0.$$

This property of $a_n(c_1, x)$ and the assumption that $c_1 \in (c_+^*, \overline{c}_+)$ yield

$$(1,0) = a(c_1, +\infty) = \lim_{x \to +\infty} \lim_{n \to +\infty} a_n(c_1, x) \le \lim_{x \to +\infty} \varphi(x) = (0,0).$$

This contradiction implies that $c_+^* = \overline{c}_+$. \square

Based on the aforementioned theorems, we know that system (2.1) possesses a single rightward spreading speed c_+^* , which is equal to the minimal wave speed for traveling waves connecting β to $\mathbf{0}$ denoted by c_{\min} . Therefore, in the next section we will discuss the selection mechanism for c_{\min} .

3. Selection mechanism for the minimal wave speed

In this section we will derive general conditions to determine the linear or nonlinear selection of the minimal wave speed for traveling waves connecting β to **0**. Firstly, we present the wave profile system related to system (2.1):

$$\begin{cases} U'' + cU' + (1 - U) (a_1 V^2 - U) = 0, \\ dV'' + cV' + rV (1 - V - a_2 (1 - U)^2) = 0 \end{cases}$$
(3.1)

subject to the boundary conditions

$$(U,V)(-\infty) = (1,1), \quad (U,V)(+\infty) = (0,0),$$
 (3.2)

where (U,V)(z)=(u,v)(x,t) and z=x-ct. Linearizing (3.1) at **0** yields a linear system

$$\begin{cases} U'' + cU' - U = 0, \\ dV'' + cV' + r(1 - a_2)V = 0, \\ U(\infty) = V(\infty) = 0. \end{cases}$$
 (3.3)

Let $(U,V)(z)=(\eta_1,\eta_2)e^{-\mu z}$, where η_1,η_2 , and μ are positive constants. Substituting it into (3.3) gives

$$B(\mu) = \begin{pmatrix} \mu^2 - c\mu - 1 & 0 \\ 0 & d\mu^2 - c\mu + r(1 - a_2) \end{pmatrix} \begin{pmatrix} \eta_1 \\ \eta_2 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}.$$
 (3.4)

Then μ solves the characteristic equations

$$\mu^2 - c\mu - 1 = 0$$
, $d\mu^2 - c\mu + r(1 - a_2) = 0$.

Solving the first equation for μ yields

$$\mu_1(c) = \frac{c + \sqrt{c^2 + 4}}{2} > 0, \quad \mu_2(c) = \frac{c - \sqrt{c^2 + 4}}{2} < 0,$$
(3.5)

and the second equation leads to

$$\mu_3(c) = \frac{c - \sqrt{c^2 - 4dr(1 - a_2)}}{2d}, \quad \mu_4(c) = \frac{c + \sqrt{c^2 - 4dr(1 - a_2)}}{2d}.$$
(3.6)

Taking into account that (U, V) is positive, we have $c \ge 2\sqrt{dr(1-a_2)}$, and thus $\mu_4(c) \ge \mu_3(c) > 0$. It is easy to see that $\mu_1(c) > \mu_4(c) \ge \mu_3(c) > 0$ if $d \ge 1$. By convention, $c_0 := 2\sqrt{dr(1-a_2)}$ is called the linear speed. Clearly, we have

$$\overline{\mu} := \mu_4(c_0) = \mu_3(c_0) = \sqrt{\frac{r(1-a_2)}{d}}.$$
 (3.7)

By (3.4), we know that the eigenvectors of the matrix $B(\mu)$ corresponding to μ_1 and μ_i , i = 3,4 are $(\eta_1, \eta_2)^T = (1,0)^T$ and $(\eta_1, \eta_2)^T = (0,1)^T$, respectively. Hence near **0** the positive solution of (U, V) with $c > c_0$ satisfies

$$\begin{pmatrix} U(z) \\ V(z) \end{pmatrix} \sim C_1 \begin{pmatrix} 1 \\ 0 \end{pmatrix} e^{-\mu_1(c)z} + C_2 \begin{pmatrix} 0 \\ 1 \end{pmatrix} e^{-\mu_3(c)z} \text{ as } z \to \infty, \tag{3.8}$$

where C_i , i = 1, 2 are constants and $C_1 > 0$, $C_2 > 0$. We now present the definition of selection mechanism of the minimal wave speed and the definition of an upper/lower solution for system (3.1).

Definition 3.1. If the minimal wave speed c_{\min} is equal to c_0 , then we say that the minimal wave speed is linearly selected; Otherwise, i.e., $c_{\min} > c_0$, we say that the minimal wave speed is nonlinearly selected.

Definition 3.2. (see Section 6 in [1]) An upper solution to system (3.1)-(3.2) is defined to be a pair of continuous functions (U, V)(z) which are twice-differentiable on $z \in (-\infty, \infty)$ except at a finite number of points $z_i, i = 1, \dots, n$, and which satisfy

$$\begin{cases}
U'' + cU' + (1 - U) \left(a_1 V^2 - U \right) \le 0, \\
dV'' + cV' + rV \left(1 - V - a_2 (1 - U)^2 \right) \le 0, \\
(U, V)(-\infty) \ge 1, \quad (U, V)(\infty) \ge 0,
\end{cases}$$
(3.9)

for $z \neq z_i, i = 1, \dots, n$, and $(U', V')(z_i^-) \geq (U', V')(z_i^+)$ for $i = 1, \dots, n$. A lower solution is given by reversing all the inequalities.

The following theorem gives a sufficient condition for the linear selection of the minimal wave speed.

Theorem 3.1. Assume that, for a given $\overline{c} \geq c_0$, there exists a positive and non-increasing upper solution $(\overline{U}, \overline{V})(z), z = x - \overline{c}t$ of system (3.1)-(3.2) satisfying

$$\lim_{z \to -\infty} \inf(\overline{U}, \overline{V})(z) > (0,0), \quad \lim_{z \to \infty} (\overline{U}, \overline{V})(z) = (0,0). \tag{3.10}$$

Then we have that $c_{\min} \leq \overline{c}$. Particularly, if $\overline{c} = c_0$, then the minimal wave speed is linearly selected.

Proof. By (2.6) and Theorem 2.3, we know that the minimal wave speed is equal to the single rightward spreading speed, i.e.,

$$c_{\min} = c_{+}^{*} = \sup\{c : a(c, +\infty) = \beta\}.$$
 (3.11)

The non-increasing function ψ in (2.5) is taken as

$$\psi(x) = \mathbf{0}, \quad x > 0 \quad \text{and} \lim_{x \to -\infty} (\psi(x) - \overline{\omega}) = \mathbf{0}, \quad \mathbf{0} \ll \overline{\omega} \ll \beta.$$

Now let $\psi(-\infty)$ be sufficiently small such that the upper solution $(\overline{U}, \overline{V})$ (or a shift if needed) satisfies

$$\psi(x) = a_0(\overline{c}; x) \le (\overline{U}, \overline{V})(x) \triangleq \varphi(x), \quad x \in \mathbb{R}.$$

Thus, by (2.4) and (2.5), it follows that

$$a_{1}(\overline{c}; x) = \max\{\psi(x), T_{-\overline{c}}Q[a_{0}(\overline{c}; \cdot)](x)\}$$

$$= \max\{\psi(x), Q[a_{0}(\overline{c}; \cdot)](x + \overline{c})\}$$

$$\leq \max\{\varphi(x), Q[\varphi](x + \overline{c})\}$$

$$\leq \max\{\varphi(x), (\overline{U}, \overline{V})(x)\} = (\overline{U}, \overline{V})(x),$$

where the definition of a upper solution $(\overline{U}, \overline{V})$ of the map Q is used, that is, $Q(\overline{U}, \overline{V})(x) \leq (\overline{U}, \overline{V})(x-c)$. By induction, we have

$$a_n(\overline{c}; x) \le (\overline{U}, \overline{V})(x), \quad n \ge 0.$$

By letting $n \to +\infty, x \to +\infty$, it follows that $a(\overline{c}; +\infty) \leq (\overline{U}, \overline{V})(\infty) = (0, 0)$, which indicates that $a(\overline{c}, +\infty) = \mathbf{0}$. Then (3.11) implies that $\overline{c} \geq c_{\min}$. Hence the first result of the theorem is proved.

The second part of the theorem directly follows from the result of the first part and from the definition of c_0 . \Box

Generic conditions for nonlinear selection are presented in the following two theorems.

Theorem 3.2. Suppose that $d \ge 1$, and for a given $c = \underline{c} > c_0$, $(\underline{U},\underline{V})(z)$ is a pair of nonnegative and non-increasing functions, which satisfy

$$\lim_{z \to -\infty} \sup(\underline{U}, \underline{V})(z) < 1, \quad (\underline{U}, \underline{V})(z) \sim (\xi_1 e^{-\mu_1(\underline{c})z}, \xi_2 e^{-\mu_1(\underline{c})z}), \quad z \to \infty, \tag{3.12}$$

where $z = x - \underline{c}t$, $\mu_1(\underline{c})$ is defined in (3.5), and ξ_1, ξ_2 are positive constants. If $(\underline{U}, \underline{V})(z)$ is a lower solution of system (3.1)-(3.2), then system (2.1) has no traveling wave with speed $c \in [c_0, \underline{c})$, i.e., $c_{\min} \geq \underline{c}$.

Proof. Following the proof (by contradiction) of Lemma 2.8 in [1], it will be assumed now that there exists a non-increasing traveling wave solution (U, V)(x - ct) to (2.1) with initial conditions

$$u(x,0) = U(x), v(x,0) = V(x)$$

for some c located in $[c_0, \underline{c})$. Since $d \ge 1$ implies that $\mu_1(c) \ge \mu_4(c)$, and by $\mu_1(c)$ is increasing in c, we have that $\mu_1(\underline{c}) \ge \max\{\mu_1(c), \mu_4(c)\}$. Then from (3.12) it is possible (by shifting if necessary) to have

$$(\underline{U},\underline{V})(x) \le (U,V)(x), x \in \mathbb{R}.$$

By applying the comparison principle, it follows that

$$\underline{U}(x - \underline{c}t) \le U(x - ct), \quad \underline{V}(x - \underline{c}t) \le V(x - ct) \tag{3.13}$$

for all $(x,t) \in (-\infty,\infty) \times [0,\infty)$. Now fix $z^* = x - \underline{c}t$ such that $\underline{U}(z^*) > 0$. Then, it follows that

$$U(z^*) = U(x - ct) \le U(x - ct) = U(z^* + (c - c)t) \sim U(\infty) = 0 \text{ as } t \to \infty.$$
 (3.14)

This contradicts the fact that $\underline{U}(z^*) > 0$. Hence the proof is complete. \Box

Due to the fact that $\mu_4(c)$ is increasing with respect to c, and by applying Theorem 3.2, we can now easily obtain the following general condition for nonlinear selection.

Theorem 3.3. Let $(\underline{U},\underline{V})(z)$ be a pair of nonnegative and non-increasing functions, satisfying

$$\lim_{z \to -\infty} \sup(\underline{U}, \underline{V})(z) < 1, \quad (\underline{U}, \underline{V})(z) \sim (\eta_1 e^{-\mu_1(\underline{c})z}, \eta_2 e^{-\mu_4(\underline{c})z}), \quad z \to \infty, \tag{3.15}$$

for a given $c = \underline{c} > c_0$, where $z = x - \underline{c}t$, where $\mu_1(\underline{c})$, and $\mu_4(\underline{c})$ are defined in (3.5)-(3.6), and where η_1, η_2 are positive constants. If $(\underline{U}, \underline{V})(z)$ is a lower solution of system (3.1)-(3.2), then system (2.1) has no traveling wave with speed $c \in [c_0, \underline{c})$, and so: $c_{\min} \geq \underline{c}$.

4. Explicit conditions for linear selection

Based on the Theorem 3.1, we derive in this section some explicit conditions for linear selection of the spreading speed by explicitly constructing upper solutions to system (3.1)-(3.2). In what follows, c_0 and $\bar{\mu}$ are defined as in Section 3, that is,

$$c_0 = 2\sqrt{dr(1-a_2)}, \quad \overline{\mu} = \mu(c_0) = \sqrt{\frac{r(1-a_2)}{d}}, \text{ and } d\overline{\mu}^2 - c_0\overline{\mu} + r(1-a_2) = 0.$$

Theorem 4.1. For the fixed parameters d, r, a_1 and a_2 , assumed that either

$$d > 1, \ a_1^2 + 2 \ge \frac{2}{a_2} \ge \min\{2a_1 + 1, \sqrt{a_1} + 2\},$$
 (4.1)

or

$$d > 1, \ a_1^2 + 2 \le \frac{2}{a_2}$$
 (4.2)

is satisfied. Then the minimal wave speed is linearly selected.

Proof. Define a pair of functions $(\overline{U_1}, \overline{V_1})$ by

$$\overline{V_1} = \frac{1}{1 + e^{\overline{\mu}z}}, \quad \overline{U_1} = \begin{cases} 1, & z \le z_1, \\ a_1 \overline{V_1}^2, & z \ge z_1, \end{cases}$$
(4.3)

where z_1 satisfies $a_1\overline{V_1}^2(z_1)=1$ and $\overline{\mu}=\overline{\mu}(c_0)$. It is easy to check that

$$\overline{V_1}' = -\overline{\mu}\overline{V_1}(1 - \overline{V_1}), \quad \overline{V_1}'' = \overline{\mu}^2 \overline{V_1}(1 - \overline{V_1})(1 - 2\overline{V_1}),$$

$$\overline{U}_1' = -2a_1\overline{\mu}\overline{V}_1^2(1 - \overline{V}_1), \quad \overline{U}_1'' = 2a_1\overline{\mu}^2 \overline{V}_1^2(1 - \overline{V}_1)(2 - 3\overline{V}_1).$$

By substituting $(\overline{U_1}, \overline{V_1})$ into the first equation of (3.1), and by using the assumptions that d > 1 and (1.5), we obtain

$$\begin{aligned} & \overline{U_1}'' + c_0 \overline{U_1}' + (1 - \overline{U_1}) \left(a_1 \overline{V_1}^2 - \overline{U_1} \right) \\ = & 2a_1 \overline{V_1}^2 (1 - \overline{V_1}) \left(2\overline{\mu}^2 - c_0 \overline{\mu} - 3\overline{\mu}^2 \overline{V_1} \right) \\ = & 2a_1 \overline{V_1}^2 (1 - \overline{V_1}) \left(\frac{2r(1 - d)(1 - a_2)}{d} - 3\overline{\mu}^2 \overline{V_1} \right) \le 0. \end{aligned}$$

For the second equation in (3.1), when $z \leq z_1$, by using the fact that $\overline{V}_1(z) \geq \overline{V}_1(z_1) = \frac{1}{\sqrt{a_1}}$ and (4.1), we have

$$d\overline{V}_{1}'' + c_{0}\overline{V}_{1}' + r\overline{V}_{1}\left(1 - \overline{V}_{1} - a_{2}(1 - \overline{U}_{1})^{2}\right)$$

$$= \overline{V}_{1}(1 - \overline{V}_{1})(ra_{2} - 2d\overline{\mu}^{2}\overline{V}_{1})$$

$$\leq \overline{V}_{1}(1 - \overline{V}_{1})\left(ra_{2} - \frac{2r(1 - a_{2})}{\sqrt{a_{1}}}\right)$$

$$= \frac{ra_{2}}{\sqrt{a_{1}}}\overline{V}_{1}(1 - \overline{V}_{1})\left(\sqrt{a_{1}} + 2 - \frac{2}{a_{2}}\right) \leq 0,$$
(4.4)

when $z \geq z_1$, by noting the fact that $1 - a_1 \overline{V}_1^2 \geq 1 - a_1 \overline{V}_1$, it follows that

$$\begin{split} & d\overline{V}_1'' + c_0\overline{V}_1' + r\overline{V}_1 \left(1 - \overline{V}_1 - a_2(1 - \overline{U}_1)^2\right) \\ \leq & \overline{V}_1(1 - \overline{V}_1) \left[ra_2 - ra_2 \frac{(1 - a_1\overline{V}_1)^2}{1 - \overline{V}_1} - 2d\overline{\mu}^2 \overline{V}_1 \right] \\ = & \overline{V}_1 \left[ra_2(1 - \overline{V}_1) - ra_2(1 - a_1\overline{V}_1)^2 - 2d\overline{\mu}^2 \overline{V}_1(1 - \overline{V}_1) \right]. \end{split}$$

The condition (4.1) leads to

$$\overline{V}_1 \left[ra_2 (1 - \overline{V}_1) - ra_2 (1 - a_1 \overline{V}_1)^2 - 2d\overline{\mu}^2 \overline{V}_1 (1 - \overline{V}_1) \right]$$

$$= ra_2 \overline{V}_1 \left[\overline{V}_1 (2a_1 + 1 - \frac{2}{a_2}) + \overline{V}_1^2 (\frac{2}{a_2} - a_1^2 - 2) \right] \le 0.$$

The condition (4.2) also yields

$$\overline{V}_1 \left[ra_2 (1 - \overline{V}_1) - ra_2 (1 - a_1 \overline{V}_1)^2 - 2d\overline{\mu}^2 \overline{V}_1 (1 - \overline{V}_1) \right]$$

$$\leq ra_2 \overline{V}_1 \left[\overline{V}_1 (2a_1 + 1 - \frac{2}{a_2}) + \overline{V}_1 (\frac{2}{a_2} - a_1^2 - 2) \right] = -ra_2 \overline{V}_1^2 (a_1 - 1)^2 \leq 0.$$

Moreover, since (4.2) implies $\sqrt{a_1} + 2 \le \frac{2}{a_2}$, hence (4.4) is still true under the condition (4.2). Thus, $(\overline{U_1}, \overline{V_1})$ is an upper solution to system (3.1)-(3.2) under the condition (4.1) or (4.2). Then, by Theorem 3.1, the desired result follows. \square

Now by defining an upper solution whose two component functions are linear dependent, we derive conditions for the linear selection of the spreading speed.

Theorem 4.2. For the fixed parameters d, r, a_1 and a_2 , suppose that either

$$\begin{cases}
0 < d < \frac{1}{2}, \\
a_2(1+a_1) \ge 1, \\
\frac{a_1 d}{2(1-a_2)} \le r \le \frac{d}{(1-2d)(1-a_2)},
\end{cases}$$
(4.5)

or

$$\begin{cases}
d > \frac{1}{2}, \\
a_2(1+a_1) \ge 1, \\
r \ge \frac{a_1 d}{2(1-a_2)}
\end{cases}$$
(4.6)

holds. Then the minimal wave speed is linearly selected.

Proof. Define a pair of functions $(\overline{U_2}, \overline{V_2})$ by

$$\overline{V_2} = \frac{1}{1 + e^{\overline{\mu}z}}, \quad \overline{U_2} = \begin{cases} 1, & z \le z_2, \\ \frac{1 - a_2}{a_2} \overline{V_2}, & z \ge z_2, \end{cases}$$
(4.7)

where z_2 satisfies $\frac{1-a_2}{a_2}\overline{V_2}(z_2)=1$ and $\overline{\mu}=\overline{\mu}(c_0)$. It is easy to check that

$$\overline{V_2}' = -\overline{\mu}\overline{V_2}(1 - \overline{V_2}), \quad \overline{V_2}'' = \overline{\mu}^2\overline{V_2}(1 - \overline{V_2})(1 - 2\overline{V_2}).$$

Substituting $(\overline{U_2}, \overline{V_2})$ into the first equation in (3.1), for $z \leq z_2$ we then easily obtain

$$\overline{U_2}'' + c_0 \overline{U_2}' + (1 - \overline{U_2}) \left(a_1 \overline{V_2}^2 - \overline{U_2} \right) = 0.$$

For $z \geq z_2$ we obtain

$$\begin{split} & \overline{U_2}'' + c_0 \overline{U_2}' + (1 - \overline{U_2}) \left(a_1 \overline{V_2}^2 - \overline{U_2} \right) \\ &= \frac{1 - a_2}{a_2} \overline{V_2} \left[\overline{\mu}^2 (1 - \overline{V_2}) (1 - 2\overline{V_2}) - \overline{\mu} c_0 (1 - \overline{V_2}) + \frac{a_2}{1 - a_2} (1 - \frac{1 - a_2}{a_2} \overline{V_2}) (a_1 \overline{V_2} - \frac{1 - a_2}{a_2}) \right] \\ &=: \frac{1 - a_2}{a_2} \overline{V_2} G(\overline{V_2}), \end{split}$$

where

$$G(\overline{V_2}) = \overline{\mu}^2 (1 - \overline{V_2})(1 - 2\overline{V_2}) - \overline{\mu}c_0(1 - \overline{V_2}) + \frac{a_2}{1 - a_2} (1 - \frac{1 - a_2}{a_2} \overline{V_2})(a_1 \overline{V_2} - \frac{1 - a_2}{a_2})$$

$$= (2\overline{\mu}^2 - a_1)\overline{V_2}^2 + \left(c_0\overline{\mu} + \frac{a_1 a_2}{1 - a_2} - 3\overline{\mu}^2 + \frac{1 - a_2}{a_2}\right)\overline{V_2} + \overline{\mu}^2 - c_0\overline{\mu} - 1.$$

From the third inequality in (4.5) or (4.6), one has $G''(\overline{V_2}) = 2\left(\frac{2(1-a_2)r}{d} - a_1\right) \ge 0$. Furthermore, from the first inequality and the third inequality in (4.5) or the first inequality in (4.6), we obtain that

$$G(0) = \overline{\mu}^2 - c_0 \overline{\mu} - 1 = \frac{r(1 - 2d)(1 - a_2)}{d} - 1 \le 0,$$

using (1.5) and the second inequality in (4.5) or (4.6) give

$$G(1) = \frac{1}{a_2} (1 - \frac{a_2}{1 - a_2}) [1 - a_2(1 + a_1)] \le 0.$$

Thus, $G(\overline{V_2}) \leq 0$ for $0 \leq \overline{V_2} \leq 1$, and then

$$\overline{U_2}'' + c_0 \overline{U_2}' + (1 - \overline{U_2}) \left(a_1 \overline{V_2}^2 - \overline{U_2} \right) \le 0, \ z \in (-\infty, \infty).$$

From the second equation in (3.1), when $z \leq z_2$, and by using $\overline{V}_2(z) \geq \overline{V}_2(z_2) = \frac{a_2}{1-a_2}$, we obtain

$$\begin{split} & d\overline{V}_2'' + c_0 \overline{V}_2' + r \overline{V}_2 \left(1 - \overline{V}_2 - a_2 (1 - \overline{U}_2)^2 \right) \\ = & \overline{V}_2 (1 - \overline{V}_2) (r a_2 - 2 d\overline{\mu}^2 \overline{V}_2) \\ \leq & \overline{V}_2 (1 - \overline{V}_2) (r a_2 - 2r (1 - a_2) \frac{a_2}{1 - a_2}) = -r a_2 \overline{V}_2 (1 - \overline{V}_2) \leq 0. \end{split}$$

When $z \geq z_2$, we obtain

$$\begin{split} & d\overline{V}_2'' + c_0\overline{V}_2' + r\overline{V}_2 \left(1 - \overline{V}_2 - a_2(1 - \overline{U}_2)^2\right) \\ = & \overline{V}_2(1 - \overline{V}_2) \{ d\overline{\mu}^2 (1 - 2\overline{V}_2) - c\overline{\mu} + r - ra_2 \frac{\left(1 - \frac{1 - a_2}{a_2} \overline{V}_2\right)^2}{1 - \overline{V}_2} \} \\ \leq & \overline{V}_2(1 - \overline{V}_2) \{ d\overline{\mu}^2 (1 - 2\overline{V}_2) - c\overline{\mu} + r - ra_2(1 - \frac{1 - a_2}{a_2} \overline{V}_2)^2 \} \\ = & \overline{V}_2(1 - \overline{V}_2) \left[ra_2 - 2r(1 - a_2)\overline{V}_2 - ra_2(1 - \frac{1 - a_2}{a_2} \overline{V}_2)^2 \right] = -\frac{r(1 - a_2)^2}{a_2} \overline{V}_2^3 (1 - \overline{V}_2) \leq 0. \end{split}$$

Therefore, $(\overline{U_2}, \overline{V_2})$ is an upper solution to system (3.1)-(3.2) when the condition (4.5) or (4.6) is satisfied. Then Theorem 3.1 implies the desired result. \Box

We next construct an upper solution for which both components are twice continuously differentiable functions on \mathbb{R} in order to obtain conditions for the linear selection of the spreading speed.

Theorem 4.3. Suppose that the given parameters d, r, a_1 , and a_2 satisfy

$$d > \frac{1}{2}, \ r \ge \frac{d(a_1 - 1)}{2(1 - a_2)(2d - 1)}.$$
 (4.8)

Then the minimal wave speed is linearly selected.

Proof. We define a pair of functions $(\overline{U}_3, \overline{V}_3)$ by

$$\overline{U}_3 = \overline{V}_3 = \left(\frac{1}{1 + e^{2\overline{\mu}z}}\right)^{\frac{1}{2}}$$

with $\overline{\mu} = \overline{\mu}(c_0)$. Again by using Theorem 3.1, it suffices to prove that $(\overline{U}_3, \overline{V}_3)$ is an upper solution of system (3.1)-(3.2). A simple computation leads to

$$\overline{V}_3' = -\overline{\mu}\overline{V}_3(1 - \overline{V}_3)(1 + \overline{V}_3), \quad V_3'' = \overline{\mu}^2\overline{V}_3(1 - \overline{V}_3)(1 + \overline{V}_3)(1 - 3\overline{V}_3^2).$$

By using $0 \le \overline{V}_3 \le 1$, and (4.8), and from the first equation in (3.1), it follows that

$$\begin{split} & \overline{U}_{3}'' + c_{0}\overline{U}_{3}' + (1 - \overline{U}_{3}) \left(a_{1}\overline{V}_{3}^{2} - \overline{U}_{3} \right) \\ &= \overline{V}_{3} (1 - \overline{V}_{3}^{2}) \left(\overline{\mu}^{2} - 3\overline{\mu}^{2}\overline{V}_{3}^{2} - c_{0}\overline{\mu} + \frac{a_{1}\overline{V}_{3} - 1}{1 + \overline{V}_{3}} \right) \\ &= \overline{V}_{3} (1 - \overline{V}_{3}^{2}) \left(\frac{r(1 - a_{2})}{d} - 2r(1 - a_{2}) - \frac{3r(1 - a_{2})}{d} \overline{V}_{3}^{2} + a_{1} \frac{\overline{V}_{3}}{1 + \overline{V}_{3}} - \frac{1}{1 + \overline{V}_{3}} \right) \\ &\leq \overline{V}_{3} (1 - \overline{V}_{3}^{2}) \left(\frac{r(1 - a_{2})}{d} - 2r(1 - a_{2}) + \frac{1}{2}a_{1} - \frac{1}{2} \right) \\ &= \frac{1}{2} \overline{V}_{3} (1 - \overline{V}_{3}^{2}) \left(a_{1} - 1 - \frac{2(1 - a_{2})(2d - 1)}{d} \right) \leq 0. \end{split}$$

From the second equation in (3.1), and by using (1.5), it follows that

$$d\overline{V}_{3}'' + c_{0}\overline{V}_{3}' + r\overline{V}_{3}(1 - \overline{V}_{3}) - ra_{2}\overline{V}_{3}(1 - \overline{U}_{3})^{2}$$

$$= \overline{V}_{3}(1 - \overline{V}_{3}^{2}) \left(-3d\overline{\mu}^{2}\overline{V}_{3}^{2} - r(1 - a_{2}) + r\frac{1 - a_{2}(1 - \overline{V}_{3})}{1 + \overline{V}_{3}} \right)$$

$$= \overline{V}_{3}(1 - \overline{V}_{3}^{2}) \left(-3r(1 - a_{2})\overline{V}_{3}^{2} - \frac{\overline{V}_{3}(1 - 2a_{2})}{1 + \overline{V}_{3}}r \right) \leq 0.$$

Thus, $(\overline{U}_3, \overline{V}_3)$ is an upper solution of system (3.1)-(3.2), and the proof is completed. \Box

5. Conclusion and discussion

In this paper we have proved the existence of traveling wave solutions connecting some of the steady states of system (1.3). We have also verified that the spreading speed is unique and equal to the minimal wave speed. These proofs mainly rely on the propagation theory for monotone semiflows. The generic selection mechanisms of the spreading speed have been obtained by using the comparison principle and the decay rates of traveling waves (see Theorems 3.1-3.3). Three explicit conditions for linear selection (i.e., Theorems 4.1-4.3) have been proved by giving explicit upper solutions. Compared to the results on linear selection for the Lotka-Volterra model with linear competition in [1,8,13], some striking differences are found for the Lotka-Volterra problems as considered in this paper. For instance, this paper finds explicit conditions for both $d \in (0, 1/2)$ and $d \in (1/2, \infty)$. However, in all the known references [1,8,13], it is required that d is located in a finite interval. Furthermore, in [1,9,13] some sufficient conditions for nonlinear selection were obtained. However, for the Lotka-Volterra model (1.1) with nonlinear competition it is very difficult to find an appropriate lower solution satisfying the Theorems 3.2-3.3. An explicit condition for nonlinear selection has not yet been derived so far, and remains an open problem.

In this paper we only studied the case for which system (1.3) has three uniform steady states, that is, condition (1.5) is required. But if condition (1.5) is not satisfied, system (1.3) may have four uniform steady states including a co-existence equilibrium. Then individual species possibly invade into the far end with different spreading speeds. Hence the basic question to solve is whether spreading speeds are unique or not. This is an interesting and challenging question, and efforts to answer this question are currently made, and will be presented in future publications.

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