

## SPEED DETERMINACY OF TRAVELING WAVES TO A STREAM-POPULATION MODEL WITH ALLEE EFFECT\*

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**Abstract.** In this paper, we investigate the speed determinacy (or selection mechanism) of traveling waves to a reaction-advection-diffusion stream-population model. We concentrate on how the spreading speed (the minimal wave speed) is impacted by the Allee effect in the model. Linear and nonlinear selection mechanisms for the minimal speed (or the spreading speed) are first defined, and the determinacy is further established by way of the upper and lower solutions method. It is found that the nonlinear determinacy is realized if there exists a lower solution with a faster decay. The results obtained are novel, and numerical simulations are carried out to illustrate our discovery.

**Key words.** stream population, traveling wavefronts, minimal wave speed, speed selection, Allee effect

**AMS subject classifications.** 35K57, 35B40, 92D25

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**1. Introduction.** The study of the biological population of species in streams, rivers, and estuaries has been attracting considerable attention recently (see, e.g., [9, 11, 12, 13, 14]). As in these investigations of stream ecology, the so-called *drift paradox* is an interesting phenomenon, according to which the species at any fixed location will not become extinct, even though there exists a downstream drift that washes away the species. Perhaps the first reasonable explanation was the theory of the colonization cycle proposed by Müller [11, 12]. Afterward, different from Müller’s idea, Speirs and Gurney [14] further formulated a constant-coefficient scalar partial differential equation to describe the situation. Their model demonstrated a simplified one-dimensional representation of a species residing in a stream, a river, or an estuary subject to advection (stream drift flow) and diffusion (random movement), with

$$(1.1) \quad \frac{\partial u}{\partial t} = g(u)u - \alpha \frac{\partial u}{\partial x} + d \frac{\partial^2 u}{\partial x^2}.$$

Here,  $u(x, t)$  is the density of the species,  $g(u)$  is the per capita growth rate of the population,  $\alpha$  is the advection speed (i.e., the speed of the flow), and  $d$  is the diffusion coefficient. They concentrated on the role of diffusion, variable river flow direction, and the swimming of organisms in the persistence of the species.

Later, Pachepsky et al. [13] extended (1.1) to a coupled system, investigating the persistence of benthic aquatic organisms. They assumed the total population to be divided into two interacting compartments: individuals (called “benthos”) residing in the benthic zone (the bottom of the stream) and individuals drifting in the flow.

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Their nondimensional system is given by

$$(1.2) \quad \begin{cases} \frac{\partial u}{\partial t} = -\sigma u + \mu v - \alpha \frac{\partial u}{\partial x} + d \frac{\partial^2 u}{\partial x^2}, \\ \frac{\partial v}{\partial t} = +\sigma u - \mu v + (1-v)v, \end{cases}$$

where the newly introduced coefficient  $\mu$  is the per capita rate at which individuals in the benthic population enter the drift;  $\sigma$  is the per capita rate at which the species returns to the benthic population from drifting, e.g., the number of the species that settle down to the benthic zone to give birth or find food. This separation has significant implications for the population persistence (for full details, please see [9, 13]). Except for the persistence or the critical domain size, for such a model, academics were also interested in the propagation speed. Since the system includes advection, it can distinguish the propagation speed with two cases: downstream (same direction of advection) and upstream (opposite direction of advection). Clearly the downstream propagation speed increases with the advection, whereas the upstream speed decreases. However, from the mathematical point of view, the analysis for an upstream-facing traveling wave solution will be similar to that of the downstream's; thus we will only consider a downstream-facing traveling wave solution that demonstrates a situation where a species invades an uninhabited downstream terrain. The main model in this paper is extended from (1.2) with the reaction term possibly having the Allee effect and the residing individuals having a weak diffusive behavior:

$$(1.3) \quad \begin{cases} \frac{\partial u}{\partial t} = -\sigma u + \mu v - \alpha \frac{\partial u}{\partial x} + d \frac{\partial^2 u}{\partial x^2}, \\ \frac{\partial v}{\partial t} = +\sigma u - \mu v + f(v) + \epsilon \frac{\partial^2 v}{\partial x^2}, \end{cases}$$

where  $\epsilon$  is a small nonnegative number due to the fact that the population living in the benthic zone barely move horizontally; the reaction term  $f(v)$  is a smooth function (say, with second-order derivative) satisfying  $f(0) = f(1) = 0$ ,  $f'(0) > 0 > f'(1)$ , and  $f(v) > 0$  for  $v \in (0, 1)$ ;  $d, \sigma, \alpha, \mu$  are positive constants with similar biological meanings to those in the model (1.2). The spatially homogeneous solutions to (1.3) are  $e_0 = (0, 0)$  and  $e_1 = (\frac{\mu}{\sigma}, 1)$ . Moreover, one can easily find that  $e_0$  is unstable and  $e_1$  is stable for the corresponding spatially homogeneous system.

To investigate the propagation phenomena, we change the model with the wave moving coordinates so as to introduce the following wave profile:

$$(1.4) \quad u(x, t) = U(\xi), \quad v(x, t) = V(\xi), \quad \xi = x - ct,$$

where  $c \geq 0$  is the unknown wave speed. Now, for a downstream-facing wave, the system for the wave profile is

$$(1.5) \quad \begin{cases} -cU' = -\sigma U + \mu V - \alpha U' + dU'', \\ -cV' = +\sigma U - \mu V + f(V) + \epsilon V'', \end{cases}$$

subject to

$$(1.6) \quad (U, V)(-\infty) = \left(\frac{\mu}{\sigma}, 1\right), \quad (U, V)(+\infty) = (0, 0).$$

A typical example for  $f(V)$  is  $V(1-V)(1+\rho V)$ , which has an Allee factor  $\rho$  (see [15]), compared to the conventional logistic growth.

By Theorems 4.1 and 4.2 in [7], it is known that there exists a critical number  $c_{\min}$  defined as

$$c_{\min} := \inf\{c \mid c \in \mathbb{R} \text{ such that (1.5)–(1.6) has a nonnegative solution}\},$$

so that the system (1.5)–(1.6) has a nonnegative solution if and only if  $c \geq c_{\min}$ . Biologically and significantly, this speed is also equal to the asymptotic spreading speed that indicates the velocity of biological invasion. Usually, the exact value of this speed is difficult to determine, even for the simple Fisher–KPP scalar model with the Allee effect. What we are able to do is to find the speed for the linearized system around zero and use it to estimate the spreading speed. For instance, for our model, by linearizing the system (1.5) near zero, we can obtain the linear speed  $c_0$  whose details will be shown in the next section, and by which it can be seen that  $c_{\min} \geq c_0$ , a fact that is believed to be true for all cooperative systems. Whether they are equal becomes a challenging problem, and this results in the following definition of linear or nonlinear determinacy, classifying the speed selection.

**DEFINITION 1.1.** *If  $c_{\min} = c_0$ , we say the minimal speed of the system (1.5)–(1.6) is linearly selected; otherwise, if  $c_{\min} > c_0$ , we say the minimal speed is nonlinearly selected.*

Currently, there are a few references that work on the speed determinacy to scalar reaction-diffusion equations or the diffusive Lotka–Volterra competition model (see [1, 2, 8, 16]). As we notice that the variation principle in [8] does not work here, we will investigate the speed selection by the upper and lower solutions technique to the wave profile system coupled with the comparison principle to the partial differential equations (1.3). Our construction of the upper or lower solution is different from the classical upper (or lower) solution of [4] that is an exponential function (a solution to the linear system) capped by the positive constant solution, and it usually gives the mechanism of the linear speed determinacy, with a further requirement that the nonlinear model is bounded by its linearized system. Our new upper solution comes directly from the solution of a nonlinear system. It can effectively approximate the real wavefront, and thus it provides better or superior conditions for the linear speed selection. Furthermore, by analyzing the nature of the *pushed* wavefront (wavefront with  $c_{\min} > c_0$ ), we will construct a lower solution with a fast decay rate to establish the nonlinear selection mechanism. The spreading speed is shown to be an increasing function of the Allee factor. Numerical simulations are carried out to obtain the linear speed and to indicate the linear and nonlinear speed determinacy.

The remaining part of this paper is organized as follows. In section 2, we will study the wave profile behavior locally near the equilibrium  $e_0$ . In section 3, we will present our main results for the speed selection mechanism. In section 4, we will apply our results to a cubic reaction term to obtain further results by choosing subtle forms of upper and lower solutions. In the last section, we append the idea of the upper and lower solutions method.

**2. Linearization at  $e_0 = (0, 0)$ .** In this section, we focus on the local analysis near  $e_0$ , i.e.,  $(U, V) = (0, 0)$ . To begin with, we linearize system (1.5) near  $e_0$  to derive the following system:

$$(2.1) \quad \begin{cases} -cU' = dU'' - \alpha U' - \sigma U + \mu V, \\ -cV' = \epsilon V'' + \sigma U - \mu V + f'(0)V. \end{cases}$$

This can be regarded as a fourth-order linear differential system with constant coefficients. Let  $(U, V) = (A_1, A_2)e^{-\lambda\xi}$  with  $\lambda > 0$  and  $A_1, A_2$  being constants. We then

obtain the following eigenvalue problem:

$$(2.2) \quad \begin{cases} c\lambda A_1 = d\lambda^2 A_1 + \alpha\lambda A_1 - \sigma A_1 + \mu A_2, \\ c\lambda A_2 = \epsilon\lambda^2 A_2 + \sigma A_1 - \mu A_2 + f'(0)A_2. \end{cases}$$

For simplicity of notation, we denote it in a matrix form:

$$(2.3) \quad c\lambda A = \begin{pmatrix} d\lambda^2 + \alpha\lambda - \sigma & \mu \\ \sigma & \epsilon\lambda^2 - \mu + f'(0) \end{pmatrix} A,$$

where  $A = (A_1 \ A_2)^T$ . To solve the above eigenvalue problem, we first consider the eigenvalue problem of the right-side operator:

$$(2.4) \quad k(\lambda)A = B(\lambda)A,$$

where  $k(\lambda)$  denotes the principal eigenvalue and

$$(2.5) \quad B(\lambda) = \begin{pmatrix} B_1(\lambda) & \mu \\ \sigma & B_2(\lambda) \end{pmatrix}, \quad B_1(\lambda) = d\lambda^2 + \alpha\lambda - \sigma, \quad B_2(\lambda) = \epsilon\lambda^2 - \mu + f'(0).$$

Clearly, to obtain a nonzero solution of (2.4), we require

$$k^2 - (B_1 + B_2)k + B_1B_2 - \sigma\mu = 0.$$

Thus, we obtain

$$k_{\pm} = \frac{(B_1 + B_2) \pm \sqrt{(B_1 + B_2)^2 - 4(B_1B_2 - \sigma\mu)}}{2}.$$

Notice that the determinant  $\Delta = (B_1 + B_2)^2 - 4(B_1B_2 - \sigma\mu) = (B_1 - B_2)^2 + 4\sigma\mu > 0$ . This means that  $k_- < k_+$ , and they both are real. Substituting  $B_1$  and  $B_2$  into it, the exact formula of  $k_+$  is given by

$$(2.6) \quad k_+ = \frac{(d + \epsilon)\lambda^2 + \alpha\lambda - \sigma - \mu + f'(0) + \sqrt{[(d + \epsilon)\lambda^2 + \alpha\lambda - \sigma + \mu - f'(0)]^2 + 4\sigma\mu}}{2}.$$

Furthermore, since all the parameters are positive, from the above formula, we have the following result.

**PROPOSITION 2.1.**  $k_+ > 0$  for all  $\lambda \in (0, +\infty)$ .

The principal eigenvalue of the cooperative matrix  $B(\lambda)$  is

$$(2.7) \quad k(\lambda) = k_+(\lambda),$$

where  $k_+$  is defined in (2.6). Moreover, due to the term  $d\lambda^2$ , it follows that  $k$  is convex with respect to  $\lambda$  (see, e.g., [3]).

From (2.3), we want to find  $c$  such that  $c\lambda = k(\lambda)$  has a solution  $\lambda \in (0, +\infty)$ . It is not hard to find the following property of the function  $k(\lambda)$ .

**LEMMA 2.2.**  $k(\lambda)$  defined in (2.7) is a real, continuous, and convex function with respect to  $\lambda \in \mathbb{R}$ . If we define

$$(2.8) \quad c_0 = \inf_{\lambda \in (0, +\infty)} \frac{k(\lambda)}{\lambda} \in \mathbb{R}_+,$$

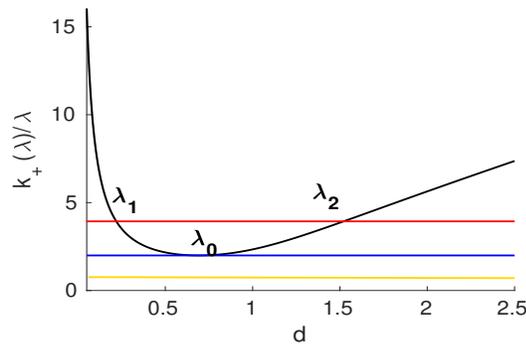


FIG. 1. (Color online.) The function  $\frac{k(\lambda)}{\lambda}$ . This figure is obtained in the parameter set  $d = 3$ ,  $\alpha = 1$ ,  $\mu = 1$ ,  $\sigma = 3$ ,  $\epsilon = 0.1$ , and  $f'(0) = 1$ . The black curve denotes the function  $\frac{k(\lambda)}{\lambda}$ , and the blue line is the value of  $c_0 = 1.99456$ .

which is called the linear speed, then the equation  $c\lambda = k(\lambda)$  has

- (1) no solution if  $c < c_0$ ;
- (2) exactly one solution  $\lambda_0(c_0)$  if  $c = c_0$ ;
- (3) two solutions  $\lambda_1(c)$  and  $\lambda_2(c)$  with  $\lambda_1(c) < \lambda_2(c)$  if  $c > c_0$ .

Here, we manifest this lemma with a particular example; see Figure 1. Letting  $d = 3$ ,  $\epsilon = 0.1$ ,  $\alpha = 1$ ,  $\mu = 1$ ,  $\sigma = 3$ , and  $f'(0) = 1$ , we obtain that  $c_0 = 1.99456$  and  $\lambda_0 = 0.6906$ . In the figure, the black curve denotes  $\frac{k(\lambda)}{\lambda}$ . As we can see from the figure, there is no intersection when  $c < c_0$  (see the yellow line); there is exactly one intersection when  $c = c_0$  (see the blue line); there are two intersections when  $c > c_0$  (see the red line).

Moreover, based on the above lemma, we can give the exact exponential behavior of the waves  $(U, V)(\xi)$  as  $\xi \rightarrow +\infty$  in the following lemma.

LEMMA 2.3. Under the definition of  $c_0$  in Lemma 2.2, for any  $c > c_0$ , the wave profile (if it exists) has the following asymptotic behavior:

$$(2.9) \quad \begin{pmatrix} U \\ V \end{pmatrix} \sim C_1 \begin{pmatrix} -\frac{\mu}{B_1(\lambda_1(c)) - c\lambda_1(c)} \\ 1 \end{pmatrix} e^{-\lambda_1(c)\xi} + C_2 \begin{pmatrix} -\frac{\mu}{B_1(\lambda_2(c)) - c\lambda_2(c)} \\ 1 \end{pmatrix} e^{-\lambda_2(c)\xi}$$

with  $C_1 > 0$ , or  $C_1 = 0$ ,  $C_2 > 0$ . Here  $B_1$  is as defined in (2.5).

*Proof.* For any given  $c > c_0$ , the traveling wave satisfies  $(U, V) \rightarrow (0, 0)$  as  $\xi \rightarrow \infty$ . Therefore, as  $\xi \rightarrow \infty$ , we have  $f(V) \sim f'(0)V$ , and the positive wave solution  $(U, V)$  of (1.5) (or the leading term of  $(U, V)$ ) should satisfy (2.1). Since  $k(\lambda) = k_+$  is the principal eigenvalue of  $B(\lambda)$ , we can derive that the corresponding eigenvector  $A = (A_1 \ A_2)^T$  is positive. Indeed, by Taylor's expansion, we obtain  $e^{B(\lambda)}A = e^{k(\lambda)}A$  and  $A$  is also the eigenvector of the operator  $e^{B(\lambda)}$  with the principal eigenvalue  $e^{k(\lambda)}$ . A theorem of Frobenius states that any nonzero irreducible matrix with nonnegative entries has a unique positive principal eigenvalue, with a corresponding principal eigenvector  $A$  with strictly positive coordinates. Therefore, via the characteristic equation of the linear system, the decaying solution of (2.1) can be obtained as the right side of (2.9) after normalizing  $A_2 = 1$ . Here we do not intake  $k_-$  since its

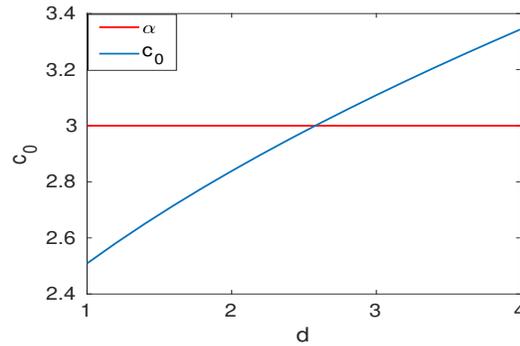


FIG. 2. (Color online.) The relation between the linear speed  $c_0$  and  $d$ . This figure is obtained when  $\alpha = 3$ ,  $\mu = 1$ ,  $\sigma = 2$ ,  $\epsilon = 0.1$ ,  $f'(0) = 1$ , and  $d$  varies from 1 to 4. The blue curve denotes the linear speed corresponding to each  $d$ , while the black line is the value of  $\alpha$ .

associated eigenvector is nonpositive. In other words, the positive wave profile satisfies

$$\begin{pmatrix} U \\ V \end{pmatrix} \sim C_1 \begin{pmatrix} -\frac{\mu}{B_1(\lambda_1) - c\lambda_1} \\ 1 \end{pmatrix} e^{-\lambda_1 \xi} + C_2 \begin{pmatrix} -\frac{\mu}{B_1(\lambda_2) - c\lambda_2} \\ 1 \end{pmatrix} e^{-\lambda_2 \xi},$$

with  $C_1 > 0$ , or  $C_1 = 0$ ,  $C_2 > 0$ . This completes the proof.  $\square$

*Remark 2.4.* According to Lemma 2.3 and the eigenvalue problem (2.3), when  $c > c_0$ , the asymptotic behavior of the wave can also be given by

$$\begin{pmatrix} U \\ V \end{pmatrix} \sim C_1 \begin{pmatrix} -\frac{B_2(\lambda_1(c)) - c\lambda_1(c)}{1} \\ 1 \end{pmatrix} e^{-\lambda_1(c)\xi} + C_2 \begin{pmatrix} -\frac{B_2(\lambda_2(c)) - c\lambda_2(c)}{1} \\ 1 \end{pmatrix} e^{-\lambda_2(c)\xi},$$

which is equivalent to (2.9).

*Remark 2.5.* Lemma 2.2 implies  $c_{\min} \geq c_0$ . It is impossible to expect a nonnegative wavefront for  $\xi$  near infinity when  $c < c_0$  since  $\lambda$  has a nontrivial imaginary part, and  $(0, 0)$  becomes a spiral point. When  $c > c_0$ ,  $\lambda_1(c)$  is decreasing in  $c$  and  $\lambda_2(c)$  is increasing in  $c$ .

From the formula of  $c_0$  (see (2.8)), it is clear to see that  $c_0$  is increasing in  $d$ . By numerical simulations, we show their relation in Figure 2. It is interesting to observe that  $c_0$  may even be less than  $\alpha$  (the drift speed of the stream) when  $d$  is small enough, in which the species is fighting with the drift flow to stay via the choice of residing at the bottom.

*Remark 2.6.* Moreover, if we normalize by setting  $A_2 = 1$ , then the eigenvalue problem (2.2) can be rewritten as

$$\begin{cases} d\lambda^2 A_1 - (c - \alpha)\lambda A_1 = \sigma A_1 - \mu, \\ \epsilon\lambda^2 - c\lambda + f'(0) = -(\sigma A_1 - \mu). \end{cases}$$

When  $c = c_0$ , we have

$$(2.10) \quad A_1(c_0) = -\frac{\mu}{B_1(\lambda_0) - c_0\lambda_0},$$

where  $\lambda_0$  is as given in Lemma 2.2(2).

**3. The speed selection mechanism.** In this section, we want to study the speed selection mechanism of the system (1.5). The method used is the upper and lower solutions technique (please see Appendix A for details). Notice that the first equation in (1.5) is always a linear equation in  $U$ ; thus by the variation of parameters, we can solve  $U$  in terms of  $V$  as

$$(3.1) \quad U(\xi) = \frac{\mu}{d(\tau_2 - \tau_1)} \left\{ \int_{-\infty}^{\xi} e^{\tau_1(\xi-s)} V(s) ds + \int_{\xi}^{\infty} e^{\tau_2(\xi-s)} V(s) ds \right\} := H(V),$$

where  $\tau_1, \tau_2$  satisfy

$$d\tau^2 + (c - \alpha)\tau - \sigma = 0,$$

with

$$(3.2) \quad \tau_1 = \frac{-(c - \alpha) - \sqrt{(c - \alpha)^2 + 4\sigma d}}{2d} < 0 < \tau_2 = \frac{-(c - \alpha) + \sqrt{(c - \alpha)^2 + 4\sigma d}}{2d}.$$

For any  $c > c_0$ , by Lemmas 2.2 and 2.3, it is easy to verify that

$$H(e^{-\lambda_i(c)\xi}) = A_{1,i}(c)e^{-\lambda_i(c)\xi} \quad \text{and} \quad H(1) = \frac{\mu}{\sigma}, \quad i = 1, 2,$$

where

$$A_{1,i}(c) = \frac{-\mu}{B_1(\lambda_i(c)) - c\lambda_i(c)}.$$

Clearly, for any given continuous function  $V(\xi)$  satisfying  $V(-\infty) = 1$  and  $V(+\infty) = 0$ , by (3.1), we have the existence of  $U$  subject to  $U(-\infty) = \frac{\mu}{\sigma}$  and  $U(+\infty) = 0$ .

For simplicity of notation, we denote

$$\begin{aligned} L_1(U, V) &:= dU'' + (c - \alpha)U' - \sigma U + \mu V, \\ L_2(U, V) &:= \epsilon V'' + cV' + \sigma U - \mu V + f(V). \end{aligned}$$

By the  $U$ 's formula, (1.5) reduces to a nonlocal equation

$$(3.3) \quad \begin{cases} \epsilon V'' + cV' + \sigma U - \mu V + f(V) = 0, \\ V(-\infty) = 1, \quad V(+\infty) = 0, \end{cases}$$

where  $U = H(V)$  is the integral given in (3.1).

From now on, we will focus on constructing a pair of suitable upper and lower solutions to the above  $V$ -equation (see Theorem 6.4).

For any  $c = c_0 + \varepsilon_1$ , by Lemma 2.2, there exist  $0 < \lambda_1(c) < \lambda_2(c)$ . Inspired by Lemma 2.3, we proceed to construct upper or lower solutions with suitable decaying behaviors. Let

$$(3.4) \quad \bar{V}(\xi) = \frac{\bar{k}_v}{[1 + (\bar{k}_v e^{\lambda_1(c)\xi})^m]^{\frac{1}{m}}}, \quad m \geq 1, \quad \bar{k}_v \geq 1.$$

It is easy to see that this  $\bar{V}$  function has the asymptotic behaviors  $\bar{V} \sim e^{-\lambda_1(c)\xi}$  as  $\xi \rightarrow +\infty$  and  $\bar{V} \rightarrow \bar{k}_v$  as  $\xi \rightarrow -\infty$ . Then, through a simple computation, its first and second derivatives are found as follows:

$$\bar{V}' = -\lambda_1(c)\bar{V}(1 - \bar{V}_1^m) \quad \text{and} \quad \bar{V}'' = \lambda_1^2(c)\bar{V}(1 - \bar{V}_1^m)(1 - (m+1)\bar{V}_1^m),$$

where  $\bar{V}_1 = \frac{\bar{V}}{\bar{k}_v}$ . Substituting all of the above formulas into the left-hand side of (3.3), we obtain

$$\begin{aligned} L_2(\bar{U}, \bar{V}) &= \bar{V}^2(1 - \bar{V}_1^m) \left\{ - (m + 1)\epsilon\lambda_1^2(c) \frac{1}{\bar{k}_v} \bar{V}_1^{m-1} + \frac{\sigma[\frac{H(\bar{V})}{\bar{V}} - A_1(1 - \bar{V}_1^m)] - \mu\bar{V}_1^m}{\bar{V}(1 - \bar{V}_1^m)} \right. \\ &\quad \left. + \frac{\frac{f(\bar{V})}{\bar{V}} - f'(0)(1 - \bar{V}_1^m)}{\bar{V}(1 - \bar{V}_1^m)} \right\} \\ &=: \bar{V}^2(1 - \bar{V}_1^m) \cdot J_{\lambda_1}(m, \bar{k}_v). \end{aligned}$$

In view of the definition of an upper solution (see Definition A.1 and Lemma A.2 for details) and  $\lambda_1 \rightarrow \lambda_0$  as  $\epsilon \rightarrow 0$ , we can easily derive that the continuous function  $\bar{V}$  given by (3.4) is an upper solution to (3.3) if

$$(3.5) \quad J_{\lambda_0}(m, \bar{k}_v) < 0,$$

with  $m$  and  $\bar{k}_v$  suitably chosen. Now, we summarize the above discussion into the following lemma.

LEMMA 3.1. *If the inequality (3.5) holds, then the continuous function  $\bar{V}$  given by (3.4) is an upper solution to (3.3) (i.e.,  $L_2(\bar{U}, \bar{V}) \leq 0$ ).*

To apply Theorem A.4 on (3.3), we need to construct a lower solution to (1.5) when  $c = c_0 + \epsilon_1$ . To this end, we define a continuous function  $\underline{V}$  as

$$(3.6) \quad \underline{V} = \begin{cases} e^{-\lambda_1(c)\xi}(1 - Me^{-\epsilon_2\xi}), & \xi > \xi_0, \\ 0, & \xi \leq \xi_0, \end{cases}$$

where  $0 < \epsilon_2 \ll 1$ ,  $M$  is a positive number to be determined, and  $\xi_0 = \frac{\log M}{\epsilon_2}$ .

LEMMA 3.2. *When  $c = c_0 + \epsilon_1$ , there exist  $0 < \epsilon_2 \ll 1$  and  $M \gg 1$  such that the pair of continuous functions  $(\underline{U}, \underline{V})(z)$ , where  $\underline{V}$  is defined in (3.6) and  $\underline{U} = H(\underline{V})$  is defined by (3.1), is a lower solution to the system (1.5)–(1.6).*

*Proof.* To prove the chosen function satisfying the definition of a lower solution, we need to show that for all  $\xi \in \mathbb{R}$ ,

$$\begin{aligned} d\underline{U}'' + (c - \alpha)\underline{U}' - \sigma\underline{U} + \mu\underline{V} &\geq 0, \\ \epsilon\underline{V}'' + c\underline{V}' + \sigma\underline{U} - \mu\underline{V} + f(\underline{V}) &\geq 0. \end{aligned}$$

Notice that the first inequality is always true for all  $\xi \in \mathbb{R}$ , and the second one holds for  $\xi \leq \xi_0$ . As for  $\xi > \xi_0$ , by direct substitution, we have

$$\begin{aligned} &\epsilon\underline{V}'' + c\underline{V}' + \sigma\underline{U} - \mu\underline{V} + f(\underline{V}) \\ &= e^{-\lambda_1(c)\xi} [\epsilon\lambda_1^2(c) - c\lambda_1(c) + \sigma A_1 - \mu + f'(0)] - Me^{-(\lambda_1(c) + \epsilon_2)\xi} [\epsilon(\lambda_1(c) + \epsilon_2)^2 \\ &\quad - c(\lambda_1(c) + \epsilon_2) - \mu + f'(0)] - \sigma MH(e^{-(\lambda_1(c) + \epsilon_2)\xi}) + [f(\underline{V}) - f'(0)\underline{V}] \\ &> -Me^{-(\lambda_1(c) + \epsilon_2)\xi} [\epsilon(\lambda_1(c) + \epsilon_2)^2 - c(\lambda_1(c) + \epsilon_2) + \sigma A_1 - \mu + f'(0)] + [f(\underline{V}) - f'(0)\underline{V}]. \end{aligned}$$

The last inequality is guaranteed by  $H(e^{-(\lambda_1(c) + \epsilon_2)\xi}) < A_1 e^{-(\lambda_1(c) + \epsilon_2)\xi}$ , which can be derived by direct computation. For the last line, it is easy to see that the first term is always positive when  $\epsilon_2$  is sufficiently small. By choosing  $M$  to be sufficiently large, we can have  $\xi_0 > 0$  and  $\underline{V} \ll 1$  so that  $[f(\underline{V}) - f'(0)\underline{V}] \sim O(e^{-2\lambda_1(c)\xi})$ ; thus the first term dominates the second one. Hence, the proof is complete.  $\square$

The condition  $V'(\xi_0^-) \leq V'(\xi_0^+)$  can be easily verified, and, by translation if necessary, we can have  $\underline{U}(\xi) \leq \bar{U}(\xi)$  and  $\underline{V}(\xi) \leq \bar{V}(\xi)$  for  $\xi \in (-\infty, +\infty)$ . Then we conclude that  $(\bar{U}, \bar{V})(\xi)$  and  $(\underline{U}, \underline{V})(\xi)$  are a pair of upper and lower solutions, respectively. By Theorem A.4, we obtain the following linear selection result.

**THEOREM 3.3** (Linear selection). *When (3.5) is satisfied, the minimal speed of the system (1.5)–(1.6) is linearly selected (i.e.,  $c_{\min} = c_0$ ).*

We then turn to study the nonlinear selection through the upper and lower solutions method. The key observation is that, when a lower solution has an asymptotic behavior  $e^{-\lambda_2 \xi}$  (i.e., the faster decay rate) as  $\xi \rightarrow +\infty$ , the nonlinear selection will be realized. We give the following theorem as a justification.

**THEOREM 3.4.** *For a given  $c_1 > c_0$ , assume that there exists a pair of nonnegative functions  $(\underline{U}, \underline{V})(\xi)$  with  $\xi = x - c_1 t$ , as a pair of lower solutions to the partial differential system*

$$(3.7) \quad \begin{cases} u_t = du_{xx} - \alpha u_x - \sigma u + \mu v, \\ v_t = \epsilon v_{xx} + \sigma u - \mu v + f(v). \end{cases}$$

*We further suppose that  $\underline{V}(\xi)$  is monotone, satisfies*

$$\limsup_{\xi \rightarrow -\infty} \underline{V}(\xi) < 1,$$

*and has the asymptotic behavior  $Ce^{-\lambda_2 \xi}$  as  $\xi \rightarrow +\infty$  for some positive constant  $C$ . Then there exists no traveling solution to (1.5)–(1.6) for  $c \in [c_0, c_1]$ .*

*Proof.* We prove here by contradiction. Assume that there exists a monotone traveling wave solution  $(U, V)(\xi)$ ,  $\xi = x - ct$ , with  $c \in [c_0, c_1]$ , subject to the initial conditions

$$u(x, 0) = U(x) \text{ and } v(x, 0) = V(x).$$

We should note that if  $c = c_0$ , then we have traveling wave solutions for all  $c > c_0$  by Theorems 4.1 and 4.2 in [7]. Thus we can always assume that  $c \in (c_0, c_1)$ .

Moreover,  $(U, V)$  satisfies (1.5), and their decaying behavior near  $+\infty$  can be easily analyzed (see, e.g., section 2). By the monotonicity of  $\lambda_1(c)$  and  $\lambda_2(c)$  in terms of  $c$ , we can always assume (by shifting if necessary) that  $(\underline{U}, \underline{V})(x) \leq (U, V)(x)$  for all  $x \in \mathbb{R}$ . Since  $(\underline{U}, \underline{V})(x - c_1 t)$  is a lower solution to the system (3.7) with the initial data  $(\underline{U}, \underline{V})(x)$ , by comparison, we obtain

$$(3.8) \quad \underline{U}(x - c_1 t) \leq U(x - ct) \text{ and } \underline{V}(x - c_1 t) \leq V(x - ct)$$

for all  $(x, t) \in \mathbb{R} \times \mathbb{R}_+$ . Now, if we fix  $\xi = x - c_1 t$ , then  $\underline{V}(\xi) > 0$  is fixed. On the other hand, from  $V(x - ct)$ , it is clear that

$$V(x - ct) = V(\xi + (c_1 - c)t) \rightarrow V(+\infty) = 0 \quad \text{as } t \rightarrow +\infty.$$

By (3.8), we thus get  $\underline{V}(\xi) \leq 0$ . This is a contradiction. Therefore, there is no traveling wave solution for  $c \in [c_0, c_1]$ . This completes the proof.  $\square$

*Remark 3.5.* Due to the above theorem, for the nonlinear selection, we only need to find a lower solution that has an asymptotic behavior  $e^{-\lambda_2(c)\xi}$  as  $\xi \rightarrow +\infty$  for some  $c > c_0$ .

Now, suppose  $\underline{V}_2$  has the following form:

$$(3.9) \quad \underline{V}_2(\xi) = \frac{\underline{k}_v}{[1 + (\underline{k}_v e^{\lambda_2(c)\xi})^m]^{\frac{1}{m}}}, \quad m \geq 1, \quad 0 < \underline{k}_v < 1.$$

Clearly, this function connects  $\underline{k}_v$  to 0 and has the asymptotic behavior  $e^{-\lambda_2\xi}$  as  $\xi \rightarrow +\infty$ . By substituting the above formula into the left-hand side of (3.3), we obtain

$$\begin{aligned} L_2(\underline{U}_2, \underline{V}_2) &= \underline{V}_2^2(1 - \underline{V}_1^m) \left\{ - (m+1)\epsilon\lambda_2^2(c) \frac{1}{\underline{k}_v} \underline{V}_1^{m-1} \right. \\ &\quad \left. + \frac{\sigma[\frac{H(\underline{V}_2)}{\underline{V}_2} - A_1(1 - \underline{V}_1^m)] - \mu\underline{V}_1^m}{\underline{V}_2(1 - \underline{V}_1^m)} + \frac{\frac{f(\underline{V}_2)}{\underline{V}_2} - f'(0)(1 - \underline{V}_1^m)}{\underline{V}_2(1 - \underline{V}_1^m)} \right\} \\ &=: \underline{V}_2^2(1 - \underline{V}_1^m) \cdot J_{\lambda_2}(m, \underline{k}_v), \end{aligned}$$

where  $\underline{V}_1 = \frac{\underline{V}_2}{\underline{k}_v}$ . For suitably chosen  $m$  and  $\underline{k}_v$ , it follows that  $\underline{V}_1$  is a lower solution to (3.3) (i.e.,  $L_2(\underline{U}_1, \underline{V}_1) \geq 0$ ) if

$$(3.10) \quad J_{\lambda_2}(m, \underline{k}_v) > 0.$$

Then, by Theorem 3.4, the following result holds.

**THEOREM 3.6** (Nonlinear selection). *If the inequality (3.10) holds for some  $m$  and  $\underline{k}_v$ , then the minimal speed of traveling waves to the system (1.5)–(1.6) is nonlinearly selected.*

**4. Applications.** In this section, we will apply the linear and nonlinear selection theorems proved in the previous section to the model with a cubic nonlinear reaction term, i.e.,  $f(v) = v(1-v)(1+\rho v)$  with  $\rho$  being a nonnegative constant. This cubic reaction term can be viewed as the classical logistic growth with a weak Allee effect (see [15]) and can be applied to model a lot of biological phenomena. We want to investigate how the Allee effect impacts the spreading speed. In current references such as [6, 18], they require that  $f(v)$  is sublinear in the sense that  $f(v) \leq f'(0)v$ , and thus a linear selection result is obtained. Following this, we immediately obtain that the minimal wave speed is linearly selected when  $\rho \leq 1$ . Now, with our methods, conclusions on the speed selection can be considerably extended. To proceed, we start with the system of the wave profile

$$(4.1) \quad \begin{cases} dU'' + (c - \alpha)U' - \sigma U + \mu V = 0, \\ \epsilon V'' + cV' + \sigma U - \mu V + (1 - V)(1 + \rho V)V = 0, \\ (U, V)(-\infty) = (\frac{\mu}{\sigma}, 1), \quad (U, V)(+\infty) = (0, 0). \end{cases}$$

With the values of  $d$ ,  $\epsilon$ ,  $\mu$ ,  $\sigma$ ,  $\alpha$ , and  $f'(0)$  being fixed, we first show the existence of a threshold  $\bar{\rho}$  so that, when  $\rho$  increases to cross over this critical value, the speed selection changes from linear to nonlinear. To see this, we will prove the following lemma.

**LEMMA 4.1.** *If the minimal wave speed of (4.1) is linearly selected when  $\rho = \rho_l$  for some  $\rho_l$ , then it is linearly selected for all  $\rho < \rho_l$ .*

*Proof.* From the assumption that  $\rho = \rho_l$ , we have  $(U_l, V_l)$  as a pair of solutions, which are decreasing with respect to  $\xi \in \mathbb{R}$ , with  $c = c_0 + \epsilon_1$  to (4.1) for any small

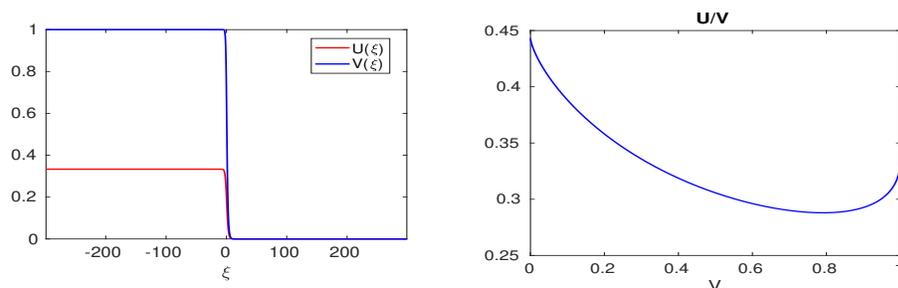


FIG. 3. (Color online.) The functions  $U, V$  and  $\frac{U}{V}$ . These figures are obtained in the parameter set  $d = 3$ ,  $\alpha = 1$ ,  $\mu = 1$ ,  $\sigma = 3$ ,  $\epsilon = 0.1$ , and  $f'(0) = 1$ .

$\varepsilon_1 > 0$ . Thus, they satisfy

$$\begin{cases} dU_l'' + (c - \alpha)U_l' - \sigma U_l + \mu V_l = 0, \\ \epsilon V_l'' + cV_l' + \sigma U_l - \mu V_l + (1 - V_l)(1 + \rho_l V_l)V_l = 0. \end{cases}$$

Then, by substituting  $(U_l, V_l)$  into (4.1) with  $\rho < \rho_l$ , we see that the first equation is always zero and the second one becomes

$$\begin{aligned} & \epsilon V_l'' + cV_l' + \sigma U_l - \mu V_l + (1 - V_l)(1 + \rho V_l)V_l \\ &= (1 - V_l)V_l^2(\rho - \rho_l) < 0. \end{aligned}$$

This means that  $(U_l, V_l)$  is an upper solution to (4.1) for  $\rho < \rho_l$ . Then, by taking the lower solution defined in Lemma 3.2, we conclude that the minimal wave speed is linearly selected for all  $\rho < \rho_l$ . This completes the proof.  $\square$

From the above lemma, we can define the threshold value of  $\rho$  as

$$\bar{\rho} := \sup\{\rho \mid \text{the linear speed selection is realized for (4.1)}\}.$$

Although we obtained the existence of the threshold  $\bar{\rho}$ , its exact value is hard to derive. In practice, we want to give an estimate of it. Moreover, the exact formula of  $U$  in terms of  $V$  (see (3.1)) is too complicated to determine the conditions in the speed selection, so we will establish some novel upper (lower) solutions to the  $U$ -equation simultaneously, i.e.,  $L_1(\bar{U}, \bar{V}) \leq 0$  ( $L_1(\underline{U}, \underline{V}) \geq 0$ ), instead of using the formula  $H(V)$ .

To carry on, we numerically compute the value of  $\frac{U}{V} = \frac{H(V)}{V}$ , where  $V$  is as defined in (3.4) with  $m = 2$ ,  $\bar{k}_v = 1$ , and  $c = c_0$ . An example is shown in Figure 3. These figures are depicted when  $d = 3$ ,  $\epsilon = 0.1$ ,  $\alpha = 1$ ,  $\mu = 1$ , and  $\sigma = 3$ . With the parameter set, we find that  $A_1 = 0.44325$ ,  $c_0 = 1.9945625$ , and  $\lambda_0 = 0.6906$ . The left panel shows the functions of  $V$  and  $U = H(V)$ . The right panel shows the value of  $\frac{U}{V}$ . As we can see,  $\frac{U}{V} \rightarrow \frac{\mu}{\sigma}$  as  $\xi \rightarrow +\infty$ ,  $\frac{U}{V} \rightarrow A_1$  as  $\xi \rightarrow -\infty$ , and the curve looks like a vertical parabola. When  $m = 1$ , similar phenomena can happen. Inspired by this observation, we will construct innovative approximate formulas of  $U$  in terms of  $V$ , which are much simpler than the abstract one  $U = H(V)$ . The details are shown as follows.

Motivated by this observation, we first give results on the speed selection by using the trial function  $U = V \cdot (A_1 + bV + aV^2)$  with  $b = \frac{\mu}{\sigma} - A_1 - a$  and  $a \in \mathbb{R}_+$  to be determined. We give the following notation to state our theorems more fluently. Denote

$$h_{c_0}(a) := a^2 \{33d^2\lambda_0^4 + 6d\lambda_0^3(c_0 - \alpha) + 9\lambda_0^2(c_0 - \alpha)^2 + 48d\lambda_0^2\sigma\} + a \left\{12d^2\lambda_0^4 \frac{\mu}{\sigma}\right.$$

$$(4.2) \quad -108d^2\lambda_0^4 A_1(c_0) - 60d\lambda_0^3 \left( \frac{\mu}{\sigma} - A_1(c_0) \right) (c_0 - \alpha) \Big\} + 36d^2\lambda_0^4 \left( \frac{\mu}{\sigma} - A_1(c_0) \right)^2,$$

and

$$(4.3) \quad \begin{cases} a_3(c_0, \lambda_0) = \frac{2d\lambda_0(\frac{\mu}{\sigma} - A_1(c_0))}{5d\lambda_0 - (c_0 - \alpha)}, & a_4(c_0, \lambda_0) = \frac{d\lambda_0^2(\frac{4\mu}{\sigma} - 6A_1(c_0)) - 2\lambda_0(c_0 - \alpha)(\frac{\mu}{\sigma} - A_1(c_0))}{4d\lambda_0^2 - 2\lambda_0(c_0 - \alpha) - \sigma}, \\ a_5(c_0, \lambda_0) = \frac{2[d\lambda_0^2\frac{\mu}{\sigma} + \lambda_0(c_0 - \alpha)(\frac{\mu}{\sigma} - A_1(c_0))]}{[-d\lambda_0^2 - \lambda_0(c_0 - \alpha) + \sigma]}. \end{cases}$$

Notice that  $h_{c_0}(a)$  is a quadratic polynomial and  $h_{c_0}(0) = 36d^2\lambda_0^4 \left( \frac{\mu}{\sigma} - A_1(c_0) \right)^2 > 0$ ; thus, if  $h_{c_0}(a) = 0$  has solutions  $a_1(c_0, \lambda_0)$  and  $a_2(c_0, \lambda_0)$ , then they must satisfy that  $0 < a_1(c_0, \lambda_0) \leq a_2(c_0, \lambda_0)$  or  $a_1(c_0, \lambda_0) \leq a_2(c_0, \lambda_0) < 0$ . Due to the requirement  $a > 0$ , we only consider the former case. Furthermore, define the sets

$$(4.4) \quad \begin{cases} S_1(c_0, \lambda_0) := \{a : a \leq a_1(c_0, \lambda_0) \text{ or } a \geq a_2(c_0, \lambda_0)\} \\ \text{and } S'_1(c_0, \lambda_0) := \{a : a_1(c_0, \lambda_0) < a < a_2(c_0, \lambda_0)\}, \\ S_2(c_0, \lambda_0) := \{a : a < a_3(c_0, \lambda_0)\} \text{ and } S'_2(c_0, \lambda_0) := \{a : a > a_3(c_0, \lambda_0)\}, \\ S_3(c_0, \lambda_0) := \{a : a \leq a_4(c_0, \lambda_0)\} \text{ and } S'_3(c_0, \lambda_0) := \{a : a \geq a_4(c_0, \lambda_0)\}, \\ S_4(c_0, \lambda_0) := \{a : a \leq a_5(c_0, \lambda_0)\} \text{ and } S'_4(c_0, \lambda_0) := \{a : a \geq a_5(c_0, \lambda_0)\}. \end{cases}$$

To proceed, we summarize the above notation into an assumption as follows.

(H1) Let  $c_0, \lambda_0, A_1(c_0)$ , and  $h_{c_0}(a)$  be as defined in (2.8), Lemma 2.2, (2.10), and (4.2), respectively. Assume that  $h_{c_0}(a) = 0$  has two nonnegative solutions  $0 \leq a_1(c_0, \lambda_0) < a_2(c_0, \lambda_0)$ , and then define  $a_i$  ( $i = 1, \dots, 5$ ) and  $S_j, S'_j$  ( $j = 1, \dots, 4$ ) as shown in (4.3) and (4.4), respectively.

THEOREM 4.2. *Let the assumption (H1) hold. Define*

$$\bar{M}(c_0, \lambda_0) := \bar{M}_1 \cup \bar{M}_2 \cup \bar{M}_3 \cup \bar{M}_4 \cap \{a : a > 0\},$$

where

$$\begin{cases} \bar{M}_1 := (S_2(c_0, \lambda_0) \cap S_3(c_0, \lambda_0)) \cup S'_1(c_0, \lambda_0), & \bar{M}_2 := (S_2(c_0, \lambda_0) \cap S'_3(c_0, \lambda_0)) \cup S'_1(c_0, \lambda_0), \\ \bar{M}_3 := (S'_2(c_0, \lambda_0) \cap S_3(c_0, \lambda_0)) \cup S'_1(c_0, \lambda_0), & \bar{M}_4 := (S'_2(c_0, \lambda_0) \cap S'_3(c_0, \lambda_0)) \cup S'_1(c_0, \lambda_0). \end{cases}$$

Then the linear selection is realized if there exists a positive constant  $a \in \bar{M}$  and

$$(4.5) \quad \rho \leq \sigma\bar{a} + 2\epsilon\lambda_0^2, \text{ where } \bar{a} = \sup \bar{M}.$$

*Proof.* When  $c = c_0 + \epsilon_1$ , let  $\bar{V}$  be as defined in (3.4) with  $m = 1$  and  $\bar{k}_v = 1$  (which implies  $\bar{V}_1 = \bar{V}$ ). Define

$$(4.6) \quad \bar{U} = \bar{V} \cdot [A_1(c) + b\bar{V} + a\bar{V}^2], \quad a > 0,$$

where  $b = \frac{\mu}{\sigma} - A_1(c) - a$  and  $a$  is to be determined. Here, we emphasize that such a  $\bar{U}$  function satisfies  $\frac{\bar{U}}{\bar{V}} \rightarrow \frac{\mu}{\sigma}$  as  $\xi \rightarrow -\infty$  and  $\frac{\bar{U}}{\bar{V}} \rightarrow A_1(c)$  as  $\xi \rightarrow +\infty$ . In the following context, we denote  $\lambda_1 = \lambda_1(c)$  and  $A_1 = A_1(c)$  for short unless otherwise specified. Then, through tedious computations, we obtain the first and second derivatives of  $\bar{U}$  as follows:

$$\bar{U}' = -\lambda_1\bar{V}(1 - \bar{V})(A_1 + 2b\bar{V} + 3a\bar{V}^2),$$

and

$$\bar{U}'' = \lambda_1^2 \bar{V}(1 - \bar{V})[A_1 + (4b - 2A_1)\bar{V} + (9a - 6b)\bar{V}^2 - 12a\bar{V}^3].$$

By substituting  $\bar{U}$ ,  $\bar{U}'$ , and  $\bar{U}''$  into  $L_1$ , we obtain

$$(4.7) \quad L_1(\bar{U}, \bar{V}) = \bar{V}^2(1 - \bar{V})G_1(\bar{V}),$$

where

$$\begin{aligned} G_1(\bar{V}) &= -12d\lambda_1^2 a \bar{V}^2 + \bar{V} \cdot [d\lambda_1^2(9a - 6b) - 3\lambda_1 a(c - \alpha)] + d\lambda_1^2(4b - 2A_1) - 2\lambda_1(c - \alpha)b + \sigma a \\ &= -12d\lambda_1^2 a \bar{V}^2 + 3\lambda_1 \bar{V} \left[ (5d\lambda_1 - (c - \alpha))a - 2d\lambda_1 \left( \frac{\mu}{\sigma} - A_1 \right) \right] \\ &\quad + a [-4d\lambda_1^2 + 2\lambda_1(c - \alpha) + \sigma] + d\lambda_1^2 \left( \frac{4\mu}{\sigma} - 6A_1 \right) - 2\lambda_1(c - \alpha) \left( \frac{\mu}{\sigma} - A_1 \right). \end{aligned}$$

It is clear that  $\bar{G}_1(\bar{V})$  is a parabolic function, which opens down, in  $\bar{V}$ . Through a direct computation, its determinant can be found as

$$\begin{aligned} \Delta &= a^2 \{ 33d^2 \lambda_1^4 + 6d\lambda_1^3(c - \alpha) + 9\lambda_1^2(c - \alpha)^2 + 48d\lambda_1^2 \sigma \} + a \left\{ 12d^2 \lambda_1^4 \frac{\mu}{\sigma} \right. \\ &\quad \left. - 108d^2 \lambda_1^4 A_1 - 60d\lambda_1^3 \left( \frac{\mu}{\sigma} - A_1 \right) (c - \alpha) \right\} + 36d^2 \lambda_1^4 \left( \frac{\mu}{\sigma} - A_1 \right)^2, \end{aligned}$$

which is  $h_c(a)$  by replacing  $c_0$  and  $\lambda_0$  with  $c$  and  $\lambda_1$  in  $h_{c_0}(a)$ . When  $\varepsilon_1$  is small enough and, by assumption, the equation  $h_c(a) = 0$  has two roots  $0 \leq a_1(c, \lambda_1) \leq a_2(c, \lambda_1)$ , then there are two cases to discuss.

When  $a_1(c, \lambda_1) < a < a_2(c, \lambda_1)$  (i.e.,  $a \in S'_1(c, \lambda_1)$ ), it follows that  $h_c(a) \leq 0$ . In other words,  $\Delta < 0$ , which implies that  $G_1(\bar{V}) = 0$  has no solution. Therefore,  $L_1(\bar{U}, \bar{V}) \leq 0$  if  $a \in S_1(c, \lambda_1)$ .

When  $0 \leq a \leq a_1(c, \lambda_1)$  or  $a \geq a_2(c, \lambda_1)$  (i.e.,  $a \in S_1(c, \lambda_1)$ ), we immediately obtain that  $\Delta \geq 0$ . Thus, under this condition,  $G_1(\bar{V}) = 0$  must have solutions. Furthermore, if the symmetric axis of  $G_1(\bar{V})$  is less than zero and  $G_1(0) \leq 0$ , then  $L_1(\bar{U}, \bar{V}) \leq 0$ . The first condition means

$$(5d\lambda_1 - (c - \alpha))a - 2d\lambda_1 \left( \frac{\mu}{\sigma} - A_1 \right) < 0.$$

The second condition ( $G_1(0) \leq 0$ ) shows that

$$a [-4d\lambda_1^2 + 2\lambda_1(c - \alpha) + \sigma] + d\lambda_1^2 \left( \frac{4\mu}{\sigma} - 6A_1 \right) - 2\lambda_1(c - \alpha) \left( \frac{\mu}{\sigma} - A_1 \right) \leq 0.$$

When  $5d\lambda_1 - (c - \alpha) > 0$  and  $4d\lambda_1^2 - 2\lambda_1(c - \alpha) - \sigma > 0$ , then

$$(4.8) \quad a < a_3(c, \lambda_1) \text{ and } a \geq a_4(c, \lambda_1).$$

Thus, when  $a \in S_1(c, \lambda_1) \cap S_2(c, \lambda_1) \cap S'_3(c, \lambda_1)$ , we have  $L_1 \leq 0$ . Summarizing the above discussion, we obtain that if

$$\begin{aligned} a &\in (S_1(c, \lambda_1) \cap S_2(c, \lambda_1) \cap S'_3(c, \lambda_1)) \cup S'_1(c, \lambda_1) \\ &= (S_2(c, \lambda_1) \cap S'_3(c, \lambda_1)) \cup S'_1(c, \lambda_1) = \bar{M}_1(c, \lambda_1), \end{aligned}$$

then  $L_1(\bar{U}, \bar{V}) \leq 0$ . It is clear that, depending on the signs of  $5d\lambda_1 - (c - \alpha)$  and  $4d\lambda_1^2 - 2\lambda_1(c - \alpha) - \sigma$ , we will obtain sets  $\bar{M}_2(c, \lambda_1)$ ,  $\bar{M}_3(c, \lambda_1)$ , and  $\bar{M}_4(c, \lambda_1)$ . In summary, if  $a \in \bar{M}(c, \lambda_1)$ , then  $L_1(\bar{U}, \bar{V}) \leq 0$ .

By inserting the  $\bar{U}$ -formula into  $L_2$ , we have

$$L_2(\bar{U}, \bar{V}) = \bar{V}^2(1 - \bar{V})(-2\epsilon\lambda_1^2 - \sigma a + \rho).$$

Now, it is clear that, if  $\rho \leq \sigma\bar{a}_1 + 2\epsilon\lambda_1^2$  with  $\bar{a}_1 = \sup \bar{M}(c, \lambda_1)$ , then  $L_2 \leq 0$ . Thus,  $(\bar{U}, \bar{V})$  is a pair of upper solutions when  $a \in \bar{M}(c, \lambda_1)$  and  $\rho < \sigma\bar{a} + 2\epsilon\lambda_1^2$  hold. Combining a pair of lower solutions from Lemma 3.2 and using Theorem A.4, we obtain the existence of  $(U, V)(\xi)$  when  $c = c_0 + \epsilon_1$ , which implies the linear selection of (4.1). Then, a limiting argument can show that the linear selection is realized when  $a \in \bar{M}(c_0, \lambda_0)$  and  $\rho \leq 2\epsilon\lambda_0^2 + \sigma\bar{a}$ . This completes the proof.  $\square$

*Remark 4.3.* If  $h_{c_0}(a) = 0$  has no solution when  $a > 0$ , then the above theorem still holds by replacing  $S'_1 = \phi$  where  $\phi$  is the empty set.

Since the minimal wave speed is always linearly selected when  $\rho \leq 1$ , the following corollary is immediately implied.

**COROLLARY 4.4.** *Let (H1) be true. The minimal wave speed is linearly selected if  $a \in \bar{M}(c_0, \lambda_0)$  and*

$$(4.9) \quad \rho \leq \max\{\sigma\bar{a} + 2\epsilon\lambda_0^2, 1\}.$$

For the nonlinear selection, we first give the following theorem.

**THEOREM 4.5.** *Let the assumption (H1) hold and*

$$\underline{M}(c_0, \lambda_0) := (\underline{M}_1 \cup \underline{M}_2 \cup \underline{M}_3 \cup \underline{M}_4) \cap \{a : a > 0\},$$

where

$$\begin{cases} \underline{M}_1 := S_1(c_0, \lambda_0) \cap S_3(c_0, \lambda_0) \cap S_4(c_0, \lambda_0), & \underline{M}_2 := S_1(c_0, \lambda_0) \cap S'_3(c_0, \lambda_0) \cap S_4(c_0, \lambda_0), \\ \underline{M}_3 := S_1(c_0, \lambda_0) \cap S_3(c_0, \lambda_0) \cap S'_4(c_0, \lambda_0), & \underline{M}_4 := S_1(c_0, \lambda_0) \cap S'_3(c_0, \lambda_0) \cap S'_4(c_0, \lambda_0). \end{cases}$$

Then the nonlinear selection is realized if there exists  $a \in \underline{M}$  and

$$(4.10) \quad \rho > \sigma\underline{a} + 2\epsilon\lambda_0^2, \text{ where } \underline{a} = \inf \underline{M} > 0.$$

*Proof.* When  $c = c_0 + \epsilon_2$ , let  $\underline{V}$  be defined in (3.9) with  $m = 1$  and  $k_v = 1$ , and

$$\underline{U} = \underline{V}[A_1(c) + b\underline{V} + a\underline{V}^2], \quad a > 0,$$

with  $b = \frac{\mu}{\sigma} - A_1(c) - a$  and  $a$  to be determined. For simplicity, we will denote  $\lambda_2 = \lambda_2(c)$  and  $A_1 = A_1(c)$  unless otherwise specified. With the help of calculations done in Theorem 4.2, we can relatively easily derive the following formulas for  $L_1$ :

$$(4.11) \quad L_1(\underline{U}, \underline{V}) = \underline{V}^2(1 - \underline{V})G_2(\underline{V}),$$

where

$$\begin{aligned} G_2(\underline{V}) = & -12d\lambda_2^2 a \underline{V}^2 + 3\lambda_2 \underline{V} \left[ (5d\lambda_2 - (c - \alpha))a - 2d\lambda_2 \left( \frac{\mu}{\sigma} - A_1 \right) \right] \\ & + a [-4d\lambda_2^2 + 2\lambda_2(c - \alpha) + \sigma] + d\lambda_2^2 \left( \frac{4\mu}{\sigma} - 6A_1 \right) - 2\lambda_2(c - \alpha) \left( \frac{\mu}{\sigma} - A_1 \right). \end{aligned}$$

Notice that  $G_2(V)$  is a parabolic function in  $V$ . Through a similar analysis on its determinant done in Theorem 4.2, we obtain that  $G_2(V) = 0$  has solutions when  $a \in S_1(c, \lambda_2)$ . Under this condition, the inequalities  $G_2(0) \geq 0$  and  $G_2(1) \geq 0$  ensure  $L_1 \geq 0$ . That means

$$G_2(0) = a [-4d\lambda_2^2 + 2\lambda_2(c - \alpha) + \sigma] + d\lambda_2^2 \left( \frac{4\mu}{\sigma} - 6A_1 \right) - 2\lambda_2(c - \alpha) \left( \frac{\mu}{\sigma} - A_1 \right) \geq 0$$

and

$$G_2(1) = a [-d\lambda_2^2 - \lambda_2(c - \alpha) + \sigma] - 2 \left[ d\lambda_2^2 \frac{\mu}{\sigma} + \lambda_2(c - \alpha) \left( \frac{\mu}{\sigma} - A_1 \right) \right] \geq 0.$$

Depending on the sign of  $-4d\lambda_2^2 + 2\lambda_2(c - \alpha) + \sigma$  and  $-d\lambda_2^2 - \lambda_2(c - \alpha) + \sigma$ , we have four cases. Since the analyses on those four cases are similar, we only present the case when  $-4d\lambda_2^2 + 2\lambda_2(c - \alpha) + \sigma > 0$  and  $-d\lambda_2^2 - \lambda_2(c - \alpha) + \sigma > 0$  in detail. Under this condition,

$$a \geq \frac{d\lambda_2^2 \left( \frac{4\mu}{\sigma} - 6A_1 \right) - 2\lambda_2(c - \alpha) \left( \frac{\mu}{\sigma} - A_1 \right)}{4d\lambda_2^2 - 2\lambda_2(c - \alpha) - \sigma} \quad \text{and} \quad a \geq \frac{2 \left[ d\lambda_2^2 \frac{\mu}{\sigma} + \lambda_2(c - \alpha) \left( \frac{\mu}{\sigma} - A_1 \right) \right]}{-d\lambda_2^2 - \lambda_2(c - \alpha) + \sigma}.$$

That means if  $a \in S'_3(c, \lambda_2) \cap S'_4(c, \lambda_2) \cap S_1(c, \lambda_2)$ , then  $L_1(\underline{U}, \underline{V}) \geq 0$ . In other words, when  $a \in \underline{M}_3(c, \lambda_2)$ , we have  $L_1(\underline{U}, \underline{V}) \geq 0$ .

For the  $V$ -equation, we obtain

$$L_2(\underline{U}, \underline{V}) = \underline{V}^2(1 - \underline{V})J_{\lambda_2}(\underline{V}) = \underline{V}^2(1 - \underline{V})(-2\epsilon\lambda_2^2 - \sigma a + \rho).$$

It is easy to see that if the strict inequality (4.10) holds, then  $\rho > \sigma \underline{a} + 2\epsilon\lambda_2^2$  with  $\underline{a} = \inf \underline{M}$ , which means  $L_2(\underline{U}, \underline{V}) > 0$ . Therefore, we have found a pair of lower solutions with the faster decay rate. If we take  $k_v = 1 - \eta$  for sufficiently small  $\eta$ , by continuity, the above derivation is still true. By Theorem 3.4, the nonlinear selection is realized.  $\square$

Since the ratio  $\frac{U}{V}$  has a parabolic behavior as shown in the right panel in Figure 3, we can give another approach to find conditions for the nonlinear selection.

**THEOREM 4.6.** *Let  $\kappa = \frac{A_1(c_0)}{\frac{\mu}{\sigma} + A_1(c_0)}$ . Suppose that*

$$(4.12) \quad \begin{cases} 2\lambda_0(c_0 - \alpha)A_1(c_0) + \mu - 6d\lambda_0^2 A_1(c_0) > 0, \\ \sigma A_1(c_0) + 2\mu + 2\lambda_0(c_0 - \alpha)A_1(c_0) > 0, \\ -6d\lambda_0^2 A_1^2(c_0) + 2A_1(c_0) \left( \frac{\mu}{\sigma} + A_1(c_0) \right) (2d\lambda_0^2 - \lambda_0(c_0 - \alpha)) + \sigma \left( \frac{\mu}{\sigma} + A_1(c_0) \right)^2 > 0, \\ -2d\lambda_0^2 - 2\lambda_0(c_0 - \alpha) + \sigma > 0. \end{cases}$$

*Then the minimal wave speed of system (4.1) is nonlinearly selected if*

$$(4.13) \quad \rho > 2\epsilon\lambda_0^2 + \frac{\mu\kappa}{1 - \kappa},$$

*where  $A_1(c_0)$  and  $\lambda_0$  are as defined in (2.10) and Lemma 2.2, respectively.*

*Proof.* When  $c = c_0 + \epsilon_3$  with  $\epsilon_3 > 0$  being small, let  $\underline{V}$  be as defined in (3.9) with  $m = 1$  and  $k_v = 1$ . Define

$$\underline{U} = \underline{V} \cdot \max_{\xi \in \mathbb{R}} \left\{ A_1(c)(1 - \underline{V}), \frac{\mu}{\sigma} \underline{V} \right\} = \begin{cases} A_1(c)(1 - \underline{V})\underline{V}, & \xi \geq \xi_2, \\ \frac{\mu}{\sigma k_v} \underline{V}^2, & \xi < \xi_2, \end{cases}$$

where  $\xi_2 \in \mathbb{R}$  such that  $\underline{V}(\xi_2) = \frac{A_1(c)}{A_1(c) + \frac{\mu}{\sigma}}$ . Thus, by substituting them into  $L_1$  and  $L_2$ , we obtain

$$L_1(\underline{U}, \underline{V}) = \begin{cases} \underline{V}^2 \left\{ -6d\lambda_2^2 A_1 \underline{V}^2 + \underline{V} [12d\lambda_2^2 A_1 - 2\lambda_2(c - \alpha)A_1] + 2\lambda_2(c - \alpha)A_1 + \mu - 6d\lambda_2^2 A_1 \right\}, & \underline{V} \in [0, \underline{V}(\xi_2)], \\ \frac{\mu}{\sigma} \underline{V}(1 - \underline{V}) \left\{ -6d\lambda_2^2 \underline{V}^2 + \underline{V} [4d\lambda_2^2 - 2\lambda_2(c - \alpha)] + \sigma \right\}, & \underline{V} \in (\underline{V}(\xi_2), 1], \end{cases}$$

and

$$L_2(\underline{U}, \underline{V}) = \begin{cases} \underline{V}^2(1 - \underline{V}) \left\{ -2\epsilon\lambda_2^2 + \frac{-\mu}{1-\underline{V}} + \rho \right\}, & \underline{V} \in [0, \underline{V}(\xi_2)], \\ \frac{\mu}{\sigma} \underline{V}^2(1 - \underline{V}) \left\{ -2\epsilon\lambda_2^2 + \frac{-\sigma A_1}{\underline{V}} + \rho \right\}, & \underline{V} \in (\underline{V}(\xi_2), 1]. \end{cases}$$

For the  $L_1$  part, let  $G_3(\underline{V}) := -6d\lambda_2^2 A_1 \underline{V}^2 + \underline{V} [12d\lambda_2^2 A_1 - 2\lambda_2(c - \alpha)A_1] + 2\lambda_2(c - \alpha)A_1 + \mu - 6d\lambda_2^2 A_1$ , which is a quadratic function in  $\underline{V}$ . The first inequality in (4.12) implies that  $G_3(0) \geq 0$ , and

$$G_3(\underline{V}(\xi_2)) = \frac{\mu^2 (-6d\lambda_2^2 A_1 + 2\lambda_2(c - \alpha)A_1 + \mu) + \mu\sigma A_1 (2\lambda_2(c - \alpha)A_1 + \sigma A_1 + 2\mu)}{(\mu + \sigma A_1)^2} \geq 0$$

provided by the first and second inequalities. Therefore,  $G_3(\underline{V}) \geq 0$  for  $\underline{V} \in [0, \underline{V}(\xi_2)]$ . Then, denote  $G_4(\underline{V}) := -6d\lambda_2^2 \underline{V}^2 + \underline{V} [4d\lambda_2^2 - 2\lambda_2(c - \alpha)] + \sigma$ , which is convex down in  $\underline{V}$ . Thus, it suffices to find the values of  $G_4(\underline{V}(\xi_2))$  and  $G_4(1)$ . Through a direct computation and the third and fourth inequalities in (4.12), we obtain that  $G_4(1) = -2d\lambda_2^2 - 2\lambda_2(c - \alpha) + \sigma \geq 0$  and

$$G_4(\underline{V}(\xi_2)) = \frac{-6d\lambda_2^2 A_1^2}{\left(\frac{\mu}{\sigma} + A_1\right)^2} + \frac{A_1 [4d\lambda_2^2 - 2\lambda_2(c - \alpha)]}{\left(\frac{\mu}{\sigma} + A_1\right)} + \sigma \geq 0.$$

As for the  $L_2$  part, it is not difficult to verify that  $L_2(\underline{U}, \underline{V}) \geq 0$  if  $\rho \geq 2\epsilon\lambda_2^2 + \frac{\mu}{1-\underline{V}(\xi_2)}$  when  $\xi \geq \xi_2$ , and  $\rho \geq 2\epsilon\lambda_2^2 + \frac{\sigma A_1}{\underline{V}(\xi_2)}$  when  $\xi < \xi_2$ . Notice that  $\frac{\sigma A_1}{\underline{V}(\xi_2)} = \frac{\mu}{1-\underline{V}(\xi_2)}$ . When  $\epsilon_3$  is small enough, (4.13) implies that if  $\rho \geq 2\epsilon\lambda_2^2 + \frac{\mu}{1-\underline{V}(\xi_2)}$ , then  $L_2(\underline{U}, \underline{V}) \geq 0$  for  $\xi \in \mathbb{R}$ . Thus, the nonlinear selection result follows.  $\square$

*Remark 4.7.* In this application, we only present conditions for the speed selection when  $m = 1$ . In fact, if  $m = 2$  (the derivation is much more complicated), we can obtain the following result.

**THEOREM 4.8.** *Let*

$$F_{c_0}(a) := a^2 [469d^2 \lambda_0^4 + 135d\lambda_0^3(c_0 - \alpha)] - a [128d^2 \lambda_0^4 \frac{\mu}{\sigma} + 7d^2 \lambda_0^4 A_1(c_0)] + 64d^2 \lambda_0^4 \left(\frac{\mu}{\sigma} - A_1(c_0)\right)^2, \quad (4.14)$$

and  $F_{c_0}(a) = 0$  has two roots  $0 < a_m(c_0) < a_M(c_0)$  with  $A_1(c_0)$  and  $\lambda_0$  being defined in (2.10) and Lemma 2.2, respectively. Assume that

$$4d\lambda_0^2 - 2\lambda_0(c_0 - \alpha) - \sigma > 0. \quad (4.15)$$

Then the system (4.1) is linearly selected if

$$\rho \leq 1 + \sigma A_1(c_0) - \mu + \sigma a_M(c_0). \quad (4.16)$$

We omit the proof, since it is similar to the previous one. Later, we will demonstrate a numerical example (the first one) in which the result in the choice of  $m = 2$  may be better than that in the choice of  $m = 1$  when  $4d\lambda_0^2 - 2\lambda_0(c_0 - \alpha) - \sigma > 0$ .

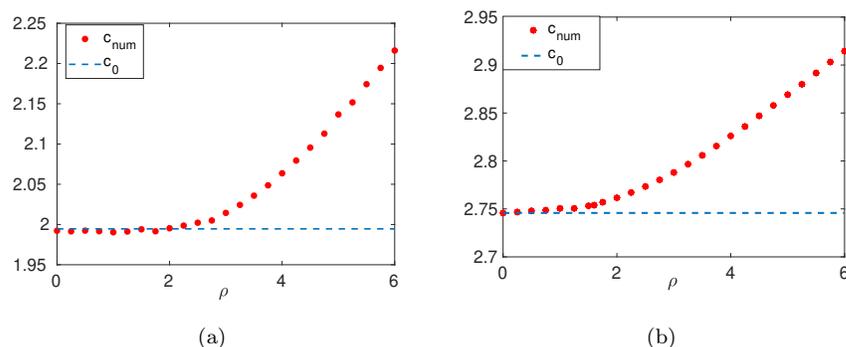


FIG. 4. (Color online.) The relation between the spreading speed and  $\rho$ . (a) This figure is depicted when  $d = 3$ ,  $\epsilon = 0.1$ ,  $\sigma = 3$ ,  $\mu = 1$ , and  $\alpha = 1$ . Here,  $c_0 = 1.9945625$ . (b) This figure is depicted when  $d = 2$ ,  $\epsilon = 0.2$ ,  $\mu = 3$ ,  $\sigma = 1$ , and  $\alpha = 2$ . Here,  $c_0 = 2.7458$ .

To complete this section, we provide two numerical examples to manifest our theoretical results. In the first example, we choose the parameter set as  $d = 3$ ,  $\epsilon = 0.1$ ,  $\mu = 1$ ,  $\sigma = 3$ , and  $\alpha = 1$ . In this set, we find that  $c_0 = 1.9946$ ,  $\lambda_0 = 0.6906$ , and  $A_1 = 0.4433$ . Then, by a simple computation, we obtain that  $4d\lambda_0^2 - 2\lambda_0(c_0 - \alpha) - \sigma = 1.3495 > 0$ ,  $5d\lambda_0 - (c_0 - \alpha) = 9.36444 > 0$ ,  $a_3 = -0.0486$ , and  $a_4 = -1.2942$ . Through Theorem 4.2 and its corollary, the linear selection result is only valid if  $\rho \leq 1$ , but Theorem 4.8 can show an improvement. We find that  $F_{c_0}(a) = 0$  has two solutions  $a_m = 0.0231$  and  $a_M = 0.0626$ . Thus, by Theorem 4.8, the system under this parameter set is linearly selected when  $\rho \leq 1.5175$ . To find numerical speeds  $c_{\text{num}}$  corresponding to different values of  $\rho$ , we use the MATLAB software to compute the solution of (1.3), where the initial conditions are

$$(4.17) \quad u(x, 0) = \frac{\frac{\mu}{\sigma}}{1 + e^{10x}} \quad \text{and} \quad v(x, 0) = \frac{1}{1 + e^{10x}}$$

such that they are steep enough to be close to the step functions. By [6, 18], the spreading speed of solutions with such initial data will evolve to  $c_{\text{min}}$ , so our numerically computed  $c_{\text{num}}$ , obtained from the level set of the solution, would give an approximation to the minimal wave speed. The values of numerically computed speed are shown in Figure 4(a). As we can see, the critical value for  $\rho$  is  $\bar{\rho} \simeq 2.2$ . Furthermore, this result illustrates our theoretical results.

In the second example, we fix  $d = 2$ ,  $\epsilon = 0.2$ ,  $\mu = 3$ ,  $\sigma = 1$ , and  $\alpha = 2$ . Under this choice of parameters, we can find that  $c_0 = 2.7458$ ,  $\lambda_0 = 0.3947$ , and  $A_1 = 3.0526$ . Through a direct computation, it follows that  $4d\lambda_0^2 - 2\lambda_0(c_0 - \alpha) - \sigma = -0.3424$ ,  $5d\lambda_0 - (c_0 - \alpha) = 3.2012$ ,  $-d\lambda_0^2 - \lambda_0(c_0 - \alpha) + \sigma = 0.3941$ ,  $a_3 = -0.0259$ ,  $a_4 = 5.6567$ , and  $a_5 = 4.6653$ . Moreover,  $h_{c_0} = 0$  has two solutions  $a_1 = 0.0003$  and  $a_2 = 1.4477$ . Thus, (4.1) is linearly selected if  $a \in [a_1, a_2]$  and  $\rho \leq \sigma a_2 + 2\epsilon\lambda_0^2 = 1.51$  by Theorem 4.2. As for the nonlinear selection, by Theorem 4.5, we obtain that the nonlinear selection is realized if  $a \geq a_4 = 5.6567$  and  $\rho > 5.7190$ . By applying the same method in the first example, the numerical speeds (spreading speeds) are obtained and shown in Figure 4(b). As we can see in the figure,  $\bar{\rho} \simeq 1.6$ , which confirms our theoretical result.

*Remark 4.9.* Finally, we would like to emphasize that the model here is com-

pletely different from the diffusive Lotka–Volterra competition system in [1, 2], where two species compete for the same resource. Here, we study a significant model describing a species in two different compartments or stages. The Allee effect appears in this model, while we cannot see this in [1, 2]. We focus here on how the spreading speed is impacted by the Allee strength. Furthermore, in [1, 2], the linearized system at  $(0, 0)$  is decoupled so that the linear speed is given by a simple formula  $c_0 = 2\sqrt{1 - a_1}$ . For the construction of upper or lower solutions to the system, we can take  $V = kU$  for different values of  $k$ , or we can assume that  $V$  admits different decay behavior than  $U$ . For the stream population model in this paper, the linear system at  $(0, 0)$  is irreducible and the linear speed is determined by an order-4 polynomial. No explicit formula  $c_0$  can be obtained. To determine the spreading speed (the minimal speed), our numerical simulation indicates that the graph of  $U/V$  looks like a vertical parabola. This provides us insight to construct novel solution pairs with  $U/V = aV^2 + bV + c$ .

**5. Conclusion.** In this paper, we investigated the speed selection mechanism (linear and nonlinear) via the upper and lower solutions method for traveling waves to a reaction-advection-diffusion model (1.3).

For this stream-population model, we focus on how the spreading speed is impacted by the Allee effect. Here, the so-called asymptotic spreading speed (which represents a critical value of biological invasion) coincides with the minimal speed  $c_{\min}$  of the traveling waves. However, its value is usually difficult to determine. We consider the case when the system is modeled with a weak Allee effect [15], i.e., with a growth function as  $f(v) = v(1 - v)(1 + \rho v)$ . For such a growth function, when  $\rho > 1$  (i.e.,  $f(v) > f'(0)v$  when  $v \in [0, 1]$ ), the per capita growth rate ( $f(v)/v$ ) of this species attains its maximum at an intermediate population size. The strength of the Allee effect increases in the parameter  $\rho$ . When  $\rho = 0$ , it reduces to the classical logistic growth. We are successful in establishing the relation between the spreading speed and the Allee effect. We also have proved that there exists a threshold value (a critical number)  $\bar{\rho}$  to divide the speed selection. Specifically, our theoretical and numerical results show that the spreading speed is an increasing function of  $\rho$ . Given values of  $\mu$ ,  $\sigma$ ,  $\alpha$ ,  $\epsilon$ , and  $d$  (through experiments), we can compute the linear speed  $c_0$  and further estimate the threshold value  $\bar{\rho}$  with analytic formulas.

In the novel construction of upper and lower solutions for the speed selection, we should emphasize that the parabolic formula for  $\frac{U}{V}$  in terms of  $V$  is entirely new and totally different from the formula given in [1, 2] (where they only assumed a linear relation, i.e.,  $\frac{U}{V} = k$ , and this idea does not work here). By this technique, we successfully establish explicit conditions for both the linear and the nonlinear selections: see Theorems 4.2 ( $m = 1$ ) and 4.8 ( $m = 2$ ) for the linear selection and Theorems 4.5–4.6 for the nonlinear selection.

We should also mention that all the coefficients of our main model are constant, but this is not essential in our method and idea. It can be interestingly extended to a more general case, such as where all the coefficients are time-periodic functions, and even with periodic habitats. Efforts on these aspects are currently in progress and will be presented in future publications.

**Appendix A.** In this appendix, we will show the upper and lower solutions method in detail. This method is originated in [5, 17] and used to prove the existence of monotone traveling wave solutions to partial differential equations. In the meantime, we can also apply it to derive the linear speed selection.

Let  $\bar{M}_1$  be a sufficiently large positive number so that

$$F(U, V) = \sigma U - \mu V + f(V) + MV$$

is monotone in  $V$ . Then the wave equations in (1.5) are equivalent to

$$(A.1) \quad \begin{cases} dU'' + (c - \alpha)U' - \sigma U = -\mu V, \\ \epsilon V'' + cV' - MV = -F(U, V). \end{cases}$$

For the first equation, we have already solved it by (3.1). For the second equation, when  $\epsilon > 0$ , the integral form is given by

$$(A.2) \quad V(\xi) = \frac{1}{\epsilon(\gamma_2 - \gamma_1)} \left\{ \int_{-\infty}^{\xi} e^{\gamma_1(\xi-s)} F(U(s), V(s)) ds + \int_{\xi}^{+\infty} e^{\gamma_2(\xi-s)} F(U(s), V(s)) ds \right\} =: T_2(U, V),$$

where

$$(A.3) \quad \gamma_1 = \frac{c - \sqrt{c^2 + 4\epsilon M}}{2\epsilon} < 0 < \gamma_2 = \frac{c + \sqrt{c^2 + 4\epsilon M}}{2\epsilon}.$$

When  $\epsilon = 0$ ,

$$(A.4) \quad V(\xi) = \frac{1}{c} \int_{\xi}^{+\infty} e^{\frac{M}{c}(\xi-s)} F(U(s), V(s)) ds =: T_2(U, V).$$

Thus, the system (A.1) in an integral form reads

$$(A.5) \quad \begin{cases} U(\xi) = H(V) = T_1(U, V), \\ V(\xi) = T_2(U, V), \end{cases}$$

where  $H(V)$  is defined by (3.1) and  $T_2(U, V)$  is defined by (A.2) when  $\epsilon > 0$  or (A.4) when  $\epsilon = 0$ . Then, with the integral form, we can define an upper (or a lower) solution.

**DEFINITION A.1.** *A pair of continuous functions  $(U, V)(\xi)$  is an upper (a lower) solution to the integral system (A.5) if*

$$\begin{cases} U(\xi) \geq (\leq) T_1(U, V)(\xi), \\ V(\xi) \geq (\leq) T_2(U, V)(\xi). \end{cases}$$

Since the above integral forms are not practical in finding upper or lower solutions, we then give inequalities in terms of differential equations themselves that imply Definition A.1 in the following lemma.

**LEMMA A.2.** *A pair of continuous functions  $(U, V)(\xi)$  which is differentiable on  $\mathbb{R}$  except at finite numbers of points  $\xi_i$ ,  $i = 1, \dots, n$ , and satisfies*

$$\begin{cases} dU'' + (c - \alpha)U' - \sigma U + \mu V \leq 0, \\ \epsilon V'' + cV' + \sigma U - \mu V + f(V)V \leq 0 \end{cases}$$

for  $\xi \neq \xi_i$  and  $(U', V')(\xi_i^-) \geq (U', V')(\xi_i^+)$  for all  $\xi_i$  is an upper solution to the integral system (A.5). A lower solution can be defined by reversing all the inequalities.

*Proof.* We give a proof for the upper solution, while a similar argument can be applied for the lower solution. From the above inequalities, we have

$$(A.6) \quad T_1(U, V)(\xi) = \frac{\mu}{d(\tau_2 - \tau_1)} \left\{ \int_{-\infty}^{\xi} e^{\tau_1(\xi-s)} V(s) ds + \int_{\xi}^{\infty} e^{\tau_2(\xi-s)} V(s) ds \right\} \\ \leq \frac{-\mu}{d(\tau_2 - \tau_1)} \left\{ \int_{-\infty}^{\xi} e^{\tau_1(\xi-s)} (dU'' + (c - \alpha)U' - \sigma U)(s) ds \right. \\ \left. + \int_{\xi}^{\infty} e^{\tau_2(\xi-s)} (dU'' + (c - \alpha)U' - \sigma U)(s) ds \right\}.$$

By a similar calculation to that of [10, proof of Lemma 2.5], we can show that

$$T_1(U, V)(\xi) \leq U(\xi).$$

The same result holds for  $T_2(U, V)(\xi) \leq V(\xi)$ . This implies that  $(U, V)(\xi)$  is an upper solution to the system (A.5). The proof for the lower solution is the same and so is omitted.  $\square$

To move on to the upper and lower solutions method, we first assume the following hypothesis.

**HYPOTHESIS A.3.** For a given  $c > c_0$ , assume there exist a monotone non-increasing upper solution  $(\bar{U}, \bar{V})(\xi)$  and a nonzero lower solution  $(\underline{U}, \underline{V})(\xi)$  to the system (A.5) with the following properties:

- (1)  $(\underline{U}, \underline{V})(\xi) \leq (\bar{U}, \bar{V})(\xi)$  for all  $\xi \in \mathbb{R}$ ;
- (2)  $(\bar{U}, \bar{V})(+\infty) = (0, 0)$  and  $(\bar{U}, \bar{V})(-\infty) = (\bar{k}_1, \bar{k}_2)$ ;
- (3)  $(\underline{U}, \underline{V})(+\infty) = (0, 0)$  and  $(\underline{U}, \underline{V})(-\infty) = (\underline{k}_1, \underline{k}_2)$  for  $(0, 0) \leq (\underline{k}_1, \underline{k}_2) \leq (\frac{\mu}{\sigma}, 1)$  and  $(\bar{k}_1, \bar{k}_2) \geq (\frac{\mu}{\sigma}, 1)$  so that no other equilibrium solution to (1.5) exists in the set  $\{(U, V) | (0, 0) \leq (U, V) \leq (\bar{k}_1, \bar{k}_2)\}$ .

Then, under the conditions of the above hypothesis, we can define an iteration scheme as

$$(A.7) \quad \begin{cases} (U_0, V_0) = (\bar{U}, \bar{V}), \\ U_{n+1} = T_1(U_n, V_n), \quad n = 0, 1, 2, \dots, \\ U_{n+1} = T_1(U_n, V_n), \quad n = 0, 1, 2, \dots \end{cases}$$

At last, by the results in [5, 17], we can arrive at the following theorem, which shows that the existence of an upper solution and a lower solution indicates the existence of the actual solution.

**THEOREM A.4.** If Hypothesis A.3 is true, then the iteration scheme (A.7) converges to a pair of nonincreasing functions  $(U, V)(\xi)$ , which is a solution to the system (1.5) with  $(U, V)(+\infty) = (0, 0)$  and  $(U, V)(-\infty) = (\frac{\mu}{\sigma}, 1)$ . Moreover,  $(\underline{U}, \underline{V})(\xi) \leq (U, V)(\xi) \leq (\bar{U}, \bar{V})(\xi)$  for all  $\xi \in \mathbb{R}$ .

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