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Bistable wave speed of the Lotka-Volterra competition model

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ABSTRACT
This work deals with the speed sign of travelling waves to the Lotka-Volterra model with diffusion and bistable nonlinearity. We obtain new conditions for the determinacy of the sign of the bistable wave speed by constructing upper or lower solutions with an inside parameter to be adjusted. The established conditions improve or supplement the results in the references and give insight into the combined effect of system parameters on the propagation direction of the bistable wave.

1. Introduction

We study the diffusive Lotka-Volterra competitive model

$$\phi_t = d_1\phi_{xx} + r_1\phi(1 - b_1\phi - a_1\varphi),$$
$$\varphi_t = d_2\varphi_{xx} + r_2\varphi(1 - a_2\phi - b_2\varphi), \tag{1}$$

where $\phi(x, t)$ and $\varphi(x, t)$ are the population densities at time t and spatial coordinate x of species ϕ and φ, respectively; d_i, r_i, a_i and $b_i, i = 1, 2$ are positive constants. Among them, d_1 and d_2 denote diffusion coefficients, r_1 and r_2 represent net birth rates, and $1/b_1$ and $1/b_2$ are carrying capacities of ϕ and φ, respectively. a_1 and a_2 measure competition strength of φ and ϕ, respectively. For the biological interpretation of this model, we refer the reader to [16,18]. By selecting dimensionless variables

$$\bar{x} = \sqrt{r_1/d_1}x, \quad \bar{t} = r_1t, \quad \bar{\phi} = b_1\phi, \quad \bar{\psi} = b_2\psi,$$

we rewrite (1) in a dimensionless form and drop the upper bars on the variables to have a new system below

$$\phi_t = \phi_{xx} + \phi(1 - \phi - a_1\varphi),$$
$$\varphi_t = d\varphi_{xx} + r\varphi(1 - a_2\phi - \varphi), \tag{2}$$

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where

$$d = d_2/d_1, \quad r = r_2/r_1, \quad a_1/b_2 \overset{\text{def}}{=} a_1, \quad a_2/b_1 \overset{\text{def}}{=} a_2. \tag{3}$$

Moreover, by setting $u = \phi$ and $v = 1 - \varphi$, we have a cooperative system of the form

$$\begin{aligned} u_t &= u_{xx} + u(1 - a_1 - u + a_1 v), \\ v_t &= d v_{xx} + r(1 - v)(a_2 u - v) \end{aligned} \tag{4}$$

with initial data

$$u(x, 0) = \phi(x, 0), \quad v(x, 0) = 1 - \varphi(x, 0), \quad \forall x \in \mathbb{R}.$$

Obviously, system (4) is monotone with respect to initial data in the phase space $C(R, R^+) \times C(R, R^+)$.

In the monostable case (i.e. $0 < a_1 < 1 < a_2$), travelling wave solutions of system (4) have been extensively investigated, for example, see [1,2,6–9–10,12,14,15,18–20] and the references therein; while for the bistable case where

$$a_1 > 1 \quad \text{and} \quad a_2 > 1, \tag{5}$$

the travelling wavefront for this model has been studied in [3–5,11,13]. Particularly, the existence and stability was discussed in Conley and Gardner [3] and Gardner [4], and the uniqueness and parameter dependence of the bistable wave speed was proved in Kanon [13]. Recently, Ma *et al.* in [17] investigated the sign of the bistable wave speed. They proved that the bistable speed is bounded via the spreading speeds of monostable travelling waves induced by the system (2), established comparison theorems on wave speed, obtained explicit conditions for determining the wave speed sign, and derived an identity

$$c(d, r, a_1, a_2) = -\sqrt{dr}\, c\left(\frac{1}{d}, \frac{1}{r}, a_2, a_1\right). \tag{6}$$

Based on these results, they established new theorems on several cases (including the cases where a_1 or a_2 is close to 1) that could not be dealt with in [5] or [12].

Due to the assumption (5), system (4) has four non-negative constant equilibria

$$\mathbf{o} = (0, 0), \quad \alpha_1 = (0, 1), \quad \alpha_2 = \left(\frac{a_1 - 1}{a_1 a_2 - 1}, \frac{a_2(a_1 - 1)}{a_1 a_2 - 1}\right) \quad \text{and} \quad \beta = (1, 1).$$

Furthermore, for the kinetic system

$$\begin{aligned} u' &= u(1 - a_1 - u + a_1 v), \\ v' &= r(1 - v)(a_2 u - v), \end{aligned} \tag{7}$$

equilibria $\mathbf{o}$ and β are stable, while α_1 and α_2 are unstable. *A bistable travelling wave solution* of (4), which connects $\mathbf{o}$ to β, is given by

$$\begin{aligned} &u(x, t) = U(z), \ v(x, t) = V(z), \ z = x + ct, \\ &(U, V)(-\infty) = \mathbf{o}, \ (U, V)(\infty) = \beta, \end{aligned} \tag{8}$$

where (U, V) is called the wavefront, z is the wave variable and $c \in \mathbb{R}$ is called *the bistable wave speed*. The wave profile $(U, V)(z)$ satisfies the following system of ordinary differential

equations:

$$U'' - cU' + U(1 - a_1 - U + a_1 V) = 0,$$
$$dV'' - cV' + r(1 - V)(a_2 U - V) = 0.$$

(9)

The sign of the bistable wave speed indicates the propagation direction of the bistable travelling wave solution. Hence it predicts which stable state has an advantage over another one and thus the outcome of competition between two species. Specifically, for model (2), if $c > 0$, then the bistable travelling wave spreads to the left, and the species ϕ will be the winner; otherwise, the species φ will win the competition. In [17], the authors obtained the following explicit conditions for the speed sign of the bistable travelling wave.

Lemma 1.1 (Theorems 4.1–4.4 in [17]): *Let the parameters a_1, a_2, d and r be fixed. Then the bistable wave speed of* (4) *is positive provided that one of the following conditions is satisfied*:

(P_1) $1 < da_1/d - r(a_2 - 1) < 2(a_2 - 1)/a_2$;
(P_2) $(r + d(a_1 - 1))/ra_2 < 3 - 2a_1$.

  The bistable wave speed of (4) *is negative if one of the following statements is true*:

(N_1) $1 < a_2 r/(r - d(a_1 - 1)) < 2(a_1 - 1)/a_1$;
(N_2) $a_1 > 5/3$, $1 < a_2 < 2$, *and either*

$$\frac{d(a_1 - 1)}{4} < r < \frac{d(a_1 - 1)}{2a_2},$$

(10)

  or

$$\frac{d(a_1 - 1)}{2a_2} < r < \frac{d(a_1 - 1)}{4(a_2 - 1)}.$$

(11)

  The purpose of this paper is to improve or supplement the results established in [17] by way of constructing novel upper or lower solutions and developing analytical techniques. Our presentation of this effort to determine the sign of the bistable wave speed can be summarized as follows: In Section 2, we introduce definitions, lemmas and decay rates at infinity of the bistable travelling wave which will be used later. Our main results and their proofs are presented in Section 3. Conclusion and discussion of how our results improve and perfect Lemma 1.1 are given in Section 4.

2. Preliminaries

We first give the definitions of upper solutions and lower solutions of system (9).

Definition 2.1: A pair of continuous functions $(U(z), V(z))$ is an upper solution to system (9) means that $(U(z), V(z))$ is twice-differentiable on $\mathbb{R}$ except at finite number of

points z_i, $i = 1, \ldots, n$ and satisfies

$$
\begin{aligned}
U'' - cU' + U(1 - a_1 - U + a_1 V) \leq 0, \quad U(-\infty) \geq 0, U(\infty) \geq 1, \\
dV'' - cV' + r(1 - V)(a_2 U - V) \leq 0, \quad V(-\infty) \geq 0, V(\infty) \geq 1,
\end{aligned}
\tag{12}
$$

for $z \neq z_i$, and $U'_-(z_i) \geq U'_+(z_i)$ and $V'_-(z_i) \geq V'_+(z_i)$ for all z_i.

A lower solution to system (9) can be defined by reversing all the above inequality signs.

The following two comparison theorems on the wave speed to system (9) were proved in [17].

Lemma 2.2 (Theorem 3.1 in [17]): *If system* (9) *has a non-negative and non-decreasing upper solution* $(\overline{U}(z), \overline{V}(z))$ *with speed* $\overline{c} < 0$, *satisfying*

$$
(\overline{U}, \overline{V})(-\infty) < (1, 1), \quad (\overline{U}, \overline{V})(\infty) \geq (1, 1),
$$

then the wave speed of the bistable travelling wave solution of (4) *is negative, i.e.*

$$
c \leq \overline{c} < 0.
\tag{13}
$$

Lemma 2.3 (Theorem 3.2 in [17]): *If system* (9) *has a non-negative and non-decreasing lower solution* $(\underline{U}, \underline{V})(x + ct)$ *with speed* $\underline{c} > 0$, *satisfying*

$$
(\underline{U}, \underline{V})(-\infty) = (0, 0) < (\underline{U}, \underline{V})(\infty) \leq (1, 1),
$$

then the wave speed of the bistable travelling wave solution of (4) *is positive, i.e.*

$$
c \geq \underline{c} > 0.
\tag{14}
$$

In order to look for upper/lower solutions of system (9) in the shape of the bistable travelling wave, we compute the decay rate μ of the bistable travelling wave as $z \to -\infty$ by linearizing system (4) at the equilibrium $\mathbf{o}$. Then μ satisfies characteristic equation

$$
\mu^2 - c\mu + (1 - a_1) = 0,
$$

which has two roots

$$
\mu_1 = \frac{c + \sqrt{c^2 + 4(a_1 - 1)}}{2} \overset{\text{def}}{=} \mu_1(c) > 0 \quad \text{and}
$$

$$
\mu_2 = \frac{c - \sqrt{c^2 + 4(a_1 - 1)}}{2} \overset{\text{def}}{=} \mu_2(c) < 0.
\tag{15}
$$

Similarly, the decay rate μ of the bistable travelling wave near β as $z \to \infty$ satisfies the characteristic equation

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

which has solutions

$$
\mu_3 = \frac{-c - \sqrt{c^2 + 4dr(a_2 - 1)}}{2d} \overset{\text{def}}{=} \mu_3(c) < 0 \quad \text{and}
$$

$$
\mu_4 = \frac{-c + \sqrt{c^2 + 4dr(a_2 - 1)}}{2d} \overset{\text{def}}{=} \mu_4(c) > 0.
\tag{16}
$$

Therefore, $\mu_1(c)$ and $\mu_4(c)$ are the decay rates near $\mathbf{o}$ and β, respectively. Moreover, $\mu_1(c)$ is increasing and $\mu_4(c)$ is decreasing in $c \in \mathbb{R}$.

3. Main result and its proof

We first establish conditions for the positive wave speed, under which the bistable travelling wave solution will spread to the left. This means that the species ϕ will survive in competition.

Theorem 3.1: *Let parameters a_1, a_2, d and r be fixed and $a_2 > 2$. If there exists an integer $m \geq 2$ such that*

$$1 < a_1 < 1 + \frac{m}{(m-1)(2m-1)}, \tag{17}$$

and either

$$\frac{2d(a_1-1)}{a_2}\frac{(m-1)^2}{m^2} < r < d(a_1-1)\frac{(m-1)^2}{m^2}, \tag{18}$$

or

$$\frac{d(a_1-1)}{a_2-1}\frac{(m-1)^2}{m^2} < r < \frac{2d(a_1-1)}{a_2}\frac{(m-1)^2}{m^2}, \tag{19}$$

then the bistable wave speed of (4) is positive.

Proof: Let $\underline{U}$ be a solution of the boundary value problem

$$\underline{U}' = \mu_1(\underline{c})\underline{U}(1 - \underline{U}^{(m-1)/m}), \quad \underline{U}(-\infty) = 0, \ \underline{U}(\infty) = 1$$

and $\underline{V} = \underline{U}^{(m-1)/m}$, where $\underline{c} = \epsilon, 0 < \epsilon \ll 1$. If $(\underline{U}, \underline{V})$ can be proved to be a lower solution of (9), then, by Lemma 2.3, we have the desired result.

Indeed, by a computation, we have

$$\underline{U}'' = \mu_1^2(\underline{c})\underline{U}\left(1 - \underline{U}^{(m-1)/m}\right)\left(1 - \frac{2m-1}{m}\underline{U}^{(m-1)/m}\right)$$

and

$$\underline{V}' = \frac{m-1}{m}\mu_1(\underline{c})\underline{V}(1 - \underline{V}), \quad \underline{V}'' = \left(\frac{m-1}{m}\right)^2 \mu_1^2(\underline{c})\underline{V}(1 - \underline{V})(1 - 2\underline{V}).$$

Substituting these expressions into system (9), and by notice of the fact that $\mu_1(\underline{c}) \to \sqrt{a_1 - 1}$ as $\epsilon \to 0$, letting $\epsilon \to 0$, by conditions (17)–(19), we have that

$$\underline{U}'' - \underline{c}\underline{U}' + \underline{U}(1 - a_1 - \underline{U} + a_1\underline{V})$$

$$= \underline{U}\left(1 - \underline{U}^{(m-1)/m}\right)\left[\mu_1^2(\underline{c}) - \underline{c}\mu_1(\underline{c}) + (1 - a_1) - \frac{2m-1}{m}\mu_1^2(\underline{c})\underline{U}^{(m-1)/m}\right.$$

$$\left. + \frac{U^{(m-1)/m}(1 - U^{1/m})}{1 - U^{(m-1)/m}}\right]$$

$$= \underline{U}^{(2m-1)/m}(1 - \underline{U}^{(m-1)/m})\left[-\frac{2m-1}{m}\mu_1^2(\underline{c}) + \frac{(1 - U^{1/m})}{1 - U^{(m-1)/m}}\right]$$

$$= \underline{U}^{(2m-1)/m}(1 - \underline{U}^{(m-1)/m})\left[-\frac{2m-1}{m}\mu_1^2(\underline{c})\right.$$

$$\left. + \frac{1}{U^{(m-2)/m} + U^{(m-3)/m} + \cdots + U^{1/m} + 1}\right]$$

$$\to \underline{U}^{(2m-1)/m}(1 - \underline{U}^{(m-1)/m})\left[-\frac{2m-1}{m}(a_1 - 1) + \frac{1}{m-1}\right] \geq 0,$$

and

$$d\underline{V}'' - \underline{c}\underline{V}' + r(1 - \underline{V})(a_2\underline{U} - \underline{V})$$

$$= \underline{V}(1 - \underline{V})\left[d\left(\frac{m-1}{m}\right)^2\mu_1^2(\underline{c})(1 - 2\underline{V}) - \underline{c}\mu_1(\underline{c})\frac{m-1}{m} - r + ra_2\underline{V}^{1/(m-1)}\right]$$

$$\geq \underline{V}(1 - \underline{V})\left[d\left(\frac{m-1}{m}\right)^2\mu_1^2(\underline{c}) - r + \left(ra_2 - \frac{2d(m-1)^2\mu_1^2(\underline{c})}{m^2}\right)\underline{V}\right]$$

$$\to \underline{V}(1 - \underline{V})\left[d\left(\frac{m-1}{m}\right)^2(a_1 - 1) - r + \left(ra_2 - \frac{2d(m-1)^2(a_1 - 1)}{m^2}\right)\underline{V}\right].$$

By this, if $r > 2d(a_1 - 1)(m - 1)^2/a_2 m^2$, then we get

$$d\left(\frac{m-1}{m}\right)^2(a_1 - 1) - r + \left(ra_2 - \frac{2d(m-1)^2(a_1 - 1)}{m^2}\right)\underline{V}$$

$$\geq d\left(\frac{m-1}{m}\right)^2(a_1 - 1) - r \geq 0,$$

or if $r < 2d(a_1 - 1)(m - 1)^2/a_2 m^2$, then it follows that

$$d\left(\frac{m-1}{m}\right)^2(a_1 - 1) - r + \left(ra_2 - \frac{2d(m-1)^2(a_1 - 1)}{m^2}\right)\underline{V}$$

$$\geq -d(a_1 - 1)\left(\frac{m-1}{m}\right)^2 + r(a_2 - 1) \geq 0.$$

Then, by Definition 2.1, when ϵ is sufficiently small, $(\underline{U}, \underline{V})$ is a lower solution of (9). Hence the proof is complete. ∎

It is easily observed that the upper bound of a_1 is decreasing in m. Thus when $m = 2$, the parameter a_1 has a maximum range. We have

Corollary 3.2: *The bistable wave speed of (4) is positive if $a_2 > 2$, $1 < a_1 < \frac{5}{3}$ and*

$$\frac{d(a_1 - 1)}{2a_2} < r < \frac{d(a_1 - 1)}{4},$$

or

$$\frac{d(a_1 - 1)}{4(a_2 - 1)} < r < \frac{d(a_1 - 1)}{2a_2}.$$

The combination of Corollary 3.2 and (N_2) explicitly shows that the competitive coefficients of two species greatly affect the outcome of their competition.

Theorem 3.3: *Fix system parameters a_1, a_2, d and r and let them satisfy*

$$\frac{2r + 4d(a_1 - 1)}{ra_2} < 3 - a_1. \tag{20}$$

Then the bistable wave speed is positive.

Proof: We first define a pair of functions $(\underline{U}, \underline{V})(z)$ by

$$\underline{U} = \frac{k}{1 + e^{-\mu_1(\underline{c})z}}, \quad \underline{V} = 1 - \left(1 - \frac{\underline{U}}{k}\right)^2$$

with $\underline{c} = \epsilon, 0 < \epsilon \ll 1, k \in (0, 1)$ to be determined and $k \geq \underline{U}(z)$. By a simple computation, it follows that

$$\underline{U}' = \mu_1(\underline{c})\underline{U}\left(1 - \frac{\underline{U}}{k}\right), \quad \underline{U}'' = \mu_1^2(\underline{c})\underline{U}\left(1 - \frac{\underline{U}}{k}\right)\left(1 - \frac{2\underline{U}}{k}\right)$$

and

$$\underline{V}' = 2\mu_1(\underline{c})\frac{\underline{U}}{k}\left(1 - \frac{\underline{U}}{k}\right)^2, \quad \underline{V}'' = 2\mu_1^2(\underline{c})\frac{\underline{U}}{k}\left(1 - \frac{\underline{U}}{k}\right)^2\left(1 - \frac{3\underline{U}}{k}\right).$$

Substituting these expressions in the left-hand sides of the two equations of (9) and using $\mu_1(\epsilon) = (\epsilon + \sqrt{\epsilon^2 + 4(a_1 - 1)})/2 \to \sqrt{a_1 - 1}$ as $\epsilon \to 0^+$, when $\varepsilon \to 0$, we have

$$\underline{U}'' - \underline{c}\underline{U}' + \underline{U}(1 - a_1 - \underline{U} + a_1\underline{V})$$

$$= \underline{U}\left(1 - \frac{\underline{U}}{k}\right)\left(\mu_1^2(\underline{c}) - \underline{c}\mu_1(\underline{c}) + 1 - a_1 - 2\mu_1^2(\underline{c})\frac{\underline{U}}{k} + \frac{a_1\underline{V} - \left(1 + \frac{a_1-1}{k}\right)\underline{U}}{1 - \frac{\underline{U}}{k}}\right)$$

$$= \frac{1}{k}\underline{U}^2\left(1 - \frac{\underline{U}}{k}\right)\left[-2\mu_1^2(\underline{c}) + \frac{a_1\underline{V} - \left(1 + \frac{a_1-1}{k}\right)\underline{U}}{\left(1 - \frac{\underline{U}}{k}\right)\frac{\underline{U}}{k}}\right]$$

$$\to \frac{1}{k}\underline{U}^2\left(1 - \frac{\underline{U}}{k}\right)\left(-2(a_1 - 1) + (a_1 + \frac{(1-k)k}{k - \underline{U}})\right)$$

$$\geq \frac{1}{k}\underline{U}^2\left(1 - \frac{\underline{U}}{k}\right)(3 - a_1 - k) \tag{21}$$

and

$$d\underline{V}'' - \underline{c}\underline{V}' + r(1 - \underline{V})(a_2\underline{U} - \underline{V})$$

$$= \frac{U}{k}\left(1 - \frac{U}{k}\right)^2\left[2d\mu_1^2(\underline{c})\left(1 - \frac{3U}{k}\right) - 2\underline{c}\mu_1(\underline{c}) + r\left(a_2k - 2 + \frac{U}{k}\right)\right]$$

$$\geq \frac{U}{k}\left(1 - \frac{U}{k}\right)^2\left[-4d\mu_1^2(\underline{c}) - 2\underline{c}\mu_1(\underline{c}) + r(a_2k - 2)\right]$$

$$\rightarrow \frac{U}{k}\left(1 - \frac{U}{k}\right)^2 ra_2\left[k - \frac{4d(a_1 - 1) + 2r}{ra_2}\right]. \tag{22}$$

Next we give a different range of allowed values of k for two cases. If $1 < a_1 \leq 2$, then k is taken as

$$\frac{2r + 4d(a_1 - 1)}{ra_2} < k < 1.$$

When $a_1 > 2$, we choose k satisfying

$$\frac{2r + 4d(a_1 - 1)}{ra_2} < k < 3 - a_1.$$

By this, when ϵ is sufficiently small, from (21) and (22), it follows that

$$\underline{U}'' - \underline{c}\underline{U}' + \underline{U}(1 - a_1 - \underline{U} + a_1\underline{V}) \geq 0,$$
$$d\underline{V}'' - \underline{c}\underline{V}' + r(1 - \underline{V})(a_2\underline{U} - \underline{V}) \geq 0.$$

Hence, by Definition 2.1, $(\underline{U}, \underline{V})(z)$ is a lower solution of (9). Then Lemma 2.3 implies that the result is true. ∎

In the following, we give conditions for the existence of negative wave speed, under which the bistable travelling wave will propagate to the right. This implies that the species φ will win competition.

Theorem 3.4: *The bistable wave speed is negative provided that for fixed system parameters a_1, a_2, d and r, there exists a constant $m = (n - 1)/n$ with integer $n \geq 2$ such that*

$$1 < a_2 < 5/3, \quad a_1 > 1 + \frac{2}{m}, \tag{23}$$

and either

$$\frac{2d(a_1 - 1)}{2 - a_2}m^2 < r < 6d(a_1 - 1)m^2, \tag{24}$$

or

$$6d(a_1 - 1)m^2 < r < \frac{4d(a_1 - 1)}{a_2 - 1}m^2. \tag{25}$$

Proof: By the assumption, we have $m \in [\frac{1}{2}, 1)$. Define a pair of functions $(\overline{U}, \overline{V})$ by

$$\overline{U}' = \mu_1(\overline{c})\overline{U}(1 - \overline{U}^m),$$
$$\overline{U}(-\infty) = 0, \ \overline{U}(\infty) = 1 \tag{26}$$

and

$$\overline{V} = 1 - (1 - \overline{U}^m)^2 \tag{27}$$

with $\overline{c} = -\epsilon, 0 < \epsilon \leq 1$. It is easy to check that

$$\overline{U}'' = \mu_1^2(\overline{c})\overline{U}(1 - \overline{U}^m)(1 - (1 + m)\overline{U}^m),$$

and

$$\overline{V}' = 2m\mu_1(\overline{c})\overline{U}^m(1 - \overline{U}^m)^2, \quad \overline{V}'' = 2m^2\mu_1^2(\overline{c})\overline{U}^m(1 - \overline{U}^m)^2(1 - 3\overline{U}^m).$$

Substituting these expressions into the left-hand sides of the two equations in system (9), likewise, by the fact that $\mu_1(-\epsilon) = (-\epsilon + \sqrt{\epsilon^2 + 4(a_1 - 1)})/2 \to \sqrt{a_1 - 1}$ as $\epsilon \to 0^+$, when $\epsilon \to 0$, for the second equation, we get

$$d\overline{V}'' - \overline{c}\overline{V}' + r(1 - \overline{V})(a_2\overline{U} - \overline{V})$$
$$= \overline{U}^m(1 - \overline{U}^m)^2 \left[2dm^2\mu_1^2(\overline{c})(1 - 3\overline{U}^m) - 2cm\mu_1(\overline{c}) + ra_2\overline{U}^{1-m} + r\overline{U}^m - 2r\right]$$
$$\leq \overline{U}^m(1 - \overline{U}^m)^2 \left[2dm^2\mu_1^2(\overline{c}) - 2r + ra_2\overline{U}^{1-m} + [r - 6dm^2\mu_1^2(\overline{c})]\overline{U}^m\right]$$
$$\to \overline{U}^m(1 - \overline{U}^m)^2 \left[2d(a_1 - 1)m^2 - 2r + ra_2\overline{U}^{1-m} + [r - 6d(a_1 - 1)m^2]\overline{U}^m\right].$$

When ϵ is sufficiently small, conditions (23), (24) and the fact that $0 \leq \overline{U} \leq 1$ lead to

$$d\overline{V}'' - \overline{c}\overline{V}' + r(1 - \overline{V})(a_2\overline{U} - \overline{V})$$
$$\leq \overline{U}^m(1 - \overline{U}^m)^2[2d(a_1 - 1)m^2 - r(2 - a_2)] \leq 0,$$

or from conditions (23), (25) and the fact that $0 \leq \overline{U} \leq 1$, it follows that

$$d\overline{V}'' - \overline{c}\overline{V}' + r(1 - \overline{V})(a_2\overline{U} - \overline{V})$$
$$\leq \overline{U}^m(1 - \overline{U}^m)^2 \left[2d(a_1 - 1)m^2 - 2r + ra_2 + [r - 6d(a_1 - 1)m^2]\right]$$
$$\leq \overline{U}^m(1 - \overline{U}^m)^2 \left[-4d(a_1 - 1)m^2 + r(a_2 - 1)]\right] \leq 0.$$

For the first equation, we need to use the equality

$$1 - U^{(n-1)/n} = (1 - U^{1/n})\left(U^{(n-2)/n} + U^{(n-3)/n} + \cdots + U^{1/n} + 1\right) \tag{28}$$

and condition (23). Then it follows that

$$\overline{U}'' - \bar{c}\overline{U}' + \overline{U}(1 - a_1 - \overline{U} + a_1\overline{V})$$

$$= \overline{U}(1 - \overline{U}^m)\left[\mu_1^2(\bar{c})(1 - (1 + m)\overline{U}^m) - \bar{c}\mu_1(\bar{c}) + \frac{1 - \overline{U} - a_1(1 - \overline{U}^m)^2}{1 - \overline{U}^m}\right]$$

$$= \overline{U}(1 - \overline{U}^m)\left[\mu_1^2(\bar{c}) - c\mu_1(\bar{c}) + 1 - a_1 - (1 + m)\mu_1^2(\bar{c})\overline{U}^m + a_1\overline{U}^m + \frac{\overline{U}^m - \overline{U}}{1 - \overline{U}^m}\right]$$

$$= \overline{U}^{1+m}(1 - \overline{U}^m)\left[-\mu_1^2(\bar{c})(1 + m) + a_1 + \frac{1 - \overline{U}^{1-m}}{1 - \overline{U}^m}\right]$$

$$= \overline{U}^{1+m}(1 - \overline{U}^m)\left[-\mu_1^2(\bar{c})(1 + m) + a_1 + \frac{1}{U^{(n-2)/n} + U^{(n-3)/n} + \cdots + U^{1/n} + 1}\right]$$

$$\rightarrow \overline{U}^{1+m}(1 - \overline{U}^m)[-(a_1 - 1)(1 + m) + a_1 + 1] \leq 0.$$

Then, by Definition 2.1, when ϵ is sufficiently small, $(\overline{U}, \overline{V})$ is an upper solution of (9). Thus, the desired result follows from Lemma 2.2. ∎

The proof of Theorem 3.4 is not applicable for the case where $m = 1$. However, by making only minor modifications to the analytical technique, we can derive the result below. The proof is omitted here.

Theorem 3.5: *Assume that*

$$1 < a_2 < 5/3, \quad a_1 > 2 \tag{29}$$

and either

$$\frac{2d(a_1 - 1)}{2 - a_2} < r < 6d(a_1 - 1), \tag{30}$$

or

$$6d(a_1 - 1) < r < \frac{4d(a_1 - 1)}{a_2 - 1}. \tag{31}$$

Then the bistable wave speed is negative.

If a pair of functions $(\overline{U}, \overline{V})$ is still defined as (26)-(27), but $m = 1/n$ with $n \geq 2$ being an integer, we can derive the condition for negative wave speed as follows:

Theorem 3.6: *The bistable wave speed is negative if there is a constant $m = 1/n$ with $n \geq 2$ being an integer such that*

$$1 < a_2 < 5, \quad a_1 > 1 + \frac{1}{m^2} \tag{32}$$

and either

$$d(a_1 - 1)m^2 < r < \frac{6d(a_1 - 1)}{(a_2 + 1)}m^2, \tag{33}$$

or

$$\frac{6d(a_1 - 1)}{(a_2 + 1)}m^2 < r < \frac{4d(a_1 - 1)}{(a_2 - 1)}m^2. \tag{34}$$

Proof: Substituting the expression of $(\overline{U}, \overline{V})$ in (26)-(27) into the left of the first equation of (9), noticing the fact that $\overline{U}^{1-m} \leq \overline{U}^m$, and using the same analysis as in Theorem 3.4 for $\mu_1(\overline{c})$, when $\epsilon \to 0$, we have

$$
d\overline{V}'' - \overline{c}\overline{V}' + r(1 - \overline{V})(a_2\overline{U} - \overline{V})
$$
$$
= \overline{U}^m(1 - \overline{U}^m)^2 \left[2dm^2\mu_1^2(\overline{c})(1 - 3\overline{U}^m) - 2\overline{c}m\mu_1(\overline{c}) + r(a_2\overline{U}^{1-m} + \overline{U}^m - 2) \right]
$$
$$
\leq \overline{U}^m(1 - \overline{U}^m)^2 \left[2dm^2\mu_1^2(\overline{c}) - 2r + [r(a_2 + 1) - 6dm^2\mu_1^2(\overline{c})]\overline{U}^m \right]
$$
$$
\to \overline{U}^m(1 - \overline{U}^m)^2 \left[2d(a_1 - 1)m^2 - 2r + [r(a_2 + 1) - 6d(a_1 - 1)m^2]\overline{U}^m \right].
$$

Now whether (32) and (33) or (32) and (34) hold, we have

$$
d\overline{V}'' - \overline{c}\overline{V}' + r(1 - \overline{V})(a_2\overline{U} - \overline{V})
$$
$$
\to \overline{U}^m(1 - \overline{U}^m)^2 \left[2d(a_1 - 1)m^2 - 2r + [r(a_2 + 1) - 6d(a_1 - 1)m^2]\overline{U}^m \right] \leq 0.
$$

From the second equation, it follows that

$$
\overline{U}'' - \overline{c}\overline{U}' + \overline{U}(1 - a_1 - \overline{U} + a_1\overline{V})
$$
$$
= \overline{U}^{1+m}(1 - \overline{U}^m) \left[-(m + 1)\mu_1^2(\overline{c}) + a_1 + \frac{1 - \overline{U}^{1-m}}{1 - \overline{U}^m} \right]
$$
$$
\leq \overline{U}^{1+m}(1 - \overline{U}^m) \left[-(m + 1)\mu_1^2(\overline{c}) + a_1 + \frac{1}{m} - 1 \right]
$$
$$
\to \overline{U}^{1+m}(1 - \overline{U}^m) \left[-(m + 1)(a_1 - 1) + a_1 + \frac{1}{m} - 1 \right] \leq 0.
$$

Here (28) and (32) are used. Thus, when ϵ is sufficiently small, Definition 2.1 and Lemma 2.2 yield the desired result. ∎

4. Conclusion and discussion

In this work, we obtain two conditions for positive wave speed (see Theorems 3.1 and 3.3) and three conditions for negative wave speed (see Theorems 3.4–3.6). Compared to that in the references [12,17], these results are different and give more biological implications for the determinacy of the speed sign.

Positive (or negative) wave speed indicates that the travelling wave solution propagates to the left (or right), which means that the stable state $(1, 0)$ (or $(0, 1)$) is more competitive than the other one $(0, 1)$ (or $(1, 0)$). Thus, only ϕ (or φ) will survive in the competition. From our theorems including the free parameter m, it is obvious to see that $a_2 > a_1$ in Theorem 3.1 and $a_2 < a_1$ in Theorems 3.4 and 3.6, which theoretically demonstrates the critical importance of competitiveness. However, for each of these theorems, there does not exist an optimal value of m such that the value domains of both a_1 and r (other parameters are fixed) can cover those for all other choices of m, which also implies that there is no best choice for the upper solution or the lower solution.

We now compare our results to those in Lemma 1.1. Due to the fact that (P_2) is invalid for $3/2 \leq a_1 < 3$, it is evident that Theorem 3.3 is a supplement of (P_2). Since (P_1) is equivalent to

$$
\begin{aligned}
1 \leq a_1 &< \frac{4(a_2 - 1)}{3a_2 - 2}, a_2 > 2, \\
\frac{d(a_1 - 1)}{a_2 - 1} &< r < \frac{d}{a_2 - 1}\left(1 - \frac{a_1 a_2}{2(a_2 - 1)}\right),
\end{aligned}
\tag{35}
$$

obviously, Corollary 3.2 improves and supplements (P_1). It is also easy to check that Theorems 3.4–3.6 improve and supplement (N_1) and (N_2).

Finally, it should be mentioned that, based on the obtained results, we could use the identity (6) to get more explicit conditions, which can be also derived by way of the decay rate μ_4 around β to construct upper or lower solutions of (9).

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