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Travelling Fronts in Nonlinear Diffusion Equations

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Summary

In Fisher's model for the migration of advantageous genes, in epidemic models and in the theory of combustion similar existence problems for travelling fronts and waves occur. For a general two-dimensional system of ordinary differential equations depending on a parameter the existence of trajectories connecting stationary points is established. For systems derived from diffusion problems these trajectories describe the shape of a travelling front, the corresponding value of the parameter is the propagation speed. The method allows to determine the exact value of the minimal speed in Fisher's model for all interesting choices of selection parameters, i.e. for intermediate heterozygotes and for inferior heterozygotes.

About forty years ago the fundamental population genetic models have been developed by Fisher, Wright, Haldane and others. For continuous time these models are described by nonlinear ordinary differential equations for genotype or gene frequencies (see e.g. [3], [8], [9]). Fisher ([5], [6]) considered also nonlinear diffusion equations for spatially distributed populations, posed the problem of travelling population fronts and conjectured the existence of a minimal propagation speed. Kolmogorov, Petrovskij, Piskunov [16] investigated a class of nonlinear diffusion equations

$$u_t = u_{ss} + F(u),\; F(u) > 0 \text{ in } (0, 1),\; F(0) = F(1) = 0 \tag{*}$$

which contains Fisher's model in the case of complete dominance of the advantageous gene. They proved the existence of a closed half-line of possible speeds. Their main object was to prove that the solution of the diffusion equation starting from a step function converges towards a front with minimal speed. Various other convergence theorems for similar equations, partially related to the theory of combustion, have been given by Kanel' ([11], [12], [13], [14]). Kendall [15] applied the idea of the proof [16] to the problem of epidemic waves.

Kolmogorov's [16] condition that the function F' assumes its maximum for $u=0$ allows to determine the minimal propagation speed explicitely, but it is not satisfied in Fisher's model with the exception of complete or almost complete dominance. Rothe [17] observed that a closed half-line of speeds exists also in the general case (*), he gave a characterization of the minimal speed and computed the minimal speed for Fisher's model for all cases of intermediate heterozygotes. Related results have been shown by Aronson and Weinberger [1]. In the present paper we consider a two-dimensional vector field depending on a parameter and give sufficient conditions for trajectories connecting singular points. In applications to diffusion problems the trajectory corresponds to a travelling front and the parameter to the speed. It turns out that a certain monotonocity property (14) is the crucial condition which allows a unified treatment of all aforementioned cases.

If in Fisher's model one gene is advantageous, but heterozygotes are inferior, then the function F in the diffusion equation has a sign change. The general theory yields immediately two classes of monotone travelling fronts with positive and negative propagation speeds, respectively. We show that there is exactly one additional monotone front, which is the only front with boundary conditions 1 at $-\infty$ and 0 at $+\infty$. Again, for Fisher's model the speeds of all fronts can be explicitely computed.

The convergence problem has been investigated by Aronson and Weinberger [1], Fife and McLeod [4], Rothe [17], Hoppensteadt [10].

1. Trajectories Connecting Singular Points

Consider a system of differential equations

$$\dot{u}=f(u,v), \quad \dot{v}=g(u,v), \tag{1}$$

where $f, g: \mathbb{R}^2 \to \mathbb{R}$ are continuously differentiable. Suppose $\mathscr{D}$ is some open and simply connected domain and (u_1, v_1), (u_2, v_2) are the only stationary points in $\mathscr{D}$. Let (u_1, v_1) be a saddle point and (u_2, v_2) a stable focus. We want to ensure that the unstable manifold of the saddle point, when continued to $t \to +\infty$, enters the focus. A possible way to do this is to construct two piecewise differentiable non-intersecting arcs ϑ and θ in $\mathscr{D}$ connecting the two singularities as indicated in Fig. 1.

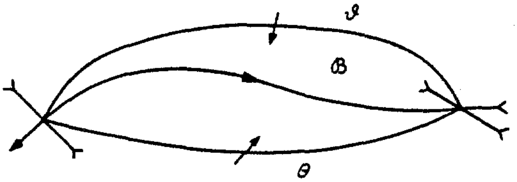

Fig. 1

If the direction of the vector field (f, g) along these arcs is always pointing inward (with respect to the open domain $\mathscr{B}$ enclosed by the two arcs) then the unstable manifold arrives finally at (u_2, v_2).

In the following we use this idea in a special situation, where the stationary points are $(\alpha, 0)$ and $(\beta, 0)$, $\alpha < \beta$, and ϑ, θ are defined as

$$\left.\begin{array}{c}\vartheta: u=\vartheta_1(t), \quad v=\vartheta_2(t), \quad -\infty<t<+\infty, \\ \alpha<\vartheta_1(t)<\beta, \quad 0<\vartheta_2(t), \\ \vartheta_1\to\beta,\ \vartheta_2\to 0 \text{ for } t\to+\infty;\ \vartheta_1\to\alpha,\ \vartheta_2\to\bar{\vartheta}\geq 0 \text{ for } t\to-\infty \\ |\dot{\vartheta}_1|+|\dot{\vartheta}_2|\neq 0;\ |\dot{\vartheta}_1|+|\dot{\vartheta}_2|\to 0 \text{ for } |t|\to\infty;\ -\infty<\lim\ \dot{\vartheta}_2/\dot{\vartheta}_1<0.\end{array}\right\} \quad (2)$$

$$u\equiv\alpha \text{ for } 0<v<\bar{\vartheta}, \quad (3)$$

$$\theta:\ v\equiv 0 \text{ for } \alpha<u<\beta. \quad (4)$$

The domain $\mathscr{B}$ is bounded by the arc (2), the u-axis, and possibly a segment of the v-axis.

The set $[\alpha, \beta]\times\mathbb{R}$ does not contain any other singularities than $(\alpha, 0)$, $(\beta, 0)$. Thus we require

$$\left.\begin{array}{c} f(u,0)=g(u,0)=0 \text{ for } u=\alpha,\beta, \\ (u,v)\in[\alpha,\beta]\times\mathbb{R}-\{(\alpha,0),(\beta,0)\}\Rightarrow|f(u,v)|+|g(u,v)|\neq 0.\end{array}\right\} \quad (5)$$

The point $(\alpha, 0)$ is a saddle point if

$$f_u g_v < f_v g_u. \quad (6)$$

The conditions

$$f_v>0, \quad g_u>0 \quad (7)$$

ensure that the unstable direction satisfies $dv/du<0$, and the stable direction $dv/du>0$. Similarly at $(\beta, 0)$ the conditions

$$f_u+g_v<0, \quad 0<4(f_u g_v-f_v g_u)\leq(f_u+g_v)^2 \quad (8)$$

guarantee a stable focus. The additional conditions

$$f_u>g_v, \quad f_v>0, \quad g_u<0 \quad (9)$$

yield that the main and the side direction are both negative and $|dv/du|$ is greater for the side direction.

The condition that the field is directed inward on the boundary of $\mathscr{B}$ can be expressed as

$$f(\vartheta_1,\vartheta_2)\dot{\vartheta}_2-g(\vartheta_1,\vartheta_2)\dot{\vartheta}_1\geq 0 \text{ for } t\in\mathbb{R}, \quad (10)$$

$$f(\alpha,v)\geq 0 \text{ for } 0<v<\bar{\vartheta}, \quad (11)$$

$$g(u,0)\geq 0 \text{ for } \alpha<u<\beta. \quad (12)$$

Theorem 1: *If conditions (2) to (12) are satisfied then the closed domain $\bar{\mathscr{B}}$ contains the unstable manifold of the saddle point. If continued to $+\infty$, this trajectory enters the stable focus $(\beta, 0)$. Thus there is a trajectory connecting $(\alpha, 0)$ and $(\beta, 0)$.*

Remark: By "unstable manifold" we mean the part of the unstable manifold leaving $(\alpha, 0)$ into $u>0$, $v>0$.

The proof of the theorem is standard and it is outlined only for completeness:
1. Suppose a trajectory is in the interior $\mathscr{B}$ at $t=0$. Then it stays in $\mathscr{B}$ for every finite t. For if $t_0<\infty$ were the smallest t for which $(u(t_0), v(t_0)) \notin \mathscr{B}$ then either $(u_0, v_0)=(u(t_0), v(t_0))$ is one of the two singular points or it is any other boundary point of $\mathscr{B}$. The first case is easily excluded. In view of (10)—(12) the trajectory is tangent to the boundary (or to one of the components of the boundary if the point is a corner). By an appropriate rotation or reflection we can achieve that the tangent direction is parallel to the positive u-axis and the domain $\mathscr{B}$ is below the arc. If we choose u as a local coordinate for the arc ϑ and the trajectory φ we have

$$f(u, \vartheta(u))\, \vartheta'(u) \geq g(u, \vartheta(u)), \; f(u, \varphi(u))\, \varphi'(u)=g(u, \varphi(u)).$$

In view of $dv/dt=0$, $du/dt>0$ we have $g(u_0, v_0)=0$, $f(u_0, v_0)>0$. For $F(u, v)=g(u, v)/f(u, v)$, $w=\vartheta-\varphi$ we have $w'(u) \geq F(u, \vartheta(u))-F(u, \varphi(u)) \geq -K\,|w(u)|$. Since t_0 was minimal, $w(u)>0$ for $u<u_0$, $w(0)=0$. But then from $w' \geq -K w$ follows $w(u) \leq 0$ for $u \leq u_0$.

2. If a trajectory is in $\partial \mathscr{B}$ for $t=t_0$ then it stays in $\bar{\mathscr{B}}$ for all t. This is obvious if the trajectory is one of the points $(\alpha, 0)$, $(\beta, 0)$. Otherwise a similar argument as in 1. can be used.

3. We show that the unstable manifold φ is contained in $\bar{\mathscr{B}}$. It is sufficient to show that the unstable manifold is in $\bar{\mathscr{B}}$ for $-\infty<t<t_0$ for some finite t_0. This is trivial for $\bar{\vartheta}>0$. Now let $\bar{\vartheta}=0$. Suppose the unstable manifold arrives at some point $P \notin \bar{\mathscr{B}}$. Choose any point $\bar{P} \notin \bar{\mathscr{B}}$ between φ and ϑ close to P and consider the trajectory $\bar{\varphi}$ through $\bar{P}$ for $t \to -\infty$. For $\bar{P}$ sufficiently close to P the trajectory follows the unstable manifold arbitrary close and has common points with the interior $\mathscr{B}$. Following this trajectory to $-\infty$ we obtain a contradiction to 1.

Lemma 2: *The closed domain $\bar{\mathscr{B}}$ contains the main direction of the focus at $(\beta, 0)$. The side manifold of the focus at $(\beta, 0)$ has no points in common with the open domain $\mathscr{B}$.*

Proof: There are trajectories beginning in the interior of $\mathscr{B}$ which enter $(\beta, 0)$ in the main direction. If the main direction were not contained in $\mathscr{B}$, these trajectories would leave $\bar{\mathscr{B}}$, which gives a contradiction to part 1 of the proof of theorem 1. Suppose the side manifold has a point P in common with the interior $\mathscr{B}$. There are trajectories starting in the interior of $\mathscr{B}$, close to P, which enter the focus along the two opposite main directions. Some of these must leave $\bar{\mathscr{B}}$ in contradiction to part 1 of the proof of theorem 1.

2. General Results on Travelling Fronts

In this paragraph we assume that the system (1) depends on an additional parameter $c \in \mathbb{R}$ such that $f, g\colon \mathbb{R}^3 \to \mathbb{R}$ are continuously differentiable,

$$\dot{u}=f(u, v, c), \qquad \dot{v}=g(u, v, c). \tag{13}$$

We require that conditions (5) to (7) are satisfied for all c and that conditions (8), (9) are satisfied for all $c>c^*$, whereas the stationary point $(\beta, 0)$ is a stable vortex for $c<c^*$.

Definition: *A solution $\varphi=(\varphi_1, \varphi_2)$ of the system (13) for a particular c with $\varphi(t)\in[\alpha,\beta]\times[0,\infty)$ for all $t\in\mathbb{R}$,*

$$\varphi(t)\to(\alpha,0) \text{ for } t\to-\infty, \quad \varphi(t)\to(\beta,0) \text{ for } t\to+\infty,$$

is called a front, and c is called the speed of the front.

It is clear that there are no fronts for speeds less than c^*.

Theorem 3: *Let f, g have the following monotonocity property. If $c_2>c_1\geq c^*$ then for all $(u,v)\in[\alpha,\beta]\times[0,\infty)$*

$$g(u,v,c_1)\,f(u,v,c_2)\geq f(u,v,c_1)\;g(u,v,c_2). \tag{14}$$

In addition, let condition (12) be fulfilled for all $c\geq c^*$. Then the set of possible speeds is an upper half-line or empty.

Proof: Suppose c_1 is a speed. To c_1 corresponds a trajectory $u(t)=\varphi_1(t)$, $v(t)=\varphi_2(t)$,

$$\dot\varphi_1=f(\varphi_1,\varphi_2,c_1), \qquad \dot\varphi_2=g(\varphi_1,\varphi_2,c_1).$$

For $c>c_1$ follows from (14)

$$f(\varphi_1,\varphi_2,c)\,\dot\varphi_2\geq g(\varphi_1,\varphi_2,c)\,\dot\varphi_1.$$

Then theorem 1 shows that c is a speed.

Define c_0 as the infinum of all speeds. Clearly $c^*\leq c_0\leq+\infty$.

Corollary 4: *Assume the hypothesis of theorem 3. If c_1, c_2 are speeds, $c_2>c_1\geq c^*$, and φ_1, φ_2 are the corresponding fronts, then the trajectory of φ_1 is contained in the closed domain formed by φ_2 and the u-axis.*

Theorem 5: *Assume the hypothesis of theorem 3, in addition:*

For every $c\geq c^*$ there is $\bar v=\bar v(c)>0$ such that $g(u,\bar v,c)<0$ for all $u\in(\alpha,\beta)$. (15)

Then: If $c_0<+\infty$ then c_0 is a speed.

Proof: Assume c_0 is not a speed. Let $c>c_0$ be any speed with front ϑ and let $\mathscr{B}$ be the domain bounded by ϑ and the u-axis. In view of (14) the vector field for $c=c_0$ points outward. Using the same arguments as in the proof of theorem 1, we see that the unstable manifold φ for $c=c_0$ does not enter the open domain $\mathscr{B}$ as long as it remains in $[\alpha,\beta]\times\mathbb{R}_+$. Condition (15) prevents that φ goes to infinity in the domain $[\alpha,\beta]\times\mathbb{R}_+$. Thus φ arrives at $u=\alpha$ or $u=\beta$ for some finite t. In both cases the unstable manifold for $c>c_0$, where $c-c_0$ is sufficiently small, has the same behaviour, which leads immediately to a contradiction.

Remark: Without an additional assumption like (15) theorem 4 seems to be wrong: Consider an example where φ and the side manifold (for $t\to-\infty$) both go to infinity, and all trajectories between these two bend downward and go into the main direction.

Corollary 6: *Under the hypothesis of theorem 5 the minimal speed c_0 can be characterized as the infimum of all c for which a function ϑ satisfying* (2) *and* (10) *exists.*

Theorem 7: *Let the conditions of theorem 5 be satisfied.*

i) *If $c_0 > c^*$ is finite then the front corresponding to c_0 is the side manifold of the focus $(\beta, 0)$.*

ii) *For $c > c_0$ the front with speed c arrives in the main direction at $(\beta, 0)$ unless for all $\tilde{c} \in [c_0, c]$ the fronts have identical trajectories.*

Proof:
i) Let φ_0 be the front with speed c_0 and let $\mathscr{B}$ be the domain between φ_0 and the u-axis. Let φ be the unstable manifold for a $c \in (c^*, c_0)$. The trajectory φ does not enter the open domain $\mathscr{B}$ and does not arrive at $(\beta, 0)$. But for this c the side manifold of the focus (traced backward for $t \to -\infty$) is in $\mathscr{B}$ and thus separates all other trajectories entering $(\beta, 0)$ from φ. For $c \to c_0$ the trajectory φ merges with the side manifold before it can meet any other trajectory entering $(\beta, 0)$.

ii) Suppose $c_1 > c > c_0$. Let ϑ, ϑ_1 be the front with speed c, c_1 and $\mathscr{B}$ the domain between ϑ and the u-axis. ϑ_1 is contained in $\bar{\mathscr{B}}$. By lemma 2 the side manifold at $(\beta, 0)$ for c_1 has no points in common with $\mathscr{B}$. Thus, if ϑ_1 does not arrive in the main direction at $(\beta, 0)$ then the trajectories of ϑ and ϑ_1 coincide. (Note that, according to the proof of theorem 1, a trajectory from $\mathscr{B}$ cannot arrive on the boundary of $\mathscr{B}$ in finite time.)

3. Travelling Fronts for a Nonlinear Diffusion Equation

We consider a diffusion equation

$$u_t = u_{ss} + F(u), \tag{16}$$

where F is continuously differentiable and satisfies the conditions

$$F(0) = F(1) = 0, \ F(u) > 0 \text{ in } (0, 1), \ F'(0) > 0, \ F'(1) < 0. \tag{17}$$

A travelling front is a solution $u(s, t) = u(s - ct)$ with

$$u(-\infty) = 1, \quad u(+\infty) = 0, \quad 0 \le u \le 1. \tag{18}$$

If such a front exists then the function u of one variable is a solution of the boundary value problem of the ordinary differential equation

$$\ddot{u} = -c\,\dot{u} + F(u) \tag{19}$$

with boundary conditions (18). We apply the substitutions $u \to 1 - u$, $v = \dot{u}$, then

$$\dot{u} = v, \quad \dot{v} = -c\,v + F(1 - u). \tag{20}$$

This system has the form (13) and satisfies all required conditions. The saddle point is $(\alpha, 0)=(0,0)$, the focus $(\beta, 0)=(1,0)$, and $c^*=2\sqrt{F'(0)}$. Condition (12), (11), the monotonocity property (14) and condition (15) are fulfilled. By theorem 3 and 4 there is a possibly empty closed upper half-line of speeds. We use corollary 5 to exclude $c_0=+\infty$ and to compute c_0. Since along any front $\dot{u}=v>0$, we can represent the arc ϑ in (2), (10) in the form $v=\varrho(u)$, where $\varrho:[0,1]\to[0,\infty)$ is continuously differentiable and satisfies

$$\varrho(u)>0 \text{ for } u\in(0,1), \qquad \varrho(1)=0, \qquad \varrho'(1)<0. \tag{21}$$

Then condition (10) is equivalent with

$$\varrho\,\varrho'+c\,\varrho-F(1-u)\geq 0$$

or

$$c\geq \sup_{0<u<1}\left\{-\varrho'(u)+\frac{F(1-u)}{\varrho(u)}\right\}. \tag{22}$$

Since there are functions of the required type the existence of large speeds is established.

If we choose for ϱ the function $\bar{\varrho}$ representing the front with speed $\bar{c}$ then $\bar{\varrho}'=-\bar{c}+F(1-u)/\bar{\varrho}$ and the supremum is $\bar{c}$. In particular, for $\bar{c}=c_0$, we have (going back to the notation of (19)) the

Theorem 8: *The minimal speed in problem* (19) (18) *is finite. It is characterized by*

$$c_0=\inf_{\varrho}\sup_{0<u<1}\left\{\varrho'(u)+\frac{F(u)}{\varrho(u)}\right\}, \tag{23}$$

where ϱ is any continuously differentiable function on $[0,1]$ *with the properties* (21).

Corollary 9: *The minimal speed in problem* (19) *satisfies*

$$2\sqrt{F'(0)}\leq c_0\leq 2\sqrt{L}, \text{ where } L=\sup_{0<u<1}\frac{F(u)}{u}. \tag{24}$$

Proof: In (23) choose $\varrho(u)=\varkappa u$ with $\varkappa>0$. Then $c_0\leq\varkappa+L/\varkappa$. Minimize over $\varkappa$.

Corollary 10: *The front with speed c enters* $(0,0)$ *in the direction*

$$\frac{dv}{du}=\begin{cases}\dfrac{1}{2}\sqrt{c^2-4F'(0)}-\dfrac{c}{2} & \text{for } c>c_0,\\[2mm] -\dfrac{1}{2}\sqrt{c^2-4F'(0)}-\dfrac{c}{2} & \text{for } c=c_0.\end{cases} \tag{25}$$

Proof: Follows from theorem 7.

4. Fisher's Population Genetic Model

In Fisher's model for the migration of advantageous genes we have an equation for the gene frequency

$$u_t = u_{ss} + u(1-u)\left(1-\tau-(2-\sigma-\tau)u\right) \tag{26}$$

where σ, 1, τ are the viabilities of the three genotypes. For $\sigma \geq 1 > \tau$ (heterozygotes not inferior) we can easily transform the equation into

$$u_t = u_{ss} + F(u), \qquad F(u) = u(1-u)(1+\nu u), \tag{27}$$

where

$$\nu = (\sigma-1)/(1-\tau) - 1, \qquad -1 \leq \nu < +\infty. \tag{28}$$

Theorem 11: *The minimal speed in Fisher's equation* (27) *is*

$$c_0 = \begin{cases} 2 & \text{for } -1 \leq \nu \leq 2, \\ \dfrac{\nu+2}{\sqrt{2\nu}} & \text{for } \qquad \nu \geq 2. \end{cases} \tag{29}$$

Proof: From (24) follows

$$F'(0) = 1 \leq \frac{c_0^2}{4} \leq L = \begin{cases} 1 & \text{for } -1 \leq \nu \leq 1 \\ \dfrac{(\nu+1)^2}{4\nu} & \text{for } \quad 1 \leq \nu \end{cases} \tag{30}$$

Hence we know $c_0 = 2$ for $|\nu| \leq 1$. A simple computation shows that for $\nu > 0$ the function ("Huxley pulse")

$$u(t) = [1 + \exp(\sqrt{\nu/2}\, t)]^{-1} \tag{31}$$

is a front travelling with speed $c_H = (\nu+2)/\sqrt{2\nu}$. For $\nu = 2$ we have $c_H = 2$, thus $c_0 \leq 2$, and according to (30), $c_0 = 2$. Since the function F and thus c_0 increases with ν (follows from (23)) we have $c_0 = 2$ for $1 \leq \nu \leq 2$.

For $\nu \geq 2$

$$v(t) = \dot{u}(t) = -\sqrt{\nu/2}\, \exp(\sqrt{\nu/2}\, t)\, [1 + \exp(\sqrt{\nu/2}\, t)]^{-2},$$
$$dv/du \to -\sqrt{\nu/2} \text{ for } t \to +\infty.$$

On the other hand, by (25) the slowest travelling front arrives at $(0, 0)$ with the side direction

$$\frac{dv}{du} = -\frac{1}{2}\sqrt{c_0^2 - 4} - \frac{c_0}{2},$$

which shows $c_H = c_0$. Moreover, for $\nu \geq 2$ the function u defined by (31) is the slowest travelling front. Unfortunately the slowest travelling front for $-1 \leq \nu < 2$ has not yet been determined.

5. Source Terms with a Sign Change

Suppose the function F in the diffusion equation (16) has a sign change,

$$F(0) = F(\mu) = F(1) = 0, \qquad 0 < \mu < 1 \tag{32}$$

$$F(u) < 0 \text{ for } 0 < u < \mu, \qquad F(u) > 0 \text{ for } \mu < u < 1 \tag{33}$$

$$F'(0)<0, \quad F'(\mu)>0, \quad F'(1)<0. \tag{34}$$

For any travelling front $u=u(s-ct)$ the corresponding ordinary differential equation is given by (19). Now the singularities are two saddle points at (0, 0), (1, 0) and a third stationary point at $(\mu, 0)$ which is a stable focus for $c \geq 2\sqrt{F'(0)}$, an unstable focus for $c \leq -2\sqrt{F(0)}$, and a vortex or center in between. For initial data in $\mu \leq u \leq 1$ we have the same situation as for equation (16) with conditions (17). Thus we get a half-line $[c_0, \infty)$ of speeds corresponding to monotonely decreasing fronts with boundary conditions

$$u(-\infty)=1, \quad u(+\infty)=\mu. \tag{35}$$

These fronts correspond to trajectories connecting the saddle point (1, 0) with the focus $(\mu, 0)$. On the other hand there is a half-line $(-\infty, -\bar{c}_0]$, $\bar{c}_0>0$, of speeds of monotonely decreasing fronts travelling to the left with boundary conditions

$$u(-\infty)=\mu, \quad u(+\infty)=0, \tag{36}$$

connecting the unstable focus $(\mu, 0)$ to the saddle point (0, 0). It is rather obvious that there is a certain value c_1 between c_0 and $-\bar{c}_0$ for which the unstable manifold of (1, 0) continues into the stable manifold of (0, 0). Indeed we can show

Theorem 12: *Under the conditions* (32), (33), (34) *the set of speeds of monotonely decreasing travelling fronts for equation* (16) *consists of two half-lines* $(-\infty, -\bar{c}_0]$, $[c_0, \infty)$, *and an isolated point* c_1, *whereby*

$$-\infty < -\bar{c}_0 \leq -2\sqrt{F'(\mu)} < c_1 < 2\sqrt{F'(\mu)} \leq c_0 < \infty. \tag{37}$$

c_1 *may be positive or not. For* $c \geq c_0$, $c=c_1$, $c \leq -\bar{c}_0$ *the front satisfies boundary conditions* (35), (18), (36), *respectively.*

Remark: In addition there are monotonely increasing fronts and various non-monotonous, in particular oscillating, fronts. To each front u travelling with speed c there is a front $\bar{u}$, $\bar{u}(t)=u(-t)$, travelling with speed $-c$.

Proof:
1) The assertions on c_0, $\bar{c}_0$ follow trivially from theorem 8.

2) For $c=c_0$ the unstable manifold of (1, 0) enters $(\mu, 0)$ for $t \to +\infty$. Let $\varrho:[0, 1] \to \mathbb{R}$ be a continuously differentiable function with $\varrho(0)=\varrho(1)=0$, $\varrho>0$ in (0, 1), $\varrho'(0)>0$, $\varrho'(1)<0$. Then $v=-\varrho(u)$ defines a smooth arc connecting (0, 0) and (1, 0). Denote the arc again by ϱ and let $\mathscr{B}$ be the open domain between ϱ and the segment [0, 1] of the u-axis. The condition that the field direction $(du/dt, dv/dt)$ is pointing outward with respect to $\mathscr{B}$ is expressed by

$$\varrho'(u)\,v - c\,v - F(u) \leq 0 \quad \text{for} \quad v=-\varrho(u).$$

Thus for a fixed $\hat{c}$ with

$$\hat{c} < \inf_{0<u<1} \left\{ \varrho'(u) + \frac{F(u)}{\varrho(u)} \right\} \tag{38}$$

no trajectory can enter $\mathscr{B}$ through ϱ. An argument as in the proof of theorem 1 shows that the unstable manifold φ of (1, 0) cannot enter the open domain $\mathscr{B}$

whereas the stable manifold of $(0,0)$ is contained in $\bar{\mathscr{B}}$. Consequently (with strict inequality in (38)) φ does not arrive at $(0,0)$. In view of $dv/du \approx -\hat{c}$ for large negative values of v the manifold φ arrives at $u=0$, $v<0$ for a finite t. On the other hand, for $c=c_0$, the unstable manifold of $(1,0)$ goes to $(\mu, 0)$. Thus for c slightly less than c_0 the unstable manifold of $(1,0)$ crosses the u-axis close to $(\mu, 0)$, but for $c=\hat{c}$ it crosses the negative v-axis. Since the trajectories depend continuously on c for finite values of t, there is a number $c_1 \in (\hat{c}, c_0)$ for which the unstable manifold of $(1,0)$ is connected to $(0,0)$.

3) We show that c_1 is unique. Describe the phase curve connecting $(1,0)$ to $(0,0)$ in the form $v=-\varrho(u)$, and let $\mathscr{B}$ be the domain between this trajectory and the u-axis. Choose any $c \neq c_1$, then the inner product between the field vector $(v, -cv-F(u))$ and the inner normal on ϱ with respect to $\mathscr{B}$ is

$$\varrho'(u)\,v - c\,v - F(u) = \left(c_1 + F(u)/v\right) v - c\,v - F(u) = (c-c_1)\,\varrho(u).$$

For $c>c_1$ the field is strictly pointing inward, for $c<c_1$ it is strictly pointing outward. By the argument of theorem 1 one can immediately check that for $c>c_1$ the unstable manifold of $(1,0)$ is contained in $\mathscr{B}$ and the stable manifold of $(0,0)$ is not. For $c<c_1$ the opposite holds. For $c \neq c_1$ the two singular points cannot be connected.

6. Application to Fisher's Model

If heterozygotes are inferior we have $\sigma>1$, $\tau>1$ in Fisher's equation (26). By a simple substitution we arrive at

$$u_t = u_{ss} + u\,(1-u)\,(u-\mu), \tag{39}$$

where

$$\mu = (\tau-1)/(\sigma+\tau-2), \qquad 0<\mu<1. \tag{40}$$

We give a complete description of the wave-like solutions $u(s-ct)$ of equation (39). Because of the reflection symmetry of the equation we can restrict ourselves to nonnegative speeds $c \geq 0$. Further, without loss of generality, we assume $\sigma \geq \tau$ which entails $\mu \in (0, 1/2]$.

Define the following critical values of the parameter c (see Fig. 2).

$$\begin{aligned} c^* &= 2\sqrt{\mu(1-\mu)}, \\ c_0 &= \begin{cases} (1+\mu)/\sqrt{2} & \text{for } 0<\mu\leq 1/3, \\ c^* & \text{for } 1/3 \leq \mu \leq \frac{1}{2}, \end{cases} \\ c_1 &= \frac{1}{\sqrt{2}} - \mu\sqrt{2}. \end{aligned} \tag{41}$$

Then

$$\begin{aligned} &c^* < c_1 < c_0 \quad \text{for } 0<\mu<\bar{\mu}, \\ &c_1 < c^* < c_0 \quad \text{for } \bar{\mu}<\mu<1/3, \end{aligned} \tag{42}$$

$$c_1 < c^* = c_0 \quad \text{for } 1/3 < \mu < 1/2,$$

where

$$\bar{\mu} = (1 - \sqrt{2/3})/2.$$

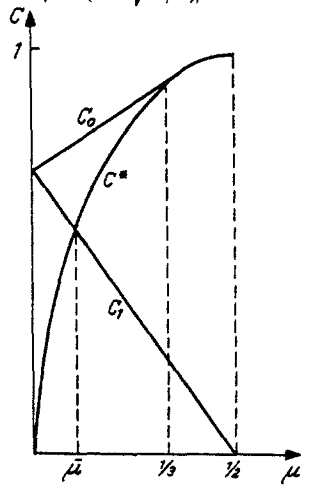

Fig. 2

Theorem 13: *Let c^*, c_0, and c_1 be defined as in* (41). *Then:*

i) *For $c \geq c_0$ there is a monotonely decreasing front with boundary conditions $u(-\infty) = 1$, $u(+\infty) = \mu$.*

ii) *For $c \geq c^*$ there is a monotonely increasing front with boundary conditions $u(-\infty) = 0$, $u(+\infty) = \mu$.*

iii) *For $c = c_1$ there is a unique monotone front with boundary condition $u(-\infty) = 1$, $u(+\infty) = 0$.*

iv) *For $0 < c < c^*$ there is an oscillating wave with boundary conditions $u(-\infty) = 0$, $u(+\infty) = \mu$.*

v) *For $c_1 < c < c^*$ (impossible for $\mu < \bar{\mu}$) there is an oscillating front with $u(-\infty) = 1$, $u(+\infty) = \mu$.*

vi) *For* $\max(c_1, c^*) < c < c_0$ *(impossible for $\mu > 1/3$) there is a front with boundary conditions $u(-\infty) = 1$, $u(+\infty) = \mu$, which decreases monotonely to some value $u < \mu$, then increases towards μ for $t \to +\infty$.*

vii) *For $c = 0$ there are periodic solutions and a unique nonvanishing front with $u(-\infty) = u(+\infty) = 0$.*

Remark: For equation (39) the number $\bar{c}_0$ defined in theorem 12 is always equal to c^*.

Proof: The assertion follows from theorem 11, formula 41, and a simple discussion of the phase plane. The function

$$u(t) = (\exp(t/\sqrt{2}) + 1)^{-1}, \qquad v = u(1-u)/\sqrt{2}, \tag{43}$$

represents the front with speed c_1 for all $\mu \in (0, 1)$.

7. Travelling Epidemic Fronts

Kendall [15] considers the diffusion equations

$$u_t = -u\,(v + v_{ss}), \qquad v_t = u\,(v + v_{ss}) - v \tag{44}$$

as a model for the spread of an epidemic (u is the density of susceptibles, v of the infectious). The boundary conditions are

$$\begin{gathered} u(-\infty, t) = \alpha, \qquad u(+\infty, t) = \beta, \qquad 0 < \alpha < \beta, \\ v(-\infty, t) = v(+\infty, t) = 0. \end{gathered} \tag{45}$$

If a travelling wave $u(s - c\,t)$, $v(s - c\,t)$ exists then

$$-c\,\dot{u} = -u\,(v + \ddot{v}), \qquad -c\,\dot{v} = u\,(v + \ddot{v}) - v. \tag{46}$$

We add the equations, $c\,\dot{u} + c\,\dot{v} = v$, and integrate the first equation after a substitution for v,

$$c \log u = \dot{v} + c\,u + c\,v - c\,\gamma.$$

Thus, after a rescaling in t,

$$\begin{aligned} \dot{u} &= \left(1 + \frac{1}{c^2}\right) v - (\gamma - u + \log u), \\ \dot{v} &= (\gamma - u + \log u) - v. \end{aligned} \tag{47}$$

From the boundary conditions at $\pm\infty$ follows $\gamma = \beta - \log\beta \geq 1$ and $\gamma = \alpha - \log\alpha$. Thus necessarily

$$\alpha - \log\alpha = \beta - \log\beta. \tag{48}$$

In view of $\alpha < \beta$ the two densities α and β determine each other uniquely.

Elementary considerations show that the system (47) satisfies conditions (5) through (9), (12), (14), (15), where

$$c^* = 2\sqrt{\beta(\beta - 1)}. \tag{49}$$

We apply theorems 3, 4 and corollary 5. We choose the arc ϑ as an isocline of the vector field (47), parametrized by u,

$$\varrho(u) = \varkappa(\gamma - u + \log u), \qquad \varkappa > 0.$$

Then condition (10) is equivalent with

$$\left[\left(1 + \frac{1}{c^2}\right)\varkappa - 1\right]\varkappa\left(1 - \frac{1}{u}\right) \leq \varkappa - 1 \quad \text{for } \alpha \leq u \leq \beta.$$

For $\varkappa = 2\beta/(2\beta - 1)$ this condition is satisfied for all $c \geq 2\sqrt{\beta(\beta - 1)}$ which shows $c_0 = c^*$. We state our result as

Theorem 14: *The boundary value problem*

$$-c\,\dot{u} = -u\,(v + \ddot{v}), \qquad -c\,\dot{v} = u\,(v + \ddot{v}),$$

$$u(-\infty) = \alpha, \qquad u(+\infty) = \beta, \qquad v(\pm\infty) = 0, \qquad 0 < \alpha < \beta,$$

has a solution iff the conditions

$$\alpha - \log \alpha = \beta - \log \beta, \qquad c \geq c^* = 2\sqrt{\beta(\beta-1)}$$

are satisfied.

The necessary condition (48) can be interpreted in epidemiological terms: suppose the density of susceptibles before infection β is fixed and $\bar{\alpha} < 1$ is the unique solution of equation (48). If the actual density of susceptibles after infection α is greater than $\bar{\alpha}$ then the epidemic wave will cease down. On the other hand, for $\alpha < \bar{\alpha}$ the epidemic front explodes.

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