TRAVELING BANDS FOR THE KELLER-SEGEL MODEL WITH POPULATION GROWTH

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Dedicated to Professor Glenn Webb on the occasion of his 70th birthday

ABSTRACT. This paper is concerned with the existence of the traveling bands to the Keller-Segel model with cell population growth in the form of a chemical uptake kinetics. We find that when the cell growth is considered, the profile of traveling bands, the minimum wave speed and the range of the chemical consumption rate for the existence of traveling wave solutions will change. Our results reveal that collective interaction of cell growth and chemical consumption rate plays an essential role in the generation of traveling bands. The research in the paper provides new insights into the mechanisms underlying the chemotactic pattern formation of wave bands.

1. **Introduction.** The study of traveling waves of chemotaxis models began with the pioneering work of Keller and Segel [11] in which the following model was proposed and investigated:

$$\begin{cases} u_t = du_{xx} - \chi[u\varphi(v)_x]_x, \\ v_t = \varepsilon v_{xx} - g(v)u \end{cases}$$
(1.1)

with the chemotactic sensitivity function $\varphi(v)$ assumed to be logarithmic:

$$\varphi(v) = \log v,$$

and the chemical degradation (or death) rate function g(v) following a power law:

$$q(v) = v^m, \ m > 0$$

where u(x,t) and v(x,t) represent the bacterial density and chemical concentration, respectively. χ is called the chemotactic sensitivity coefficient describing the strength of chemotaxis, d and ε denote the cell and chemical diffusion coefficients,

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respectively. The positive parameter m>0 is called the chemical consumption rate.

When $0 \le m < 1$, it was shown in [11] that model (1.1) with $\varepsilon = 0$ can generate traveling bands (traveling pulses, see an illustration in Fig. 1 (a)) which qualitatively were in satisfactory agreement with experimental observation of [1, 2]. Subsequently, a sequence of rigorous works on various aspects of traveling wave solutions of (1.1) with $\varepsilon > 0$ had been carried out, cf. [21, 23, 25, 26, 27, 30] and references therein. When m > 1, the model (1.1) does not admit traveling wave solutions (e.g., see [30, 33]), and the global solutions of (1.1) with other forms of chemotactic sensitivity function were studied in [5, 6, 7, 16, 31] in both bounded and unbounded domains. For the borderline case m=1, the model (1.1) was used in [24] to describe the chemotactic boundary formation by bacterial population in response to the substrate consisting of nutrients if $\varepsilon = 0$, and recently in [15] to describe the directed migration of endothelial cells toward the signaling molecule vascular endothelial growth factor (VEGF) during the initiation of angiogenesis (see further references [5, 6, 15], where u denotes the density of endothelial cells and v stands for the concentration of VEGF. The existence of traveling wavefronts of (1.1) with m=1 was obtained in [34] for $\varepsilon=0$ and in [32] for $\varepsilon>0$. Though the existence of traveling wave solutions of the Keller-Segel model (1.1) has been extensively studied and well understood, the stability of traveling wave solutions is still a challenging problem due to the singular logarithmic sensitivity $\log v$. The linear instability of traveling wave solutions to (1.1) in certain functional spaces was first obtained in [23] for a special case m=0. The linear stability/instability of traveling wave solutions for $m \neq 0$ still remains open. The nonlinear stability of traveling wave solutions to (1.1) was not obtained until recently the second author with co-workers proved the nonlinear stability of traveling waves of (1.1) with $\varepsilon = 0$ in [18, 19, 9] and with $\varepsilon > 0$ in [20, 17] for the borderline case m = 1. A kinetic description of chemotactic traveling bands can be found in [28, 29]. When g(v) is negative, results can be found in [4] and references therein.

It is evident that the cell growth (i.e. generation of biomass) was not considered in the Keller-Segel model (1.1). Since v is often a nutrient source (like energy or oxygen in the experiment of [1, 2]), it is natural to consider the cell growth in the dynamics due to the consumption of nutrient as mentioned by Keller and Segel themselves in [11]. Hence it would be of interest to investigate whether the cell growth plays a role in the generation of traveling bands. In other words, we are concerned with the traveling waves of the following Keller-Segel model with cell population growth

$$\begin{cases} u_t = du_{xx} - \chi [u\varphi(v)_x]_x + f(u, v), \\ v_t = \varepsilon v_{xx} - g(v)u. \end{cases}$$

The first work considering the cell population growth in chemotaxis models was presented in [13] where the chemotactic sensitivity function is assumed to be a receptor form: $\varphi(v) = \frac{v}{v+k}$ for some constant k>0 and growth term $f(u,v) = \sigma u$, and traveling bands (non-monotonic wavefronts, an illustration in Fig. 1 (b)) are numerically obtained at a specific growth rate $\sigma>0$. When the chemotactic sensitivity is linear: $\varphi(v)=v$ and cell growth is the Monod's model (namely f(u,v)=g(v)u with $g(v)=\frac{kv}{K+v}$ for some positive constants k and K), the existence of traveling bands was obtained in [12]. Subsequently the same Monod's kinetics was numerically investigated in [14] for three main different types of chemotactic sensitivities

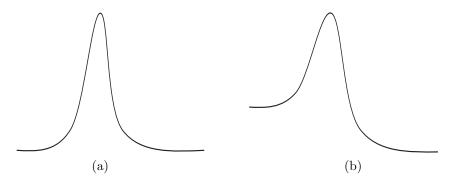


FIGURE 1. An illustration of two distinct profiles of a traveling band: (a) traveling pulse; (b) non-monotonic wavefront.

(linear, logarithmic and receptor). When both the sensitivity function and chemical kinetics are linear, namely $\varphi(v) = v$ and the term $-uv^m$ in (1.1) is replaced by u - v, the traveling wave solutions for the model (1.1) was studied in [8] for a bistable cell growth and in [22] for a logistic one. It can be clearly seen that all above-mentioned works considering traveling waves of the Keller-Segel model with cell growth either alter the chemotactic sensitivity function $\varphi(v)$ or the chemical kinetics in (1.1). Hence a fundamental question rises as follows:

• Is there an appropriate cell growth function which can be included into the Keller-Segel model (1.1) without changing any other terms such that the resulting model still admits the traveling bands?

When the logistic growth is included into the first equation of (1.1) with m=1, only monotonic traveling wavefronts can be obtained (see [3]). We stress here that it is important to keep the chemotactic sensitivity function $\varphi(v)$ as the logarithm as in the original Keller-Segel model (1.1) since it has been confirmed recently by both experiments and model simulation in [10] that bacterial (like E. coli) cells do sense the spatial gradient of the logarithmic ligand concentration. Hence the logarithmic sensitivity has its fundamental biological relevance. Mathematically the logarithmic sensitivity function is much more challenging than other types of sensitivity (like linear or receptor) due to the singularity at v=0.

Toward the basic question raised above, in this paper we shall include a nutrient uptake cell kinetics (meaning cells grow due to the nutrient uptake) into the Keller-Segel molde (1.1) directly and resulting model reads:

$$\begin{cases} u_t = du_{xx} - \chi [u(\log v)_x]_x + ruv^m, \\ v_t = \varepsilon v_{xx} - uv^m \end{cases}$$
 (1.2)

where r ($0 < r \le 1$) is the conversion rate from the consumption of nutrient to the growth of cells. As we know, the chemical uptake kinetics in chemotaxis has not been studied before. However it is natural to consider such a kind of kinetics since the bacterial consume the energy and then increase its biomass. The main goal of this paper will be to find under what conditions for the parameter m > 0, the traveling bands of the model (1.2) exist and then discuss the differences of traveling bands generated by the model (1.1) with and without cell kinetics. Furthermore we shall discuss biological implications of our results. Since the model (1.2) is a system of two parabolic equations, it is generally nontrivial to obtain the traveling

wave solutions. As the first step, we consider a simplified case $\varepsilon = 0$ (i.e., chemical diffusion is negligible) as treated in [11].

Assume that (u, v)(x, t) = (U, V)(x - ct) is a traveling wave solution of (1.2), where c > 0 denotes the wave speed. With $\varphi(v) = \log v$ and $\varepsilon = 0$, the traveling wave solution (U, V) satisfies the ODE system

$$\begin{cases} dU'' + cU' + rUV^m - \chi [U\varphi(V)']' = 0, \\ cV' - UV^m = 0. \end{cases}$$
(1.3)

Here we are only interested in the case $U \ge 0, V \ge 0$ due to the biological relevance. Since V is an increasing wavefront, which can be seen from the second equation of (1.3), we assume that $V(\infty) = 1$ without loss of generality and $U'(\infty) = U(\infty) = 0$. With these conditions, the integrated sum of equations of (1.3) gives

$$dU' + c(U + rV - r) - \chi U \frac{V'}{V} = 0.$$

Thus the travelling wave solutions (u, v) := (U, V) satisfy the system

$$\begin{cases} du' = c(r - u - rv) + \frac{\chi}{c} u^2 v^{m-1}, \\ v' = -\frac{1}{c} u v^m, \end{cases}$$
 (1.4)

and the conditions

$$u > 0$$
, $0 < v < 1$, $(u, v)(-\infty) = E_1 := (r, 0)$, $(u, v)(\infty) = E_3 := (0, 1)$. (1.5)

In the following we assume that d=1 for simplicity. Clearly, when $0 \le m < 1$, there is no solution to (1.4) - (1.5) since if there were such a solution (u,v) for some c>0, we would have $u'(\xi)=\frac{\chi}{c}[r^2+o(1)]v^{m-1}(\xi)+o(1)\to\infty$ as $\xi\to-\infty$, which contradicts $u(\xi)\to r$ as $\xi\to-\infty$. Therefore we just need to consider $m\geq 1$. Since the equilibrium points of (1.4) are different for m=1 and for m>1, we consider these two cases separately. When m=1, (1.4) has one equilibrium E_3 if $c < 2\sqrt{\chi r}$ and three equilibria E_3 , $E_1^* = (u_1^*, 0)$ and $E_2^* = (u_2^*, 0)$ with $r < u_1^* < u_2^*$ if $c > 2\sqrt{\chi r}$. When m > 1, (1.4) has two equilibria E_1 and E_3 for every c > 0. In Section 2, we consider the case m=1 and show that for every $c>\max\{2\sqrt{r},2\sqrt{\chi r}\}$, there is a unique (up to a translation) heteroclinic solution (u, v) of (1.4) connecting E_1^* to E_3 with u'<0 and v'>0. In Section 3, we consider m>1 and show that there is a minimal value $c_0(m)$ with $c_0(m) = 2\sqrt{r}$ if $\chi \leq 1$ and $2\sqrt{r} \leq c_0(m) \leq 2\sqrt{\chi r}$ if $\chi > 1$ such that for every $c \geq c_0(m)$ there is a unique solution to (1.4) - (1.5) with v'>0, u'<0 if $m\geq 2$ (so that u< r along the whole orbit), and u' changing sign exactly one time if 1 < m < 2 (so that $u(\xi) > r$ as $\xi \to -\infty$); furthermore, $c_0(m)$ is a decreasing function of $m \in (1, \infty)$. The precise statements of these results are given at the beginning of the corresponding sections. The proofs of these results are based on studying local dynamics near E_1 (or E_1^*) and constructing positive invariant sets by making use of the existence result for m=1 and the monotonic properties of the vector field of (1.4) in the region u > 0 and 0 < v < 1 with respect to m > 1 and c > 0. Since the system (1.4) for 1 < m < 2 is not smooth at E_1 , we cannot linearize (1.4) at E_1 , and hence cannot apply the unstable manifold theorem to prove that there exist solutions of (1.4) approaching E_1 as $\xi \to -\infty$. To resolve this problem, a shooting argument will be used.

2. Case of m=1. Assume that m=1. Then (1.4) reduces to the system

$$u' = c(r - u - rv) + \frac{\chi}{c}u^2, \qquad v' = \frac{1}{c}uv.$$
 (2.1)

Assuming $c^2 > 4r\chi$, (2.1) has three equilibria $E_1^* = (u_1^*, 0)$, $E_2^* = (u_2^*, 0)$ and E_3 , where u_1^* and u_2^* are the solutions of $\chi u^2 - c^2 u + c^2 r = 0$ given by

$$u_1^* = \frac{1}{2\chi} \left(c^2 - \sqrt{c^4 - 4r\chi c^2} \right), \qquad u_2^* = \frac{1}{2\chi} \left(c^2 + \sqrt{c^4 - 4r\chi c^2} \right).$$

Note that u_1^* and u_2^* are strictly decreasing and increasing functions of c respectively, with $r < u_1^* < 2r$, $2r < u_2^* < \infty$ and the asymptotic behavior

$$\left\{ \begin{array}{ll} u_1^* \to 2r & \quad (c \to \sqrt{4r\chi}), \\ u_1^* \to r & \quad (c \to \infty), \end{array} \right. \qquad \left\{ \begin{array}{ll} u_2^* \to 2r & \quad (c \to \sqrt{4r\chi}), \\ u_2^* \to \infty & \quad (c \to \infty). \end{array} \right.$$

In Lemma 2.2 below we will show that E_1^* is a saddle and E_3 is a stable node of (2.1). The features of these equilibria enable us to prove the following:

Theorem 2.1. For every $c > \max\{2\sqrt{\chi r}, 2\sqrt{r}\}$, there exists a unique (up to a translation) heteroclinic solution (u, v) of (2.1), with u' < 0, v' > 0 on $(-\infty, \infty)$, $(u, v)(-\infty) = E_1^*$, $(u, v)(\infty) = E_3$, and the following asymptotic formulas: for some positives constants C_- and C_+ ,

$$\begin{pmatrix} u(\xi) \\ v(\xi) \end{pmatrix} = \begin{pmatrix} u_1^* \\ 0 \end{pmatrix} + C_- e^{\frac{u_1^*}{c}\xi} [1 + O(e^{\frac{u_1^*}{c}\xi})] \mathcal{V}_1 \qquad (\xi \to -\infty),$$

where $V_1 := \left[1, \frac{1}{c^2 r} \left(2\chi u_1^* - c^2 - u_1^*\right)\right]^{\top}$ whose second component is negative, and

$$\begin{pmatrix} u(\xi) \\ v(\xi) \end{pmatrix} = \begin{pmatrix} 0 \\ 1 \end{pmatrix} + C_{+}e^{\lambda_{+}\xi} [1 + o(1)] \begin{pmatrix} c\lambda_{+} \\ 1 \end{pmatrix} \qquad (\xi \to \infty),$$

where $\lambda_{+} = \frac{1}{2}(-c + \sqrt{c^2 - 4r}).$

Remark 1. (i) Using a standard limiting procedure we can show the assertion of Theorem 2.1 for $c = \max\{2\sqrt{\chi r}, 2\sqrt{r}\}$. This implies that the minimal speed $c = 2\sqrt{r}$ is reached when $\chi \leq 1$ (since E_3 is a spiral of (1.4) if $c < 2\sqrt{r}$).

(ii) It is easy to verify that E_2^* is a unstable node of (2.1). We can show that there are a continuum of infinitely many solutions (u,v) of (2.1) satisfying $(u,v)(-\infty) = E_2^*$, $(u,v)(\infty) = E_3$ and v' > 0 on $(-\infty,\infty)$. Furthermore, if $(\chi-1)c^2 > r(1-2\chi)^2$, then u' change signs exactly one time on $(-\infty,\infty)$; otherwise, if $(\chi-1)c^2 < r(1-2\chi)^2$, then u' < 0 on $(-\infty,\infty)$. Due to the length of the paper, we will not give the proof here.

We need two lemmas to prove Theorem 2.1. The first one gives the local dynamics of (2.1) at E_1^* and E_3 .

Lemma 2.2. Assume $c > \max\{\sqrt{4r}, \sqrt{4r\chi}\}$.

- (i) E_1^* is a saddle point of (2.1), with the unstable manifold $W^u(E_1^*)$ tangent to the vector \mathcal{V}_1 defined in Theorem 2.1.
 - (ii) E_3 is a stable node of (2.1).

Proof. The Jacobian matrices of (2.1) at E_1^* and E_3 are, respectively,

$$J(E_1^*) = \begin{pmatrix} -c + \frac{2\chi}{c} u_1^* & -cr \\ 0 & \frac{1}{c} u_1^* \end{pmatrix}, \qquad J(E_3) = \begin{pmatrix} -c & -cr \\ \frac{1}{c} & 0 \end{pmatrix}.$$
 (2.2)

Sine $2\chi u_1^* - c^2 = -c\sqrt{c^2 - 4r\chi} < 0$, it follows that $J(E_1)$ has a negative eigenvalue $-c + \frac{2\chi}{c}u_1^*$ and a positive eigenvalue $\frac{1}{c}u_1^*$; Thus, E_1^* is a saddle point of (2.1). A direct computation shows that \mathcal{V}_1 is an eigenvector of $J(E_1^*)$ associated with the eigenvalue u_1^*/c . Applying the unstable manifold theorem we conclude $W^u(E_1^*)$ is tangent to \mathcal{V}_1 . This shows (i).

Since the characteristic polynomial of $J(E_3)$ is $\lambda^2 + c\lambda + r = 0$, we find that the eigenvalues of $J(E_3)$ are $\lambda_{\pm} = \frac{1}{2} \left(-c \pm \sqrt{c^2 - 4r} \right)$, which are negative by virtue of $c^2 > 4r$. This yields the assertion (ii) from the stable manifold theorem.

Lemma 2.3. Assume that $c > \max\{\sqrt{4r}, \sqrt{4r\chi}\}$. Let

$$k = \begin{cases} k_1 := \frac{1}{2rc^2} \left(-[c^2 + (1-\chi)u_1^*] + \sqrt{[c^2 + (1-\chi)u_1^*]^2 - 4rc^2} \right) & \text{if } \chi > 1, \\ k_2 := \frac{1}{2rc^2} \left(-c^2 + \sqrt{c^4 - 4rc^2} \right) & \text{if } \chi \le 1. \end{cases}$$

Then,

(i) k < 0

(ii) Let $E_4 = (-1/k, 0)$. Then E_4 lies between E_1^* and E_2^* on the u axis if $\chi < 1$, equals E_2^* if $\chi = 1$, and lies to the right of E_2^* if $\chi > 1$.

(iii) Let $E_5 = (u_1^*, 1 + ku_1^*)$, the intersection of the vertical line $u = u_1^*$ with the line segment $\overline{E_4E_3}$. Let \mathcal{R}_1 be the region bounded by the arc $\widetilde{E_1^*E_3}$ on the u-nullcline of (2.1) and the segments $\overline{E_1^*E_5}$ and $\overline{E_5E_3}$. Then \mathcal{R}_1 is a positively invariant set of (2.1). (See Fig. 2.)

Proof. Clearly, $k_2 < 0$. To show $k_1 < 0$, it suffices to show that $c^2 + (1 - \chi)u_1^* > 2c\sqrt{r}$. Note that, from the equation for u_1^* , $c^2 + (1 - \chi)u_1^* = \frac{1}{u_1^*}[c^2u_1^* - \chi(u_1^*)^2 + (u_1^*)^2] = \frac{1}{u_1^*}[c^2r + (u_1^*)^2]$, and $c\sqrt{r} - u_1^* > c\sqrt{r} - 2r > \sqrt{r}(c - 2\sqrt{r}) > 0$. We have

$$c^{2} + (1 - \chi)u_{1}^{*} - 2c\sqrt{r} = \frac{1}{u_{1}^{*}}[c^{2}r + (u_{1}^{*})^{2} - 2c\sqrt{r}u_{1}^{*}] = \frac{1}{u_{1}^{*}}(c\sqrt{r} - u_{1}^{*})^{2} > 0.$$

Thus $k_1 < 0$. This shows (i).

To show (ii) let

$$v = Q(u) := \frac{1}{c^2 r} (\chi u^2 - c^2 u + c^2 r), \tag{2.3}$$

whose graph (a parabola) is the u-nullcline of (2.1). Since $rc^2k_2^2+c^2k_2+1=0$ from the definition of k_2 , we have $Q(-\frac{1}{k_2})=\frac{1}{k_2^2}(rc^2k_2^2+c^2k_2+\chi)=\frac{1}{k_2^2}(\chi-1)<0$ if $\chi<1$. This shows that E_4 lies strictly between E_1^* and E_2^* . The formulas for u_2^* and k_2 show that $E_4=E_2^*$ if $\chi=1$.

We now consider the case $\chi > 1$. Using the equation $rc^2k_1^2 + [c^2 + (1-\chi)u_1^*]k_1 + 1 = 0$ we have $Q(-\frac{1}{k_1}) = \frac{1}{k_1^2}(rc^2k_1^2 + c^2k_1 + \chi) = \frac{1}{k_2^2}[\chi - (1-\chi)u_1^*k_1 - 1] = 0$

$$\frac{1}{k_1^2}(\chi - 1)(1 + u_1^*k_1)$$
. Since

$$\begin{split} 1 + u_1^* k_1 &= 1 + u_1^* \frac{1}{2rc^2} \left(-[c^2 + (1-\chi)u_1^*] + \sqrt{[c^2 + (1-\chi)u_1^*]^2 - 4rc^2} \right) \\ &= \frac{1}{2rc^2} \left(2rc^2 - [c^2 + (1-\chi)u_1^*]u_1^* + u_1^* \sqrt{[c^2 + (1-\chi)u_1^*]^2 - 4rc^2} \right) \\ &= \frac{1}{2rc^2} \left(2rc^2 - [c^2u_1^* + (1-\chi)(u_1^*)^2] + u_1^* \sqrt{[c^2 + (1-\chi)u_1^*]^2 - 4rc^2} \right) \\ &= \frac{1}{2rc^2} \left(rc^2 - (u_1^*)^2 + u_1^* \sqrt{[c^2 + (1-\chi)u_1^*]^2 - 4rc^2} \right) \\ &= \frac{1}{2rc^2} \left(c^2u_1^* + (\chi - 1)(u_1^*)^2 + u_1^* \sqrt{[c^2 + (1-\chi)u_1^*]^2 - 4rc^2} \right) \\ &> 0. \end{split}$$

it follows that $Q(-\frac{1}{k_1}) > 0$ and $u_1^* < -\frac{1}{k_1}$, and hence $-\frac{1}{k_1} > u_2^*$ from the graph of v = Q(u). This shows (ii).

To show (iii), let (u, v) be an arbitrary point on $int(\overline{E_5E_3})$, which lies on the line v-1-ku=0. If $\chi>1$, then $k=k_1$, and using $0< u< u_1^*$, we have

$$(v-1-ku)' = \frac{1}{c}u\left\{rc^2k^2 + [c^2 + (1-\chi)u]k + 1\right\}$$

$$< \frac{1}{c}u\left\{rc^2k_1^2 + [c^2 + (1-\chi)u_1^*]k_1 + 1\right\} = 0;$$

If $\chi \leq 1$, then $k = k_2$, and using $(1 - \chi)uk_2 \leq 0$, we have

$$(v-1-ku)' = \frac{1}{c}u\left\{rc^2k^2 + [c^2 + (1-\chi)u]k + 1\right\} \le \frac{1}{c}u\left\{rc^2k_2^2 + c^2k_2 + 1\right\} = 0.$$

This implies that the vector field of (2.1) points to the interior of \mathcal{R}_1 . Since the vector field of (2.1) points strictly upper-ward on the arc $int(E_3E_1^*)$, and $u'=c(r-u_1^*-rv)+\chi(u_1^*)^2/c=-crv<0$ on the segment $int(E_1^*E_5)$, it follows that \mathcal{R}_1 is a positive invariant set of (2.1). This shows (iii), thereby completing the proof of Lemma 2.3.

We are now to prove Theorem 2.1.

Proof of Theorem 2.1. Since $W^u(E_1^*)$ is tangent to \mathcal{V}_1 at E_1^* , the u-nullcline v=Q(u) is tangent to the vector $[1,Q'(u_1^*)]^{\top}$ at E_1^* , and $Q'(r)=\frac{1}{c^2r}(2\chi u_1^*-c^2)$ is bigger than the second component of \mathcal{V}_1 and less than zero, it follows that the branch of $W^u(E_1^*)$ with u< r lies in the interior of the region \mathcal{R}_1 defined in Lemma 2.3 (iii). Let $\varphi_c=(u_c,v_c)$ be a solution of (2.1) with $\varphi(0)$ lying on this branch of $W^u(E_1^*)$. The positive invariance of \mathcal{R}_1 implies that $\varphi_c(\xi)$ is defined for all $\xi\in(-\infty,\infty)$ with $\varphi_c(\xi)\in int(\mathcal{R}_1)$. The vector field of (2.1) in $int(\mathcal{R}_1)$ yields $u_c'(\xi)<0$ and $v_c'(\xi)>0$ or all $\xi\in(-\infty,\infty)$, and hence $\varphi_c(\infty)=E_3$.

It remains to show the asymptotic formulas for φ_c as stated in Theorem 2.1. Since E_1^* is saddle, the asymptotic formula for $\varphi_c(\xi)$ as $\xi \to -\infty$ follows directly from the stable manifold theorem. Recall that the Jacobian matrix of (2.1) at E_3 has two eigenvalues λ_{\pm} with associated eigenvectors $[c\lambda_{\pm}, 1]^{\top}$. Therefore, E_3 is a stable node of (2.1) with 1-dimensional strongly stable manifold $W^{ss}(E_3)$ tangent to the

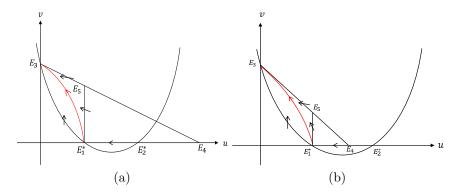


FIGURE 2. The parabolas and red curves in (a) for $\chi > 1$ and (b) for $\chi \leq 1$ are the *u*-nullcline and heteroclinic solutions of (2.1), respectively.

eigenvector $[c\lambda_-, 1]^{\top}$ at E_3 . To derive the asymptotic formula for $\varphi_c(\xi)$ as $\xi \to \infty$ it suffices to show that the orbit of φ_c does not lie on $W^{ss}(E_3)$. If this is false, since φ_c lies entirely inside the region \mathcal{R}_1 connecting E_1^* and E_3 , \mathcal{R}_1 is positively invariant for the orbits of (2.1), and $W^{ss}(E_3)$ lies above the eigenvector $[c\lambda_+, 1]^{\top}$, it follows (using different orbits cannot intersect) that all orbits of (2.1 starting from interior of the segment $E_1^*E_5$ (see Fig. 2) go to E_3 as $\xi \to \infty$ tangentially to $W^{ss}(E_3)$. This is impossible since there is at most one orbit of (2.1) lying in \mathcal{R}_1 that is allowed to have such a tangential behavior at E_3 . This shows that φ_c must be tangent to the eigenvector $[c\lambda_+, 1]^{\top}$ at E_3 , yielding its asymptotic formula as $\xi \to \infty$ as stated in Theorem 2.1. This completes the proof of Theorem 2.1.

3. Case of m > 1. Note that when m > 1, (1.4) has two equilibria E_1 and E_3 for every c > 0. The main theorem in this section is the following:

Theorem 3.1. (i) For every m > 1 there exists a minimal number $c_0(m)$ with $c_0(m) \ge 2\sqrt{r}$ such that for each $c > c_0(m)$, the problem (1.4)-(1.5) has a unique (up to a translation) solution (u_c, v_c) , which satisfies that $u_c + rv_c - r > 0$, $v'_c > 0$ on $(-\infty, \infty)$ and that for 1 < m < 2, u'_c changes sign exactly one time, namely, there exists $\xi_0 \in (-\infty, \infty)$ such that $u'_c(\xi) > 0$ for $\xi < \xi_0$ and $u'_c(\xi) < 0$ for $\xi > \xi_0$ with the global maximum $u_c(\xi_0) < \min\{2r, r + 4r^2\chi/c^2\}$; for $m \ge 2$, $u'_c(\xi) < 0$ for all $\xi \in (-\infty, \infty)$. Furthermore, (u_c, v_c) has the following asymptotic formulas: for some positive constants D_- and D_+ ,

(a) As
$$\xi \to -\infty$$
,

$$v_{c}(\xi) = D_{-} \left[\frac{(m-1)r}{c} |\xi| \right]^{-1} \frac{1}{m-1} [1 + o(1)],$$

$$u_{c}(\xi) - r = \begin{cases} \frac{\chi r^{2}}{c^{2}} [v_{c}(\xi)]^{m-1} \left[1 + O\left([v_{c}(\xi)]^{m-1}\right) \right], & \text{if } 1 < m < 2, \\ -r \left[1 - \frac{\chi r}{c^{2}} \right] v_{c}(\xi) [1 + O(v_{c}(\xi))], & \text{if } m = 2, \\ -r v_{c}(\xi) \left[1 + O(v_{c}(\xi)) + O([v_{c}(\xi)]^{m-2}) \right], & \text{if } m > 2. \end{cases}$$

$$(3.1)$$

(b) As
$$\xi \to \infty$$
,
$$\begin{pmatrix} u_c(\xi) \\ v_c(\xi) \end{pmatrix} = \begin{pmatrix} 0 \\ 1 \end{pmatrix} + D_+ e^{\lambda_+ \xi} [1 + o(1)] \begin{pmatrix} \lambda_+ c \\ 1 \end{pmatrix}, \tag{3.2}$$

where $\lambda_{+} = \frac{1}{2}(-c + \sqrt{c^2 - 4r}).$

- (ii) The following hold for $c_0(m)$:
- (a) for m > 1, $c_0(m) = 2\sqrt{r}$ if $\chi \le 1$; $c_0(m) \le 2\sqrt{\chi r}$ if $\chi > 1$.
- (b) $c_0(m) > \sqrt{\chi r} \text{ if } 1 < m \le 2.$
- (c) $c_0(m)$ is a non-increasing function for $m \in (1, \infty)$.

Remark 2. (i) Since E_3 is a spiral of (1.4) if $c < 2\sqrt{r}$, it follows from Theorem 3.1 that $c_0(m) = 2\sqrt{r}$ for $\chi \le 1$ is the smallest wave speed to guarantee that u is positive near E_3 .

(ii) When 1 < m < 2, we find that the component u_c of the wave solution (u_c, v_c) obtained in Theorem 3.1 is a profile of non-monotonic wavefront and hence generates a traveling band; however the upper bound for its maximum value $u_c(\xi_0)$ shows that $u_c(\xi_0) \to r$ as $c \to \infty$.

We need a series of lemmas to prove Theorem 3.1. The lemma 3.2 below will be used in the following subsections, and Lemma 3.3 shows that $c_0(m) > \sqrt{\chi r}$ when $1 < m \le 2$.

Lemma 3.2. The vector field of (1.4) at any point (u, v) in the interior of the segment $\overline{E_1E_3}$ (with the equation u+rv-r=0) points to the region u+rv-r>0.

Proof. Given $(u, v) \in int(\overline{E_1E_3})$ so that u > 0 and v > 0, it then follows from (1.4) that $u' + rv' - r = \frac{\chi}{c}u^2v^{m-1} + \frac{r}{c}uv^m > 0$, which implies the conclusion of the lemma.

Lemma 3.3. (i) If 1 < m < 2 and (1.4)-(1.5) has a solution (u, v) with $u(\xi) > r$ for all sufficiently negative ξ , then $c > \sqrt{\chi r}$.

(ii) If m=2 and (1.4)-(1.5) has a solution, then $c>\sqrt{\chi r}$.

Proof. (i) Since $u(\infty) = 0$, it follows that there exists the smallest $\xi = \xi_0$ such that $u(\xi_0) = r$ and $u'(\xi_0) \leq 0$. Evaluating the first equation at ξ_0 gives $u'(\xi_0) = \frac{r}{c}v(\xi_0)[-c^2 + \chi r v^{m-2}(\xi_0)] \leq 0$, and hence $c^2 \geq \chi r/v^{2-m}(\xi_0) > \chi r$ (since 0 < v < 1).

(ii) Let (u, v) be a solution of (1.4)-(1.5) with m = 2. Then the equation for u can be written as

$$u' = c(r - u) - \frac{1}{c}v[c^2r - \chi u^2] = c(r - u) - \frac{1}{c}v[c^2r - \chi r^2 + \chi r^2 - \chi u^2]$$
$$= c(r - u) - \frac{\chi}{c}v[r^2 - u^2] - \frac{r}{c}v[c^2 - \chi r] = p_0(\xi)(u - r) + \frac{r}{c}[\chi r - c^2]v,$$

where $p_0(\xi) := -c + \frac{\chi}{c}(r+u)v$. Given any $\xi \in (-\infty, \infty)$, applying the variation of constants formula on $[\xi_0, \xi]$ (with $\xi_0 < \xi$) we get

$$u(\xi) - r = e^{\int_{\xi_0}^{\xi} p_0(\eta) d\eta} [u(\xi_0) - r] + \frac{r}{c} [\chi r - c^2] \int_{\xi_0}^{\xi} e^{\int_{\eta}^{\xi} p_0(s) ds} v(\eta) d\eta.$$
 (3.3)

Since $p_0(\xi) \to -c$ as $\xi \to -\infty$, it follows that $e^{\int_{\xi_0}^{\xi} p_0(\eta) d\eta} \to 0$ as $\xi_0 \to -\infty$. Letting $\xi_0 \to -\infty$ in (3.3) gives, for $\xi \in (-\infty, \infty)$,

$$u(\xi) - r = \frac{r}{c} [\chi r - c^2] \int_{-\infty}^{\xi} e^{\int_{\eta}^{\xi} p_0(s) \, ds} v(\eta) \, d\eta.$$

Assume that $\chi r - c^2 \ge 0$. Since v > 0, it follows that $u(\xi) \ge r$ for all $\xi \in (-\infty, \infty)$, contradicting $u(\infty) = 0$. Therefore $\chi r - c^2 < 0$. This shows (ii).

3.1. Existence of solutions of (1.4) approaching E_1 as $\xi \to -\infty$. We assume that m > 1. The goal in this section is to prove the existence of solutions (u, v) of (1.4) satisfying $(u(\xi), v(\xi)) \to E_1$ as $\xi \to -\infty$. As mentioned in the introduction, since v^{m-1} is not differentiable at v = 0 for 1 < m < 2, we cannot linearize (1.4) at E_1 and then apply the unstable manifold theorem. We shall directly prove the existence of the desired solutions. For this, we need to study the vector filed of (1.4). Solving the u-nuclline equation $c^2(r - u - rv) + \chi u^2 v^{m-1} = 0$ for u in a neighborhood of E_1 with $v \ge 0$ gives a unique solution

$$u_{-}(v) = \frac{2c^{2}r(1-v)}{c^{2} + \sqrt{c^{4} - 4c^{2}r\chi v^{m-1}(1-v)}} \qquad (0 \le v \le v_{0}), \tag{3.4}$$

where

$$v_0 = \begin{cases} h^{-1}(\frac{c^2}{4r\chi}) & \text{if } c^2 < 4\chi r \frac{1}{m} (1 - \frac{1}{m})^{m-1}, \\ 1 - \frac{1}{m} & \text{if } c^2 \ge 4\chi r \frac{1}{m} (1 - \frac{1}{m})^{m-1}, \end{cases}$$

in which h^{-1} is the inverse function of $h(v):=v^{m-1}(1-v)$ that reaches its maximum value over the interval [0,1] at $v=1-\frac{1}{m}$ with the value $\frac{1}{m}(1-\frac{1}{m})^{m-1}$ and is monotonically increasing over $[0,1-\frac{1}{m}]$. It follows that as $v\to 0^+$,

$$u_{-}(v) - r = \frac{\chi}{c^{2}} u_{-}^{2}(v) v^{m-1} - rv = \begin{cases} \frac{\chi}{c^{2}} r^{2} v^{m-1} [1 + O(v^{m-1})] & \text{if } 1 < m < 2, \\ r[\frac{\chi r}{c^{2}} (1 + O(v)) - 1] v & \text{if } m = 2, \\ -rv + O(v^{m-1}) & \text{if } m > 2. \end{cases}$$
(3.5)

Implicitly differentiate the equation $c^2[r - u_-(v) - rv] + \chi u_-(v)^2 v^{m-1} = 0$ to get, for $v \in (0, v_0)$,

$$\frac{du_{-}(v)}{dv} = \frac{\chi(m-1)u_{-}^{2}(v)v^{m-2} - c^{2}r}{c^{2} - 2\chi u_{-}(v)v^{m-1}},$$
(3.6)

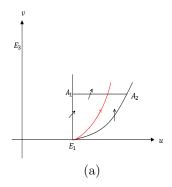
and by virtue of (3.5) to get, for sufficiently small v > 0,

$$\frac{du_{-}(v)}{dv} = \begin{cases} > 0 & \text{if } 1 < m < 2, \text{ or if } m = 2 \text{ and } c < \sqrt{\chi r} \\ < 0 & \text{if } m > 2, \text{ or if } m = 2 \text{ and } c > \sqrt{\chi r}. \end{cases}$$
(3.7)

Note that for m=2 and $c=\sqrt{\chi r}$, $u_-(v)\equiv r$ and $u'_-(v)\equiv 0$.

Therefore, the graph of $u_-(v)$ in the (u,v) plane for $v \ge 0$ small lies to the right of the vertical line u=r if 1 < m < 2 or if m=2 and $c < \sqrt{\chi r}$, and to the left if m>2 or if m=2 and $c > \sqrt{\chi r}$. Using this information we prove the following:

Lemma 3.4. (i) For every m > 1 and c > 0, there is a unique (up to a translation) solution (u, v) of (1.4) defined on $(-\infty, 0]$ such that $(u, v)(-\infty) = E_1$, u+rv-r > 0, v' > 0, and u satisfies that (a) $u \equiv r$ if m = 2 and $c = \sqrt{\chi r}$, (b) u' > 0 if 1 < m < 2 or if m = 2 and $c < \sqrt{\chi r}$; furthermore,



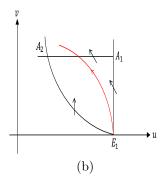


FIGURE 3. The arcs E_1A_2 in (a) and (b) are the nullclines of (1.4) for 1 < m < 2 and m > 2 respectively; the red curves are solutions of (1.4) approaching E_1 as $\xi \to -\infty$ claimed in Lemma 3.4 (i)

the following asymptotic formulas hold as $\xi \to -\infty$:

$$v(\xi) = \left[\frac{(m-1)r}{c}|\xi|\right]^{-\frac{1}{m-1}}[1+o(1)],$$

$$u(\xi) - r = \begin{cases} \frac{\chi r^2}{c^2}[v(\xi)]^{m-1}\left[1+O\left([v(\xi)]^{m-1}\right)\right] & \text{if } 1 < m < 2, \\ -rv(\xi)[1-\frac{\chi r}{c^2}][1+O(v(\xi))] & \text{if } m = 2, \\ -rv(\xi)[1+O(v(\xi))+O(v^{m-2}(\xi))] & \text{if } m > 2. \end{cases}$$

$$(3.8)$$

(ii) Let $\varphi_{m,c} = (u_{m,c}, v_{m,c})$ be the solution obtained in (i). Regarding $u_{m,c}$ as a function of $v = v_{m,c}$ for sufficiently small v > 0, we have

(a) $u_{m_1,c}(v) < u_{m_2,c}(v)$ for every $m_1 > m_2 > 1$ and every c > 0;

(b) $u_{m,c_1}(v) < u_{m,c_2}(v)$ for every m > 1 and $c_1 > c_2 > 0$.

3.2. Proof of Lemma 3.4 (i) for 1 < m < 2 and m = 2 with $c < \sqrt{\chi r}$. We divide the proof into several steps.

Step 1. Choose $\bar{v}_0 \in (0, v_0)$ sufficiently small such that $u' = -crv + \chi r^2 v^{m-1} > 0$ from (1.4) on the segment $\overline{E_1 A_1} - \{E_1\}$ where $A_1 = (r, \bar{v}_0)$, and $u'_-(v) > 0$ for $v \in (0, \bar{v}_0]$ from (3.7). Let $A_2 = (u_-(\bar{v}_0), \bar{v}_0)$. See Fig. 3 (a), where the arc $\overline{E_1 A_2}$ is the graph of $u = u_-(v)$ for $v \in [0, \bar{v}_0]$. Let $\varphi_A = (u_A, v_A)$ be the solution of (1.4) with the initial point $A \in \overline{A_1 A_2}$. Consider the backward flow of φ_A . Since u' > 0 and v' > 0 on $\overline{E_1 A_1} - \{E_1\}$, v' > 0 on $\overline{A_1 A_2}$ and u' = 0 and v' > 0 on $\overline{E_1 A_2} - \{E_1\}$, it follows from the continuous dependence of φ_A on A and the connectedness of $int(\overline{A_1 A_2})$ that there exist A_3 and A_4 (with A_3 lying to the left of A_4 if $A_3 \neq A_4$) such that the backward flow of φ_A leaves the region \mathcal{R}_0 bounded by $\overline{E_1 A_1} \cup \overline{A_1 A_2} \cup \overline{A_2 E_1}$ through a point in $int(\overline{E_1 A_1})$ (at a finite $\xi < 0$) for each $A \in int(\overline{A_1 A_3})$, through a point in $int(\overline{E_1 A_2})$ for each $A \in int(\overline{A_4 A_2})$, and remains in $int(\mathcal{R}_0)$ for each $A \in \overline{A_3 A_4}$ over the left maximal interval $(\xi_A, 0]$ of its existence. Since the vector field of (1.4) in $int(\mathcal{R}_0)$ satisfies u' > 0 and v' > 0, it follows that $\lim_{\xi \to \xi_A} \varphi_A(\xi_A) = E_1$ for every $A \in \overline{A_3 A_4}$. Since (1.4) is not smooth at E_1 , we

cannot conclude from the general global existence theorem that $\xi_A = -\infty$; instead, we prove this in the next step.

Step 2. Let $A \in \overline{A_3A_4}$ and $(u,v) := \varphi_A$. We show $\xi_A = -\infty$ and asymptotic formula (3.8). Since $\frac{dv}{d\xi} = \frac{1}{c}uv^m = \frac{1}{c}(r+o(1))v^m$ as $\xi \to \xi_A$ and v > 0, we have $v^{-m}\frac{dv}{d\xi} = \frac{1}{c}(r+o(1))$, and integrating over $[\xi,0]$ gives

$$\frac{1}{m-1} \left[\left(\frac{1}{v(\xi)} \right)^{m-1} - \left(\frac{1}{v(0)} \right)^{m-1} \right] = \frac{1}{c} \int_{\xi}^{0} [r + o(1)] d\xi = \frac{r}{c} |\xi| [1 + o(1)] \quad (\xi \to \xi_A).$$

Since $v(\xi) \to 0$ as $\xi \to \xi_A$, we conclude from the above equation that $\xi_A = -\infty$ and the asymptotic formula for v as stated in (3.8).

Next, we show the asymptotic formula of u. Since u > r, v > 0, v' > 0, u = r + o(1), and v = o(1) as $\xi \to -\infty$, we regard u as a function of v with v > 0 small to get, for 1 < m < 2 and c > 0,

$$\begin{split} \frac{du}{dv} &= -\frac{c^2(u-r)}{uv^m} + \frac{\chi u^2 v^{m-1} - c^2 r v}{uv^m} \\ &= -\frac{c^2}{rv^m} [1 + O(u-r)](u-r) + \frac{\chi r^2 [1 + O(u-r)] v^{m-1} - c^2 r v}{rv^m} [1 + O(u-r)] \\ &= -\frac{c^2}{rv^m} [1 + O(u-r)](u-r) + \frac{\chi r^2 [1 + O(u-r) + O(v^{2-m})] v^{m-1}}{rv^m} [1 + O(u-r)] \\ &= -\frac{c^2}{rv^m} [1 + O(u-r)](u-r) + \frac{\chi r}{v} [1 + O(u-r) + O(v^{2-m})], \end{split}$$
(3.9)

and for m=2 and $c<\sqrt{\chi r}$,

$$\frac{du}{dv} = -\frac{c^2}{rv^2} [1 + O(u - r)](u - r) + \frac{\chi r - c^2}{v} [1 + O(u - r)]. \tag{3.10}$$

Note that, for m > 1 and c > 0,

$$\frac{d}{dv}e^{\frac{c^2}{r(1-m)v^{m-1}}} = \frac{c^2}{rv^m}e^{\frac{c^2}{r(1-m)v^{m-1}}},$$
(3.11)

and

$$\begin{split} & \int_0^v \frac{1}{s} e^{\frac{c^2}{r(1-m)s^{m-1}}} \, ds \\ & = \frac{r}{c^2} v^{m-1} e^{\frac{c^2}{r(1-m)v^{m-1}}} - \frac{r}{c^2} (m-1) \int_0^v s^{m-2} e^{\frac{c^2}{r(1-m)s^{1-m}}} \, ds \\ & = \frac{r}{c^2} v^{m-1} e^{\frac{c^2}{r(1-m)v^{m-1}}} + O(v^{2(m-1)}) e^{\frac{c^2}{r(1-m)v^{m-1}}} \\ & = \frac{r}{c^2} v^{m-1} [1 + O(v^{m-1})] e^{\frac{c^2}{r(1-m)v^{m-1}}} \, . \end{split}$$

Applying the variation of constants formula to (3.9) we have, for 1 < m < 2 and c > 0.

$$u(v) - r = e^{-\frac{c^2}{r(1-m)v^{m-1}}} \left[O((u(v)-r)^2) \int_0^v \frac{1}{s^m} e^{\frac{c^2}{r(1-m)s^{m-1}}} dv + r\chi [1 + O(u(v)-r) + O(v^{m-1})] \int_0^v \frac{1}{s} e^{\frac{c^2}{r(1-m)s^{m-1}}} ds \right]$$

$$= O\left((u(v)-r)^2 \right) + \frac{r^2\chi}{c^2} v^{m-1} [1 + O(u(v)-r) + O(v^{m-1})] [1 + O(v^{m-1})]$$

$$= O\left((u(v)-r)^2 \right) + \frac{r^2\chi}{c^2} v^{m-1} [1 + O(u(v)-r) + O(v^{m-1})], \tag{3.12}$$

frow which we conclude

$$u(v) - r = \frac{r^2 \chi}{c^2} v^{m-1} [1 + O(v^{m-1})] \qquad (v \to 0^+).$$

Similarly, by applying the variation of constants formula to (3.10) we get for m=2 and $c<\sqrt{\chi r}$,

$$u(r) - r = \frac{r(\chi r - c^2)}{c^2} v[1 + O(v)] \qquad (v \to 0^+).$$

This shows the asymptotic formula for u as stated in (3.8).

Step 3. We prove the uniqueness of the solution as stated in the lemma. It suffices to show from Steps 1 and 2 that $A_3=A_4$. Let $(u_3,v_3):=\varphi_{A_3}$ and $(u_4,v_4):=\varphi_{A_4}$. Since $v_3'>0$ and $v_4'>0$, we can regard u_3 and u_4 as a function of $v\in(0,\bar{v}_0)$, both satisfying the scalar equation $\frac{du}{dv}=c^2r(v^{-m}-v^{1-m})\frac{1}{u}-\frac{c^2}{v^m}+\chi\frac{1}{v}u$. A substraction gives

$$\frac{d(u_4 - u_3)}{dv} = \left[-\frac{c^2 r}{u_3 u_4} \left(\frac{1}{v^m} - \frac{1}{v^{m-1}} \right) + \frac{\chi}{v} \right] (u_4 - u_3).$$

Assume by contradiction that $A_3 \neq A_4$ so that $u_4(v) > u_3(v)$ for $0 < v < \bar{v}_0$. Since $u_3(v) = r + o(1)$ and $u_4(v) = r + o(1)$ $v^{-m} \gg v^{1-m}$ and $v^{-m} \gg v^{-1}$ for v > 0 sufficiently small, we have, for sufficiently small $\tilde{v}_0 < \bar{v}_0$ and $0 < v \le \tilde{v}_0$, $-\frac{c^2r}{u_3u_4}\left(\frac{1}{v^m} - \frac{1}{v^{m-1}}\right) + \frac{\chi}{v} < -\frac{c^2}{2r}v^{-m}$, and thus $\frac{d(u_4 - u_3)}{dv} < -\frac{c^2}{2r}v^{-m}(u_4 - u_3)$. Upon an integration over $[v, \tilde{v}_0]$ gives

$$\ln \frac{u_4(\bar{v}_0) - u_3(\bar{v}_0)}{u_4(v) - u_3(v)} < -\frac{c^2}{2r} \int_v^{\bar{v}_0} v^{-m} \, dv = \frac{c^2}{2r(m-1)} (\bar{v}_0^{1-m} - v^{1-m}) < 0,$$

contradicting $u_4(v) - u_3(v) \to 0$ as $v \to 0^+$. This shows $A_3 = A_4$. The proof of Lemma 3.4 (i) for 1 < m < 2 is complete.

3.3. Proof of Lemma 3.4 (i) for m > 2 and for m = 2 with $c > \sqrt{\chi r}$. The proof is similar to that for 1 < m < 2 in the previous subsection.

Step 1. Choose $\bar{v}_0 \in (0, v_0)$ sufficiently small such that $u' = -crv + \chi r^2 v^{m-1} < 0$ on the segment $\overline{E_1 A_1} - \{E_1\}$ where $A_1 = (r, \bar{v}_0)$, and $u'_-(v) > 0$ for $v \in (0, \bar{v}_0]$ from (3.7). Let $A_2 = (u_-(\bar{v}_0), \bar{v}_0)$. See Fig. 3 (b), where the arc $E_1 A_2$ is the graph of $u = u_-(v)$ for $v \in [0, \bar{v}_0]$. It follows from the same reasoning as in the previous

proof that there exist A_3 and A_4 (with A_3 lying to the left of A_4 if $A_3 \neq A_4$) such that the backward flow of φ_A for $A \in \overline{A_3A_4}$ stays in $int(\mathcal{R}_0)$ for $A \in \overline{A_3A_4}$ where

the region \mathcal{R}_0 bounded by $\overline{E_1A_1} \cup \overline{A_1A_2} \cup \overline{E_1A_2}$. Since the vector field of (1.4) in $int(\mathcal{R}_0)$ is C^1 smooth (including on its boundary) and satisfies u' < 0 and v' > 0, it follows that φ_A is defined on $(-\infty, 0]$ with $\varphi_A(-\infty) = E_1$. The same proof in Step 3 in the previous subsection for 1 < m < 2 can be used to show that $A_3 = A_4$ for the present case, which gives the uniqueness of the solution claimed in Lemma 3.4

(i) for $m \geq 2$. From the u nullcline equation of (1.4), it follows that $\widetilde{E_1} A_2$ lies above the segment $\overline{E_1} E_3$, and hence the solution we found satisfies $u(\xi) + rv(\xi) - r > 0$ for $\xi \in [0 - \infty)$.

Step 2. It remains to show the asymptotic formula (3.8) for m > 2. The formula for v is obtained by the same proof for 1 < m < 2; so is the asymptotic formula for u when m = 2 and $c > \sqrt{\chi r}$. The asymptotic formula for u with m > 2 needs a slight modification of the proof there. In this case, since u' < 0, u < r, v' > 0 and $(u, v) \to E_1$ as $\xi \to -\infty$, (3.9) becomes

$$\frac{du}{dv} = -\frac{c^2}{rv^m}[1 + O(r-u)](u-r) - \frac{c^2}{v^{m-1}}[1 + O(r-u) + O(v^{m-2})].$$

Applying the variation of constants formula and using (3.11) and

$$\begin{split} & \int_0^v \frac{1}{s^{m-1}} e^{\frac{c^2}{r(1-m)s^{m-1}}} \, ds \\ & = \frac{r}{c^2} v e^{\frac{c^2}{r(1-m)v^{m-1}}} - \frac{r}{c^2} (m-1) \int_0^v e^{\frac{c^2}{r(1-m)s^{1-m}}} \, ds \\ & = \frac{r}{c^2} v e^{\frac{c^2}{r(1-m)v^{m-1}}} + O(v^m) e^{\frac{c^2}{r(1-m)v^{m-1}}} \\ & = \frac{r}{c^2} v [1 + O(v^{m-1})] e^{\frac{c^2}{r(1-m)v^{m-1}}}, \end{split}$$

we have, as in (3.12),

$$u(v) - r = O((u - r)^{2}) - rv[1 + O(r - u) + O(v^{m-2})],$$

and thus

$$u(v) - r = -rv[1 + O(v) + O(v^{m-2})]$$
 $(v \to 0^+),$

as desired. This completes the proof of Lemma 3.4 (i) under the current assumptions on m and c.

3.4. Proof of Lemma 3.4 (ii). (a) Let $u_i := u_{m_i,c}(v)$ (i = 1, 2), which satisfy

$$\frac{du_i}{dv} = \frac{c^2(r - u_i - rv)}{u_i v^m} - \frac{\chi}{v} u_i \qquad (i = 1, 2).$$

Upon substraction, we have

$$\begin{split} \frac{d(u_1 - u_2)}{dv} &= \frac{c^2(r - u_1 - rv)}{u_1} \left(\frac{1}{v^{m_1}} - \frac{1}{v^{m_2}}\right) \\ &+ \frac{1}{v^{m_2}} \left(\frac{c^2(r - u_1 - rv)}{u_1} - \frac{c^2(r - u_1 - rv)}{u_2}\right) - \frac{\chi}{v}(u_1 - u_2) \\ &= p(v)(u_1 - u_2) + q(v), \end{split}$$

where

$$p(v) = \frac{c^2 r(1-v)}{u_1 u_2 v^{m_2}} + \frac{\chi}{v}, \qquad q(v) = \frac{c^2 (r - u_1 - rv)}{u_1} \left(\frac{1}{v^{m_1}} - \frac{1}{v^{m_2}}\right).$$

Applying the variation of constants formula gives

$$u_{1}(v_{0}) - u_{2}(v_{0}) = exp\left(-\int_{v}^{v_{0}} p(s) ds\right) [u_{1}(v) - u_{2}(v)] + \int_{v}^{v_{0}} exp\left(-\int_{s}^{v_{0}} p(\tau) d\tau\right) q(s) ds.$$
 (3.13)

Note that $p(v) \ge \chi/v$ and so $exp\left(-\int_v^{v_0} p(s) \, ds\right) \le v^{\chi}/v_0^{\chi}$. Letting $v \to 0^+$ in (3.13) gives

$$u_1(v_0) - u_2(v_0) = \int_0^{v_0} \exp\left(-\int_s^{v_0} p(\tau) d\tau\right) q(s) ds.$$
 (3.14)

Note that q(v) < 0 (since $v^{-m_1} > v^{-m_2}$ and $r - u_1 - rv < 0$). It follows that $u_1(v_0) - u_2(v_0) < 0$ for every small $v_0 > 0$, that is, $u_1(v) - u_2(v) < 0$ for every small v > 0. This proves (ii) (a).

(b) Let $u_i := u_{m,c_i}(v)$ (i = 1, 2), which satisfy

$$\frac{du_i}{dv} = \frac{c_i^2(r - u_i - rv)}{u_i v^m} - \frac{\chi u_i}{v}.$$
 (i = 1, 2).

Upon substraction, we have

$$\frac{d(u_1 - u_2)}{dv} = \frac{(r - u_1 - rv)}{u_1 v^m} (c_1^2 - c_2^2) + \frac{c_2^2 r(1 - v)}{v^m} \left(\frac{1}{u_1} - \frac{1}{u_2}\right) - \frac{\chi}{v} (u_1 - u_2)$$
$$= p_1(v)(u_1 - u_2) + q_1(v),$$

where

$$p_1(v) = -\left(\frac{c_2^2 r(1-v)}{u_1 u_2 v^m} + \frac{\chi}{v}\right), \qquad q_1(v) = \frac{(r-u_1-rv)}{u_1 v^m} (c_1^2 - c_2^2).$$

Applying the same argument we get (3.14) in which p and q are replaced by p_1 and q_1 respectively. Since $q_1(v) < 0$ because of $c_1 > c_2$ and $r - u_1 - rv < 0$, it follows that $u_1(v_0) - u_2(v_0) < 0$ for every small $v_0 > 0$, that is, $u_1(v) - u_2(v) < 0$ for every small v > 0. This proves (ii) (b).

3.5. Further results.

Lemma 3.5. Let $(u,v) := (u_{m,c}, v_{m,c})$ be a solution given in Lemma 3.4 (i) for some m > 1 and c > 0. Assume that it is defined on $(-\infty, \infty)$ with u > 0 and $(u,v)(\infty) = E_3$. Then v' > 0 on $(-\infty, \infty)$; furthermore,

(i) if 1 < m < 2, then there is $\xi_0 \in (-\infty, \infty)$ such that $u'(\xi) > 0$ for $\xi \in (-\infty, \xi_0)$ and $u'(\xi) < 0$ for $\xi > \xi_0$, and moreover the maximum value $u(\xi_0)$ satisfies that $u(\xi_0) < r + \min\{2r, 4\chi r^2/c^2\}$;

(ii) if
$$m > 2$$
 or if $m = 2$ and $c > \sqrt{\chi r}$, then $u'(\xi) < 0$ for all $\xi \in (-\infty, \infty)$.

Proof. Since u > 0 on $(-\infty, \infty)$ and $v(\xi) > 0$ for sufficiently negative ξ , from the second equation of (1.4) we conclude that v > 0 on $(-\infty, \infty)$, and hence v' > 0 on $(-\infty, \infty)$.

(i) Let 1 < m < 2. Since $u(\xi) > r$ for sufficiently negative ξ from Lemma 3.4 (i) and $u(\infty) = 0$, it follows that there exists the smallest $\xi_0 \in (-\infty, \infty)$ such that $u'(\xi_0) = 0$ and $u'(\xi) < 0$ for $\xi \in (-\infty, \xi_0)$. Differentiating the first equation of (1.4) and evaluating at ξ_0 gives $u''(\xi_0) = \frac{1}{c}v'(\xi_0)[-c^2r + (m-1)\chi u^2(\xi_0)v^{m-2}(\xi_0)] \le 0$, so that

$$(m-1)\chi u^2(\xi_0)v^{m-2}(\xi_0) \le c^2 r. \tag{3.15}$$

We claim that $u''(\xi_0) < 0$. If this is not true, i.e. $u''(\xi_0) = 0$, then a further differentiation yields $u'''(\xi_0) = (m-1)(m-2)\frac{\chi}{c}u^2(\xi_0)v^{m-3}(\xi_0)(v')^2(\xi_0) < 0$, which implies that $u'(\xi_0) = 0$ is a local maximum value of u', contradicting that u' > 0 for $\xi < \xi_0$. We thus conclude that $u'(\xi) < 0$, for $\xi - \xi_0 > 0$ small.

We now claim that $u'(\xi) < 0$ for all $\xi > \xi_0$. Assume that this is false, and there exists $\xi_1 > \xi_0$ such that $u'(\xi_1) = 0$, $u'(\xi) < 0$ for $\xi \in (\xi_0, \xi_1)$, and $u''(\xi_1) = \frac{1}{c}v'[-c^2r + (m-1)\chi u^2(\xi_1)v^{m-2}(\xi_1)] \ge 0$, which together with (3.15) yields that $(m-1)\chi u^2(\xi_1)v^{m-2}(\xi_1) \ge c^2r \ge (m-1)\chi u^2(\xi_0)v^{m-2}(\xi_0)$. However this contradicts the fact that the function $(m-1)\chi u^2v^{m-2}$ is strictly decreasing over the interval (ξ_0, ξ_1) . Therefore, ξ_0 is the unique zero of u'. It follows from (3.4) that $u'(\xi_0) \le 2r$, and then evaluating the u equation in (1.4) at ξ_0 gives $u(\xi_0) - r < (\chi/c^2)u^2(\xi_0)v^{m-2}(\xi_0) < 4\chi r^2/c^2$, yielding the estimate for $u(\xi_0)$ as stated in the lemma. This shows (i) of the lemma.

(ii) We now consider $m \geq 2$ or, m = 2 and $c > \sqrt{\chi r}$. We have $u'(\xi) < 0$ for sufficiently negative ξ from Lemma 3.4 (i). Thus, assume on the contrary that there is ξ_0 such that u' < 0 on $(-\infty, \xi_0)$ and $u'(\xi) = 0$. Using a similar argument to the above we derive that $u'(\xi) > 0$ for all $\xi > \xi_0$, which contradicts the assumption that $u(\infty) = 0$. Therefore we must have $u'(\xi) < 0$ for all $\xi \in (-\infty, \infty)$. This shows (ii) of the lemma.

Lemma 3.6. For any m > 1 and $c > \max\{2\sqrt{r}, 2\sqrt{\chi r}\}$, $\varphi_{m,c} = (u_{m,c}, v_{m,c})$ is a solution to (1.4)-(1.5), with the prescribed properties in Theorem 3.1.

Proof. Fix m and c satisfying the conditions as stated in the lemma. Let \mathcal{R} be the region bounded by $\overline{E_1E_1^*} \cup \overline{E_1^*E_3} \cup \overline{E_3E_1}$, where the arc $\overline{E_1^*E_3}$ is the connecting orbit of (2.1) from E_1^* to E_3 obtained in Theorem 2.1 (i) (see Fig. 4). We claim that \mathcal{R} is positive invariant for (1.4) (with the fixed m and c) and show this as follows. On $\overline{E_1E_1^*} - \{E_1\}$, v' = 0 and u' = c(r - u) < 0; on $int(\overline{E_3E_1})$ the vector filed of (1.4) points to the interior of \mathcal{R} from Lemma 3.2; on $int(\overline{E_1^*E_3})$, the outer normal is given by $\overrightarrow{n} = [\frac{1}{c}uv, -c(r-u-rv) - \frac{\chi}{c}u^2]$ from (2.1), and the dot product of \overrightarrow{n} and the vector of (1.4) is equal to $\frac{1}{c}uv[c(r-u-rv) + \frac{\chi}{c}u^2v^{m-1}] - \frac{1}{c}uv^m[c(r-u-rv) + \frac{\chi}{c}u^2] = u(r-u-rv)(v^m-v) < 0$ (since r-u-rv < 0 and 0 < v < 1).

Since $\varphi_{m,c}(\xi) \to E_1$ as $\xi \to -\infty$ and E_1^* lies to the right of E_1 , it follows that the orbit of $\varphi_{m,c}(\xi)$ lies inside \mathcal{R} for sufficiently negative ξ , and thus the whole orbit of $\varphi_{m,c}(\xi)$ stays inside \mathcal{R} for all $\xi \in (-\infty, \infty)$, yielding $\varphi_{m,c}$ is defined on $(-\infty, \infty)$

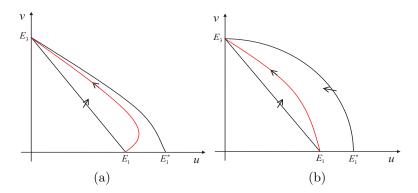


FIGURE 4. Red curves in (a) and (b) are the solutions of (1.4)-(1.5) claimed in Lemma 3.6 for 1 < m < 2 and m > 2 respectively; the curves $E_1^*E_3$ are the heteroclinic solutions of (2.1) obtained in Theorem 2.1.

with $u_{m,c} > 0$ and $v'_{m,c} > 0$, so that $\varphi_{m,c}(\infty) = E_3$. Then the assertion of the lemma follows from Lemma 3.5.

Lemma 3.7. Let m > 1. Let $\varphi_{m,c}$ be the solution of (1.4) given in Lemma 3.4 (i). Let

 $c_0 = c_0(m) = \inf\{c > 2\sqrt{r}: \varphi_{m,c} \text{ is a solution of (1.4)-(1.5)}\}.$

Then φ_{m,c_0} is a solution of (1.4)-(1.5) with the properties descried in Theorem 3.1.

Proof. We assume that 1 < m < 2. The case for $m \ge 2$ can be similarly proved. It follows from Lemma 3.6 that $c_0 := c_0(m)$ is well defined. The dentition of c_0 implies that there exists a sequence $\{c_n\}_{n=1}^{\infty}$ such that $c_n>c_0,\ c_n\to c_0$ as $n \to \infty$, and $\varphi_{c_n} = (u_n, v_n) := \varphi_{m,c_n}$ is a solution of (1.4)-(1.5) associated with $c=c_n$. Since $u_n(-\infty)=r$ and $u_n(\infty)=0$ and $u_n'(\xi)>0$ for sufficiently negative ξ , it follows from Lemma 3.5 that each u'_n changes sign exactly once and $u_n = r$ exactly once. By translation invariance we may assume that $u_n(0) = r$. Since $u'_n(0) < 0$, it follows from (1.4) that $v_n(0) > \frac{\chi r}{c_n^2}$. Furthermore, since $0 < u_n \le r$ 2r and $0 < v_n < 1$, it follows that φ_{c_n} is uniformly bounded, so are φ'_{c_n} from (1.4) and φ''_{c_n} via differentiating (1.4). Applying Arzela-Ascoli's theorem yields that there exists a subsequence of $\{\varphi_{c_n}\}$, which is still denoted by $\{\varphi_{c_n}\}$, and C^1 functions u_0 and v_0 defined on $(-\infty, \infty)$ such that $\{\varphi_{c_n}\}$ converges to (u_0, v_0) and $\{\varphi'_{c_n}\}\$ to (u'_0,v'_0) uniformly on every compact interval of $(-\infty,\infty)$, and (u_0,v_0) is a solution of (1.4) with $c = c_0$ on $(-\infty, \infty)$, satisfying $u_0(0) = r$, $u_0(\xi) \ge 0$, $0 \le v_0(\xi) \le 1$, $v_0'(\xi) \ge 0$ for $\xi \in (-\infty, \infty)$, $v_0(0) \ge \frac{\chi r}{2c_0^2}$. We claim that $u_0(\xi) > 0$ for $\xi \in (-\infty, \infty)$. For otherwise at the first point $u_0 = 0$, we would have $v_0 < 1$, and $u'_0 = cr(1 - v_0) > 0$, which is contradiction to $u_0 \ge 0$. This claim also gives $v_0'>0$ so that $(u_0,v_0)(-\infty)=E_1$ and $(u_0,v_0)(\infty)=E_3$. The uniqueness of the solution of (1.4) approaching E_1 as $\xi \to -\infty$ from Lemma 3.4 (i) implies that (u_0, v_0) is a translation of φ_{m,c_0} . Then applying Lemma 3.5 yields the assertions of the lemma.

3.6. **Proof of Theorem 3.1. Step 1.** Fix m > 1 and let $c_0 = c_0(m)$ be defined in Lemma 3.7. Let $c > c_0$ and $\varphi_c := \varphi_{m,c}$ be the solution given in Lemma 3.4. We show

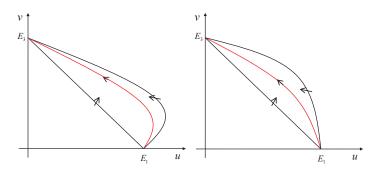


FIGURE 5. A sketch of positive invariant sets \mathcal{R} used in the Proof of Theorem 3.1.

that φ_c is a solution of (1.4)-(1.5), by using the positive invariant set \mathcal{R} of (1.4) (with the current fixed m and c) bounded by the segment $\overline{E_1E_3}\cup \overline{E_1E_3}$, where $int(\overline{E_1E_3})$ is the orbit of $\varphi_{c_0}:=\varphi_{m,c_0(m)}$ defined in Lemma 3.7 (see Fig. 5). To show the positive invariance of \mathcal{R} , from Lemma 3.2 it suffices to verify that the vector field of (1.4) on $int(\overline{E_1E_3})$ points to the interior of \mathcal{R} . Taken an arbitrary point (u,v) on $int(\overline{E_1E_3})$, the outer normal at (u,v) is given by $\overrightarrow{n}=[\frac{1}{c_0}uv^m,-c_0(r-u-rv)-\frac{\chi}{c_0}u^2v^{m-1}]$, thus the dot product of \overrightarrow{n} and the vector of (1.4) at (u,v) is equal to $\frac{1}{c_0}uv^m[c(r-u-rv)+\frac{\chi}{c_0}u^2v^{m-1}]=uv^m(r-u-rv)(\frac{c}{c_0}-\frac{c_0}{c})<0$ (since r-u-rv<0), which gives what we claimed.

Now, it follows from Lemma 3.4 (i) and (ii) (b) that φ_c lies inside \mathcal{R} near E_1 , hence the full orbit of φ_c stays in \mathcal{R} by the positive invariance of \mathcal{R} , yielding that φ_c is defined on $(-\infty,\infty)$ with $u_{m,c} > 0$ and $v'_{m,c} > 0$, so that $\varphi_c(\infty) = E_3$. It then follows from Lemma 3.5 and Lemma 3.4, φ_c is a solution of (1.4)-(1.5) with described properties in Theorem 3.1 (i), except for the asymptotic formulas given in (3.2) as $\xi \to \infty$. We show these formulas as follows.

We linearize (1.4) at E_3 and find that the linearized system has the coefficient matrix $J(E_3)$ given in (2.2) with two negative eigenvalues $\lambda_{\pm} = \frac{1}{2}(-c \pm \sqrt{c^2 - 4r})$ and associated eigenvectors $(c\lambda_{\pm},1)^{\top}$ respectively. The stable manifold theorem implies that the 1-dimensional strongly stable manifold $W_c^{ss}(E_3)$ of (1.4) is tangent to the eigenvector $(c\lambda_{-},1)^{\top}$. To show the asymptotic formulas as $\xi \to \infty$ in (3.2) for $\varphi_c = (u_c,v_c)$, it suffices to show that φ_c cannot lie on $W_c^{ss}(E_3)$. This follows from the following two facts. Fact 1. For $2\sqrt{r} < c_2 < c_1$, the portion of $W_{c_2}^{ss}(E_3)$ near E_3 in the first quadrant lies below the corresponding portion of $W_{c_1}^{ss}(E_3)$. This is because that the slope of the tangent vector $(c\lambda_{-},1)^{\top}$ given by

$$\frac{1}{c\lambda_{-}} = -\frac{1 - \sqrt{1 - \frac{4r}{c^2}}}{2r}$$

is negative and decreasing as c decreases. Fact 2. For $c_0(m) < c_2 < c_1$, the orbit of φ_{c_2} lies above the orbit of φ_{c_1} . This fact can be proved by using Lemma 3.4 (ii) and the argument as used in the first paragraph of this proof. Based on these two facts, if for some $c_0(m) < c_1$ the orbit of φ_{c_1} lies on $W_{c_1}^{ss}(E_3)$, then for any c_2 with

 $c_0(m) < c_2 < c_1$, since the eigenvector $[c_2\lambda_+, 1]^{\top}$ lies below $W_{c_2}^{ss}(E_3)$, the orbit of φ_{c_2} cannot approach to E_3 as $\xi \to \infty$. This contradicts the definition of φ_{c_2} . Therefore, the orbit of φ_c for any $c > c_0(m)$ must be tangent to the eigenvector $[c\lambda_+, 1]^{\top}$ as $\xi \to \infty$, which yields its asymptotic formula as stated in 3.1 (i). We thus complete the proof Theorem 3.1 (i).

Step 2. It is clear that the assertion (a) in Theorem 3.1 (ii) follows Lemmas 3.6 and 3.7, and the assertion (b) follows Lemma 3.3. It remains to show the assertion (c), i.e., the monotonicity of $c_0(m)$. Let $m_1 > m_2 > 1$. To show that $c_0(m_1) \le c_0(m_2)$, it suffice to show that φ_{c,m_1} is a solution of (1.4)-(1.5) where $c := c_0(m_2)$. To this end, we again use the positive invariant set \mathcal{R} as defined above except that its boundary curve $int(\widetilde{E_1E_3})$ is the orbit of φ_{c,m_2} (see Fig. 5). The positive invariance of \mathcal{R} for flows of (1.4) with $m = m_1$ and $c = c_0(m_2)$ follows from Lemma 3.2 and the following: taking an arbitrary point (u,v) on $int(\widetilde{E_1E_3})$, with the outer normal $\overrightarrow{n} = [\frac{1}{c}uv^{m_2}, -c(r-u-rv) - \frac{\chi}{c}u^2v^{m_2-1}]$, the dot product of \overrightarrow{n} and the vector of (1.4) is equal to $\frac{1}{c}uv^{m_2}[c(r-u-rv) + \frac{\chi}{c}u^2v^{m_1-1}] - \frac{1}{c}uv^{m_1}[c(r-u-rv) + \frac{\chi}{c}u^2v^{m_2-1}] = u(r-u-rv)(v^{m_2}-v^{m_1}) < 0$ (since r-u-rv < 0 and $v^{m_2}-v^{m_1} > 0$), showing that the vector field of (1.4) points to the interior of \mathcal{R} on $int(\widetilde{E_1E_3})$.

It follows from Lemma 3.4 (i) and (ii) (a) that φ_{c,m_1} lies inside \mathcal{R} near E_1 , hence the full orbit of φ_{c,m_1} stays in \mathcal{R} . It follows that φ_{c,m_1} is defined for all $\xi \in (-\infty, \infty)$ with $u_{c,m_1} > 0$ and $v'_{c,m_1} > 0$, so that $\varphi_{c,m_1}(\infty) = E_3$. Applying Lemma 3.5 gives that φ_{c,m_1} is a solution of (1.4)-(1.5). This completes the proof of Theorem 3.1 (ii).

4. **Discussion.** The propagation of traveling bands of bacterial chemotaxis was the typical picture in the chemotactic pattern formation of bacterial (see [1, 2]). When r = 0 (without cell growth), it has been shown (see the references mentioned in the introduction) that the Keller-Segel model (1.2) will produce the traveling bands (i.e. traveling pulses) only if $0 \le m < 1$, where the wave speed has a minimum value independent of the consumption rate parameter m (e.g., see [32]). Our results in this paper show that if a chemical uptake cell kinetics is included (i.e. r > 0), the resulting model (1.2) can produce the traveling bands (i.e., nonmonotonic wavefronts) only if 1 < m < 2, where the minimum wave speed exists but depends on the parameter m. As we know, this is the first result that includes the cell growth into the Keller-Segel model (1.1) directly such that the resulting model still can generate the traveling bands to recover the original motivation of Keller-Segel model. We find that the profile of traveling bands, the range of the parameter m and minimum wave speed for the existence of traveling bands are significantly different between the cases r=0 and r>0. These differences imply that the collective interaction between the cell kinetics and chemical consumption rate is vital to generate traveling bands. In particular there are two biological implications of our results. First if the uptake type cell growth occurs, the traveling bands can be generated by increasing chemical consumption rate. On the other hand if the traveling bands are formed by the non-monotonic wavefronts, the cell growth must be considered and then the chemical consumption rate will be important to determine the nature of wave propagation such as the wave speed and wave profile. Our research provides a new perspective to understand the role of cell growth in wave band formation in (bacterial) chemotaxis.

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