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A Selection-Migration Model in Population Genetics*

W. H. Fleming, Providence, R. I.

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Summary

We consider a model with two types of genes (alleles) A_1, A_2. The population lives in a bounded habitat R, contained in r-dimensional space ($r=1, 2, 3$). Let $u(t, x)$ denote the frequency of A_1 at time t and place $x \varepsilon R$. Then $u(t, x)$ is assumed to obey a nonlinear parabolic partial differential equation, describing the effects of population dispersal within R and selective advantages among the three possible genotypes $A_1 A_1$, $A_1 A_2$, $A_2 A_2$. It is assumed that the selection coefficients vary over R, so that a selective advantage at some points x becomes a disadvantage at others. The results concern the existence, stability properties, and bifurcation phenomena for equilibrium solutions.

1. Introduction

A central problem in population genetics theory is to understand the diversity of genetic types so widely observed in nature. One kind of diversity is spatial. Frequencies of types of genes (alleles) at a given gene locus often vary significantly with geographic location within the habitat of the species in question. In particular, the frequency of an allele may increase monotonically in some direction; in such a case a cline is said to occur.

We consider a model with two alleles A_1, A_2. The population lives in a bounded habitat R, contained in r-dimensional space ($r=1, 2$, or 3). Changes in gene frequencies will be assumed to occur solely through the mechanisms of dispersal within R and selective advantages for certain genotypes. Let $u(\tau, x)$ denote the frequency of allele A_1 at time τ, measured (say) in generations, and place x in R. Then u is assumed to obey the partial differential equation

$$\frac{\partial u}{\partial \tau}=\frac{m}{2r}\,\Delta u+s(x)f(u) \tag{1.1}$$

with Δ the Laplace operator in $x=(x_1, \dots, x_r)$ and with

$$f(u)=u(1-u)\,[h(1-u)+(1-h)u] \tag{1.2}$$

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for some constant h, $0<h<1$. The term $\frac{m}{2r}\Delta u$ in (1.1) represents the effect of population dispersal, with m the mean square dispersal distance per unit time. The term $s(x)f(u)$ represents the effect of natural selection, where the fitness coefficients of the genotypes $A_1 A_2$ and $A_2 A_2$ relative to $A_1 A_1$ are respectively $1-h\,s(x)$ and $1-s(x)$. For $s=$ constant and $h=\frac{1}{2}$, (1.1) is Fisher's equation.

An essential feature for our results is that $s(x)$ varies; in fact, $s(x)$ takes both positive and negative values on the habitat R. Thus a selective advantage at some points of R becomes a disadvantage at others. It may happen that both alleles A_1 and A_2 are maintained in equilibrium, even though the heterozygote $A_1 A_2$ has fitness intermediate to $A_1 A_1$ and $A_2 A_2$ $(0<h<1)$. This kind of modification of Fisher's equation was considered by Haldane [7] and Fisher [5] when $R=(-\infty,\infty)$ and $s(x)$ depends on x in a simple way. More recent work by several authors is mentioned below.

Let us take as habitat a bounded region R and impose at the boundary ∂R the zero normal derivative condition:

$$\frac{\partial u}{\partial n}=0, \quad x\in\partial R. \tag{1.3}$$

Condition (1.3) will be satisfied if there is no flow of genes into R or out of R. Since $u(\tau,x)$ is a frequency, we seek only solutions of (1.1)—(1.3) for which $0\leq u\leq 1$. Our results concern stable and unstable equilibrium solutions. There are always the trivial equilibria $u_0(x)\equiv 0$, $u_1(x)\equiv 1$, corresponding to the occurence of allele A_2 only or A_1 only. Theorem 3.1 is concerned with their stability.

In section 4 we show that there is an equilibrium u^* which minimizes a certain functional $I(u)$. Since $I(u)$ plays the role of a Lyapunov-functional in the stability analysis, it arises naturally in the problem. In cases where Theorem 3.1 implies instability of the trivial equilibria, u^* must be a third (nontrivial) equilibrium.

In sections 5—8 we take for the habitat R the 1-dimensional interval $-1\leq x\leq 1$. If $\int_{-1}^{1} s(x)\,dx<0$, then there is a critical dispersal rate m_1 such that the trivial equilibrium u_0 is stable for $m>m_1$ and unstable for $m<m_1$. In section 6 we find that as m decreases from m_1 a stable nontrivial equilibrium bifurcates from u_0, provided $h>\frac{1}{3}$ in (1.2). Numerical evidence suggests (but does not prove) that the bifurcating solution coincides with u^*. However, if $h<\frac{1}{3}$ the bifurcating solution appears for $m>m_1$ and is unstable. The situation is more complicated in that case. Similarly, if $\int_{-1}^{1} s(x)\,dx>0$ and $h<\frac{2}{3}$, a stable equilibrium bifurcates from u_1.

If $\int_{-1}^{1} s(x)\,dx=0$, then both u_0 and u_1 are unstable and u^* is nontrivial. This condition on $s(x)$ holds, in particular, for the symmetric case treated in section 7. In that case there is a unique nontrivial stable symmetric equilibrium. Fisher [5] considered $s(x)=kx$, $h=\frac{1}{2}$ on the infinite interval $-\infty<x<\infty$. In section 8 we compare his numerical results with corresponding results for a finite habitat $-L\leq x\leq L$. For the finite habitat model there is greater heterogeneity, i.e., that model predicts higher frequencies for the less common of the two alleles A_1, A_2.

Our work overlaps Karlin and McGregor [11], who obtain more detailed results for special choices of $s(x)$. Karlin and Dyn [10] give a series of results for discrete habitats. Recent interest in the continuous habitat selection-migration model was stimulated by the article of Slaktin [16]. Nagylaki [15] gave conditions for a stable nontrivial equilibrium, for semi-infinite habitat $R=[0,\infty)$ and special choices of $s(x)$. He considered, for instance, $s(x)=s_1>0$ for $0\leq x\leq a$, $s(x)=-s_2<0$ for $x>a$, corresponding to a finite "pocket" in the environment where allele A_1 is favored. Conley [4] considered $R=(-\infty,\infty)$ and any $s(x)$ not integrable near $x=\pm\infty$. If $\operatorname{sgn} s(x)=\operatorname{sgn} x$ for large $|x|$, then a nontrivial stable equilibrium exists. However, if $s(x)<0$ for large $|x|$, then an additional condition is needed to guarantee this.

Chafee [2], [3] developed the Lyapunov stability method for dynamical systems governed by a nonlinear parabolic equation (1 space dimension). He studied the asymptotic behaviour of solutions near stable and unstable equilibria. Aronson and Weinberger [1] studied the asymptotic behaviour of solutions of nonlinear parabolic equations on $R=(-\infty,\infty)$ or on $R=[0,\infty)$ with $u(\tau,0)$ given. Their results apply to (1.1) if $s(x)$ is constant; $h<0$ is allowed, corresponding to heterozygote advantage. (When $h<0$ a third constant equilibrium appears.)

The main results of the present paper were announced in [6]. Hoppensteadt [9] treats the asymptotic behaviour of $u(\tau,x)$ for large τ, if m is near the critical dispersal rate m_1 where the bifurcation in section 6 occurs and $u(\tau,x)$ is near the corresponding trivial equilibrium u_0 or u_1.

2. Problem Reformulation

The special form (1.2) of $f(u)$ will play no role in what follows. Let us assume throughout that f is of class C^1, with

$$f(0)=f(1)=0,\ f'(0)>0,\ f'(1)<0,$$
$$0<f(u)\ \text{for}\ 0<u<1.$$

It is convenient to introduce the new time scale $t=(2r)^{-1}m\tau$, and to rewrite (1.1) in the form

$$\frac{\partial u}{\partial t}=\Delta u+\lambda g(x)f(u),$$

where

$$s(x)=s_0\,g(x),\ \lambda=\frac{2rs_0}{m},\ \lambda>0. \tag{2.1}$$

The function g in piecewise continuous and takes both positive and negative values on R. The region R is bounded, with smooth boundary ∂R. The boundary condition is again (1.3), the zero Neumann condition. We regard λ as a parameter. For fixed intensity of selection s_0, small λ corresponds to m large (rapid dispersal) and large λ corresponds to m small (slow dispersal).

An *equilibrium* is a function $u(x)$ satisfying $0 \le u(x) \le 1$,

$$0 = \Delta u + \lambda g(x) f(u), \quad x \in R, \tag{2.2}$$

and the boundary conditions (1.3). There are always two trivial equilibria $u_0(x) \equiv 0$, $u_1(x) \equiv 1$. They correspond respectively to the occurence of type A_2 only, or type A_1 only, in the population. In the next section we shall give conditions for stability or instability of the trivial equilibria.

3. Stability of Equilibria

Let us use the Lyapunov concept of stability, and give a criterion (Lemma 3.1 below) for stability or instability based on linearizing equation (2.2). It is convenient to work in the Sobolev space $V = H^1(R)$; this is the space of functions $\phi(x)$ such that ϕ and ϕ_{x_i}, $i = 1, \ldots, r$, are in $L^2(R)$. Let

$$X = \{\phi \in V: 0 \le \phi(x) \le 1 \text{ a.e. in } R\}.$$

Given $\phi(x) = u(0, x)$ in V, equation (2.1) with the boundary conditions (1.3) has a solution $u(t, x)$ in the sense of the Hilbert space theory of parabolic partial differential equations. In the Appendix we review properties of solutions in this sense. Consider the semigroup $T(t)$ of operators on V defined by $u(t, \cdot) = T(t)\phi$.

From the maximum principle for parabolic equations it follows that $T(t)$ maps X into X.

An equilibrium $u(x)$ is *stable* if: given $\eta > 0$ there exists $\delta > 0$ such that $\| \phi - u \| < \delta$ implies $\| T(t)\phi - u \| < \eta$ for all $t \ge 0$. Here $\| \ \|$ is the Sobolev norm on V:

$$\| v \|^2 = \int_R [|v|^2 + |\nabla v|^2] \, dx.$$

An equilibrium u is isolated if some V-neighborhood of u contains no other equilibria. For $u \in X$ let

$$I(u) = \int_R \{\tfrac{1}{2} |\nabla u|^2 - \lambda g(x) F[u(x)]\} \, dx, \qquad F(u) = \int_0^u f(y) \, dy. \tag{3.1}$$

The Euler equation for $I(u)$ is (2.2), and (1.3) is the free boundary condition. Moreover, $I[T(t)\phi]$ is a nonincreasing function of t (Appendix). This means that I has the role of a Lyapunov functional.

Given $u \in X$, let us also consider the quadratic functional on V:

$$Q(v) = \int_R \{|\nabla v|^2 - \lambda g(x) f'[u(x)] v^2\} \, dx. \tag{3.2}$$

The Euler equation for $Q(v)$ is the linearized form of (2.2):

$$\Delta v + \lambda g(x) f'[u(x)] v = 0. \tag{3.3}$$

Lemma 3.1: *Let $u \in X$ be an equilibrium. (a) If there exists $a>0$ such that $Q(v) \geq a \| v \|^2$ for all $v \in V$, then u is stable.*

(b) If u is isolated and there exists $v \in V$ such that $Q(v)<0$, then u is unstable.

Part (a) is easily shown; in the Appendix we prove (b). For brevity let us set $A(x)=g(x) f'[u(x)]$. Consider the Rayleigh quotient

$$K(v)=\frac{\int_R |\nabla v|^2 \, dx}{\int_R A v^2 \, dx}.$$

In the following lemmas we suppose that $A(x)$ has both positive and negative values on R. We consider $K(v)$ only when the denominator is positive. Let

$$\lambda_1=\inf\left\{K(v) \colon \int_R A v^2 \, dx>0\right\}. \tag{3.4}$$

Lemma 3.2: *There exists $v \in V$ such that $Q(v)<0$ if either*

(a) $\int_R A(x) \, dx \geq 0$, *or*

(b) $\int_R A(x) \, dx<0$ *and* $\lambda>\lambda_1$.

Proof: If $\int_R A(x) \, dx>0$, then we take $v(x) \equiv c$, a constant not 0. If $\int_R A(x) \, dx=0$, then $Q(c)=0$. If $Q(v) \geq 0$ for all $v \in V$, then constants minimize $Q(v)$. However, constants $c \neq 0$ do not satisfy the Euler equation (3.3). Hence $Q(v)<0$ for some v. This proves (a). Part (b) is immediate from (3.4). ■

Lemma 3.3: *Let $\int_R A(x) \, dx<0$. Then there exist $\beta>0$, $\gamma>0$ such that*

$$\int_R |\nabla v|^2 \, dx \geq \beta \int_R v^2 \, dx \quad \text{on} \quad \left\{v \colon \int_R A v^2 \, dx>-\gamma \int_R v^2 \, dx\right\}.$$

This lemma is easily proved by contradiction, after noting that it suffices to consider those v with $\int_R v^2 \, dx=1$.

Lemma 3.3 implies the lower bound $\lambda_1 \geq \beta / \sup_R |A(x)|$.

Lemma 3.4: *Let $\int_R A(x) \, dx<0$ and $0<\lambda<\lambda_1$. Then there exists $a>0$ such that $Q(v) \geq a \| v \|^2$ for all $v \in V$.*

Proof: Write $\lambda=(1-\delta) \lambda_1$. Whenever $\int_R A v^2 \, dx>0$

$$\lambda \leq(1-\delta) K(v)=\frac{(1-\delta) \int_R |\nabla v|^2 \, dx}{\int_R A v^2 \, dx}.$$

After multiplying by the denominator and rearranging,

$$\delta \int_R |\nabla v|^2 \, dx \leq Q(v), \text{ if } \int_R A v^2 \, dx>0. \tag{*}$$

Since $\delta<1$, (*) also holds if $\int_R A v^2\,dx\le 0$. If $\int_R A v^2\,dx>-\gamma\int_R v^2\,dx$, we have from (*) and Lemma 3.3

$$Q(v)\ge\frac{\delta}{2}\int_R[|\nabla v|^2+\beta v^2]\,dx.$$

In the opposite case,

$$Q(v)\ge\int_R\{|\nabla v|^2+\lambda\gamma v^2\}\,dx.$$

Let $a=\min\left(1,\lambda\gamma,\frac{\delta}{2},\frac{\delta\beta}{2}\right)$. ■

Lemma 3.5: *Let* $\int_R A(x)\,dx<0$ *and* $\lambda=\lambda_1$. *Then* $Q(v)\ge 0$ *for all* $v\in V$. *There exists* $w(x)\not\equiv 0$ *such that* $Q(w)=0$ *and* w *satisfies* (3.3) *with the boundary condition* (1.3).

Proof: The first statement is obvious from (3.4). The second will follow if we show that $K(w)=\lambda_1$ for some w in $\{v\in V:\int_R A v^2\,dx>0,\int_R v^2\,dx=1\}$. Take a sequence w_n in this set such that $K(w_n)$ tends to the infimum λ_1. By Lemma 3.3,

$$\int_R|\nabla w_n|^2\,dx\le C,\quad\int_R A w_n^2\,dx\ge b,\quad n=1,2,\ldots,$$

for suitable positive constants C,b. A subsequence of w_n converges in L^2 norm to a limit w. By lower semicontinuity of $K(v)$ with respect to L^2 convergence, $K(w)=\lambda_1$. ■

From Lemmas 3.4 and 3.5, λ_1 is the least positive eigenvalue for the linearized problem (3.3)—(1.3).

Let us apply these results to the trivial equilibria u_0,u_1. For u_0 we have $A(x)=f'(0)g(x)$, with $f'(0)>0$; while for u_1 we have $A(x)=f'(1)g(x)$ with $f'(1)<0$. From Lemmas 3.1, 3.2, 3.4 we have:

Theorem 3.1: *Suppose that the trivial equilibria* u_0,u_1 *are isolated. Then*:

(*a*) *If* $\int_R g(x)\,dx<0$, *then* u_1 *is unstable for any* $\lambda>0$. *There exists* λ_1 *such that* u_0 *is stable for* $0<\lambda<\lambda_1$ *and unstable for* $\lambda>\lambda_1$.

(*b*) *If* $\int_R g(x)\,dx>0$, *a similar result holds with* u_0,u_1 *exchanged.*

(*c*) *If* $\int_R g(x)\,dx=0$, *then* u_0 *and* u_1 *are both unstable for any* $\lambda>0$.

We shall show in Theorem 5.1 that all equilibria are isolated at least if the habitat R is 1-dimensional and f,g are real analytic. Note that the assumption that u_0,u_1 are isolated is used, through Lemma 3.1 (b), only to establish instability.

When $\lambda<\lambda_1$ in Theorem 3.1 (a), it can be shown that $u(t,\cdot)$ converges as $t\to\infty$ at an exponential rate to u_0 starting from $u(0,x)=\phi(x)$ in some neighborhood of u_0. See Chafee [3, section 8] if $r=1$. The convergence rate for λ near λ_1 is more delicate; see Hoppensteadt [9].

There is a simple intuitive explanation of (a) and (b). Frequency $u_0(x)\equiv 0$ means that only type A_2 occurs, while $\int_R g(x)\,dx<0$ means that, averaged over the habitat R, type A_2 is advantageous. In (a) sufficiently rapid dispersal ($\lambda<\lambda_1$) implies that the population acts as a single unit in which A_2 is advantageous. For slower dispersal ($\lambda>\lambda_1$) this is no longer the case even though heterozygotes have intermediate fitnesses ($0<h<1$ in (1.2)). In the next section we shall see that a nontrivial equilibrium u^* appears when $\lambda>\lambda_1$. In (c) neither type has a selective advantage on the average. We shall see that a nontrivial u^* then appears for any $\lambda>0$.

4. Existence of an Equilibrium Minimizing I (u)

By methods of calculus of variations let us show:

Theorem 4.1: *There exists an equilibrium u^* minimizing $I(u)$ on X.*

Proof: Since $I(u)$ is lower semicontinuous with respect to L^2 convergence and subsets of X with $I(u)$ bounded are L^2-compact, existence of a minimizing u^* is immediate. We must show that u^* is an equilibrium. Except for a slight difficulty presented by the constraints $0\leq u\leq 1$, the reasoning is standard.

Let us extend $F(u)$ symmetrically outside $0\leq u\leq 1$, such that

$$F(-u)=F(2-u)=F(u).$$

Since $f(0)=f(1)=0$, $F(u)$ remains C^1. Let

$$\theta(u)=u \bmod 2,\ |\theta(u)|\leq 1.$$

If $-1\leq u(x)\leq 2$, then $I(u)=I(\tilde{u})$, with $\tilde{u}(x)=|\theta[u(x)]|$. This implies that u^* minimizes $I(u)$ among all $u\in V$ such that $-1\leq u(x)\leq 2$. Therefore, the first variation of $I(u)$ is 0:

$$\int_R \{\nabla u^*\cdot v+\lambda g(x) f[u^*(x)]\,v\}\,dx=0 \tag{4.1}$$

for all $v\in V$. But (4.1) is equivalent to (2.2) with the free boundary condition (1.3). See [13, I, chapter 2.9]. Thus u^* is an equilibrium. ■

From calculus of variations we must have

$$Q(v)=\int_R \{|\nabla v|^2-\lambda g(x) f'[u^*(x)]\,v^2\}\,dx\geq 0$$

for all $v\in V$. We then have the:

Corollary 4.1: *In case (a) or (b) of Theorem 3.1, u^* is nontrivial for $\lambda>\lambda_1$; while in case (c), u^* is nontrivial for all $\lambda>0$.*

Proof: In all these cases it was shown in section 3 that, for either $u=u_0$ or $u=u_1$, there exists v such that $Q(v)<0$. ■

5. Analysis for r = 1

Let us now suppose that the habitat is a 1-dimensional interval, which we take to be $R=[-1,1]$. Consider the following family of functions $u_\alpha(x)$ for $0\le\alpha\le 1$:

$$u_\alpha''+\lambda g(x) f[u_\alpha(x)]=0, \quad -1\le x\le 1, \tag{5.1}$$

$$u_\alpha(-1)=\alpha, \; u_\alpha'(-1)=0. \tag{5.2}$$

The equilibria are precisely those $u=u_\alpha$ which satisfy in addition

$$0\le u_\alpha(x)\le 1 \quad\text{and}\quad u_\alpha'(1)=0. \tag{5.3}$$

In particular, we have the trivial equilibria u_0, u_1. Let $v_\alpha=\partial u_\alpha/\partial\alpha$. Then v_α satisfies the linearized equation

$$v_\alpha''+\lambda g(x) f'[u_\alpha(x)]\, v_\alpha=0, \quad -1\le x\le 1, \tag{5.4}$$

$$v_\alpha(-1)=1, \; v_\alpha'(-1)=0. \tag{5.5}$$

By multiplying (5.4) by v_α and integrating by parts, we find that

$$Q(v_\alpha)=v_\alpha(1)\, v_\alpha'(1). \tag{5.6}$$

Lemma 5.1: *Let $u=u_\alpha$ be an equilibrium.*

(*a*) *If $Q(v)\ge 0$ for all $v\in V$, then:*

$$v_\alpha(x)>0 \quad for \quad -1\le x<1, \tag{5.7}$$

and

$$v_\alpha'(1)\ge 0 \quad if \quad v_\alpha(1)>0. \tag{5.8}$$

(*b*) *If* (5.7), (5.8) *hold and $v_\alpha(1)>0$, then $Q(v)\ge 0$ for all $v\in V$.*

This result is standard in calculus of variations [8, chapter 3]. Part (a) follows from the proof of the Jacobi condition and (5.6). For (b) one can construct the field of extremals $z_\mu(x)=\mu v_\alpha(x)$, $-\infty<\mu<\infty$ for the variational integrand $Q(v)$. For any $v\in V$, take μ such that $v(-1)=z_\mu(-1)$. Then

$$Q(v)\ge Q(z_\mu)=\mu^2 Q(v_\alpha)\ge 0. \quad \blacksquare$$

Note that $v_\alpha(1)=v_\alpha'(1)=0$ is impossible by (5.4), (5.5).

Lemma 5.2: *Let u_α be an equilibrium.*

(*a*) *Sufficient conditions for stability of u_α are:*

$$v_\alpha(x)>0 \quad for \quad -1\le x\le 1, \tag{5.7'}$$

and

$$v_\alpha'(1)>0. \tag{5.8'}$$

(*b*) *If u_α is isolated, then* (5.7), (5.8) *are necessary for stability.*

Proof: By Lemmas 5.1 (b) and (3.2), conditions (5.7')—(5.8') imply

$$\int_{-1}^{1} g(x) f'[u_\alpha(x)]\, dx<0$$

and $\lambda \leq \lambda_1$. Lemma 3.5 (with $w = c\,v_\alpha$) and (5.6) exclude $\lambda = \lambda_1$. Part (a) then follows from Lemmas 3.1 (a) and 3.4. Part (b) follows from Lemmas 3.1 (b) and 5.1 (a). ■

Theorem 5.1: *Let f and g be real analytic functions. Then there are only finitely many equilibria.*

Proof: Since f and g are real analytic, $u_\alpha'(1)$ is a real analytic function of α. Either u_α is an equilibrium for finitely many α $(0 \leq \alpha \leq 1)$, or there is a maximal interval G such that u_α is an equilibrium for every $\alpha \in G$. Let us exclude the second possibility. By differentiation under the integral sign and integration by parts,

$$\frac{d}{d\alpha} I(u_\alpha) = u_\alpha'(1)\, v_\alpha(1). \tag{5.9}$$

Since $u'_\alpha(1) \equiv 0$ on G, $I(u_\alpha) = \text{constant}$ on G. Let γ be the left endpoint of G. If $\gamma > 0$, then $u_\alpha(x_1) = 0$ with $-1 < x_1 \leq 1$. If $x_1 < 1$, then $u_\gamma'(x_1) = 0$ contrary to the uniqueness theorem for (5.1). Since $u_\gamma'(1) = 0$, $x_1 = 1$ is excluded for the same reason. Hence $\gamma = 0$. Similarly, the right endpoint of G is 1. Then $I(u_0) = I(u_1) = I(u^*)$, where u^* minimizes (Theorem 4.1). Thus both u_0, u_1 minimize $I(u)$. But the argument in section 3 shows that, for either $u = u_0$ or $u = u_1$ and some v, the necessary condition $Q(v) \geq 0$ for a minimum is violated. Thus, there are finitely many equilibria. ■

6. Dependence of Equilibria on λ

Let us continue with the 1-dimensional habitat $R = [-1, 1]$. The set of α for which u_α is an equilibrium depends on the parameter λ. This set always contains $\alpha = 0, 1$, corresponding to the trivial equilibria. When the minimizing u^* in section 4 is nontrivial, a third equilibrium $u_\alpha = u^*$ appears.

Let us set $\phi(\alpha, \lambda) = u_\alpha'(1)$. Equilibria correspond to roots of $\phi = 0$. Moreover, $\partial\phi/\partial\alpha = v_\alpha'(1)$. From the discussion in section 5, when $\int_{-1}^{1} g(x) f'[u_\alpha(x)]\,dx < 0$, the conditions (5.7′), (5.8′) are equivalent to $0 < \lambda < \lambda_1$. In this range, the implicit function theorem implies smooth dependence of $\alpha = \alpha(\lambda)$ on the parameter λ. For $\lambda = \lambda_1$, (5.7′) holds but $v_\alpha'(1) = 0$. At λ_1, a bifurcation may occur.

The following bifurcation theorem can be proved by a standard Lyapunov-Schmidt argument. However, we give another direct proof.

Theorem 6.1: *Assume that $f''(0) < 0$ and $\int_{-1}^{1} g(x)\,dx < 0$. Then there exists a stable nontrivial equilibrium $u_{\alpha(\lambda)}$ for $\lambda > \lambda_1$ sufficiently near λ_1, with $\alpha(\lambda) \downarrow 0$ as $\lambda \downarrow \lambda_1$.*

Proof: For $\alpha = 0$, $\lambda = \lambda_1$ one has $\phi = \partial\phi/\partial\alpha = 0$. Let us show that

$$\frac{\partial^2\phi}{\partial\alpha^2} > 0, \quad \text{when} \quad \alpha = 0,\ \lambda = \lambda_1. \tag{6.1}$$

For this purpose, let

$$z_\alpha = \frac{\partial^2 u_\alpha}{\partial \alpha^2} = \frac{\partial v_\alpha}{\partial \alpha}.$$

For $\alpha = 0$, $\lambda = \lambda_1$

$$z_0'' + \lambda_1 \, g \, [f''(0) \, v_0^2 + f'(0) \, z_0] = 0. \tag{6.2}$$

By Lemma 5.2, if $\lambda < \lambda_1$, $v_0(x) > 0$ for $-1 \le x \le 1$ and $v_0'(1) > 0$. For $\lambda = \lambda_1$, $v_0'(1) = 0$; since $v_0(1) = v_0'(1) = 0$ is impossible $v_0(x) > 0$ for $-1 \le x \le 1$ for λ in an interval containing λ_1. For such $\lambda > \lambda_1$, $v_0'(1) < 0$ since u_0 is unstable when $\lambda > \lambda_1$. Multiply (6.2) by v_0, integrate by parts twice, and use (5.4) with $\alpha = 0$ to get

$$v_0(1) \, z_0'(1) = -\lambda_1 f''(0) \int_{-1}^{1} g \, v^3{}_0 \, dx.$$

By multiplying (5.4) by v_0^2 and making another integration by parts, one gets

$$\frac{\partial^2 \phi}{\partial \alpha^2} = z_0'(1) = -\frac{2 f''(0)}{f'(0) \, v_0(1)} \int_{-1}^{1} v_0 (v_0')^2 \, dx > 0.$$

This establishes (6.1). For λ sufficiently near λ_1 the equation $\phi = 0$ has two roots $\alpha = 0$, $\alpha(\lambda)$ with $\alpha(\lambda)$ increasing and $\alpha(\lambda_1) = 0$. Moreover, for λ near enough λ_1 $(\lambda > \lambda_1)$

$$v_{\alpha(\lambda)}(x) > 0 \quad \text{for} \quad -1 \le x \le 1,$$

$$v_0'(1) = \frac{\partial \phi}{\partial \alpha}(0, \lambda) < 0, \quad v_{\alpha(\lambda)}'(1) = \frac{\partial \phi}{\partial \alpha}(\alpha(\lambda), \lambda) > 0.$$

By Lemma 5.2, $u_{\alpha(\lambda)}$ is a stable equilibrium. ■

Note: For $\lambda < \lambda_1$, $\alpha(\lambda) < 0$ is not admissible since we must have $0 \le u_\alpha(x) \le 1$. Moreover, no solution bifurcating from an eigenvalue different from λ_1 can satisfy $0 \le u_\alpha(x) \le 1$.

In Theorem 6.1 we assumed $f''(0) < 0$. For $f(u)$ as in (1.2) this means $h > \frac{1}{3}$. If $\int_{-1}^{1} g(x) \, dx > 0$, a stable nontrivial equilibrium bifurcates from u_1 for $\lambda > \lambda_1$ provided $f''(1) < 0$. This means $h < \frac{2}{3}$. In numerical examples with $h = \frac{1}{2}$ only three equilibria were found for $\lambda > \lambda_1$, including the two trivial ones u_0, u_1. In such cases, the minimizing u^* in section 4 is the same as the bifurcating equilibrium.

If $h < \frac{1}{3}$ or $h > \frac{2}{3}$, then matters are more complicated. Suppose for instance, $\int_{-1}^{1} g(x) \, dx < 0$ and $h < \frac{1}{3}$ $(f''(0) > 0)$. The bifurcating solution with $\alpha(\lambda) > 0$ occurs for $\lambda < \lambda_1$ and is unstable. The minimizing equilibrium u^* could arise in several ways; we have not investigated which actually occur. One can show that $u^* = u_0$ for $0 < \lambda < \lambda_2 \le \lambda_1$. Perhaps the simplest situation which could occur is that $u^* = u_{\beta(\lambda)}$ for $\lambda > \lambda_2$, where $\alpha = \beta(\lambda)$ is the upper branch of a curve in the (α, λ)-plane whose lower branch $\alpha = \alpha(\lambda)$ corresponds to the unstable equilibrium bifurcating backward from $(0, \lambda_1)$. In this situation, u_0 would give a local (not absolute) minimum to $I(u)$ for $\lambda_2 < \lambda < \lambda_1$.

The case $\int_{-1}^{1} g(x)\,dx=0$. By Corollary 4.1, there are always at least three equilibria u_0, u_1, u^*. The behaviour of nontrivial equilibria for λ near 0 can be treated as follows. We omit some tedious calculations. One has $\phi(\alpha, 0)=0$. By differentiating (5.1) with respect to λ and using (5.2) and $\int_{-1}^{1} g\,dx=0$, one finds that $\partial\phi/\partial\lambda=0$ when $\lambda=0$. Now consider c satisfying $f'(c)=0, f''(c)\neq 0$. By further differentiations with respect to λ and α one finds that when $\alpha=c$, $\lambda=0$

$$\frac{\partial^2\phi}{\partial\lambda^2}=0,\ \frac{\partial^3\phi}{\partial\lambda^2\,\partial\alpha}=-\frac{2f''(c)}{f(c)}\int_{-1}^{1}\left(\frac{\partial u'_\alpha}{\partial\lambda}\right)^2 dx\neq 0.$$

By applying the implicit function theorem to $\lambda^{-2}\phi$, one gets an equilibrium $u_{\alpha(\lambda)}$ for λ near 0, with $\alpha(0)=c$. This equilibrium is stable if $f''(c)<0$ and unstable if $f''(c)>0$. For the genetics model, with $f(u)$ as in (1.2), c is the unique maximum of $f(u)$ and $f''(c)<0$. At least for small λ, $u_{\alpha(\lambda)}=u^*$.

7. The Symmetric Case

Let us now suppose that

$$g(-x)=-g(x),\ g(x)>0 \text{ for } x>0,$$
$$f(u)=f(1-u),\ f(0)=f(1)=0,\ f''(u)<0.$$

For the genetic model, this implies $h=\frac{1}{2}$, $f(u)=\frac{1}{2}u(1-u)$. Let us call an equilibrium *symmetric* if

$$u(x)=1-u(-x).$$

Note that a nontrivial symmetric equilibrium is increasing in x, with $u(0)=\frac{1}{2}$, $u''(x)>0$ for $x<0$, $u''(x)<0$ for $x>0$.

Theorem 7.1: *For any* $\lambda>0$ *there exists a unique nontrivial stable symmetric equilibrium.*

Proof: Using the notation of section 5, let

$$\beta=\sup\{\alpha\colon u_\alpha(x)\leq\tfrac{1}{2} \text{ for } -1\leq x\leq 0\}.$$

Then u_β is a symmetric equilibrium. To prove uniqueness, we must exclude a symmetric equilibrium u_α with $0<\alpha<\beta$. For $-1\leq x<0$ and such α, $g(x)\,f'[u_\alpha(x)]<0$. From (5.4) and (5.5) we have $v''_\alpha(x)\geq 0$ for such x and α, and $v_\alpha(0)\geq 1$. Since $v_\alpha=\partial u_\alpha/\partial\alpha$, $u_\alpha(0)<\frac{1}{2}$ for $0<\alpha<\beta$, proving uniqueness of u_β (among symmetric equilibria). To prove stability,

$$\begin{gathered} g(x)\,f'[u_\beta(x)]<0 \text{ for } -1\leq x\leq 1,\ x\neq 0,\\ Q(v)=\int_{-1}^{1}\left[(v')^2-\lambda g(x)\,f'[u_\beta(x)]\,v^2\right]dx>0 \end{gathered} \tag{7.1}$$

for any $v(x)\not\equiv 0$. In particular, $Q(v_\beta)=v_\beta(1)\,v'_\beta(1)>0$. Since the coefficient of v_β in (5.4) is negative and v_β satisfies (5.5), $v_\beta(x)>0$ on $-1\leq x\leq 1$. By Lemma 5.2, u_β is stable.

Let us show that $\beta=\beta(\lambda)$ is a smooth, decreasing function of λ. For this purpose, let $\psi(\alpha,\lambda)=u_\alpha(0)-\frac{1}{2}$. For $\alpha=\beta(\lambda)$,

$$\psi=0,\ \frac{\partial\psi}{\partial\alpha}=v_\beta(0)>0.$$

By differentiating (5.1) with respect to λ and using (7.1), one finds that $\partial u_\alpha/\partial\lambda<0$ for $-1\le x\le 0$, $\alpha=\beta(\lambda)$. In particular, $\partial\psi/\partial\lambda>0$ when $\beta=\beta(\lambda)$, and therefore $d\beta/d\lambda<0$.

From these inequalities it also follows that $\partial u_{\beta(\lambda)}(x)/\partial\lambda<0$, and thus $u_{\beta(\lambda)}(x)$ is a decreasing function of λ for $-1\le x<0$. By symmetry $u_{\beta(\lambda)}(x)$ is increasing in λ for $0<x\le 1$. Intuitively, this result is expected. Since λ is proportional to m^{-1}, increasing λ means decreasing dispersal rate m. As λ increases each of the alleles A_1, A_2 becomes in equilibrium more frequent in those parts of the habitat where it is favored. Moreover,

$$\lim_{\lambda\to\infty} u_{\beta(\lambda)}(x)=\begin{cases}0, & -1\le x<0\\ 1, & 0<x\le 1.\end{cases}$$

In the limit $(m=0)$ there is no dispersal; then selection eliminates A_1 completely in the interval $-1\le x<0$ and A_2 completely in $0<x\le 1$.

8. Numerical Examples

Let us consider two examples, in both of which

$$R=[-1,1],\ f(u)=\tfrac{1}{2}u(1-u).$$

The first example exhibits the bifurcation phenomenon in section 6, while the second is a symmetric case (section 7). In the latter example, the results are compared with Fisher's [5].

The numerical results were found by C. P. Tsai.

Table 1. *Frequency of Allele A_1 in Stable Equilibrium*

			x		
λ	-1	$-.5$	0	$.5$	1
8	0	0	0	0	0
12	.27	.17	.06	.012	*
20	.54	.33	.09	.012	*
40	.77	.45	.08	.02	*

* Small; numerical method inaccurate for x near 1

$g(x)=-(2x+1)$, $\lambda_1=8.45$

Example 1: Let $g(x)=-(2x+1)$. This is case (a), Theorem 3.1. It was found that $\lambda_1=8.45$ with only the trivial equilibria for $\lambda<\lambda_1$. For $\lambda>\lambda_1$, one additional equilibrium $u=u_{\alpha(\lambda)}$ was found; $\alpha(\lambda)$ appears in the left column of Table 1 $(x=-1)$. This must be the bifurcating equilibrium, and also the equilibrium minimizing $I(u)$.

Example 2: Let $g(x)=2x$, a symmetric problem. A single nontrivial equilibrium was found. It is the symmetric one in Theorem 7.1, and also the equilibrium minimizing $I(u)$.

Table 2. *Frequency of Allele A_1 in Stable Equilibrium*

		x -1	$-.5$	0
	1	.43 (.21)	.45 (.33)	.5 (.5)
λ	5	.20 (.084)	.29 (.24)	.5 (.5)
	10	.10 (.044)	.21 (.19)	.5 (.5)

$g(x)=2x$, $u(x)=1-u(-x)$ for $x>0$

Fisher [5] for infinite habitat in parentheses

To compare the numerical results of Fisher [5] with ours, we first consider the steady state form of (1.1) on a habitat $-L\leq X\leq L$, with $s(X)=kX$:

$$0=\frac{m}{2}\frac{d^2u}{dX^2}+\frac{kX}{2}u(1-u), \tag{8.1}$$

and with $u'(\pm L)=0$. This reduces to Example 2 upon setting

$$\lambda=\frac{kL^3}{m},\quad X=Lx,\quad -1\leq x\leq 1.$$

For comparison, also consider (8.1) for $-\infty<X<\infty$ with $u(-\infty)=0$, $u(\infty)=1$. This takes the form $d^2u/d\xi^2+4\xi u(1-u)=0$ considered by Fisher after the substitution $x=(4\lambda^{-1})^{1/3}\xi$. From Table 2, we see that the finite habitat model consistently predicts higher frequencies for the less favored allele. For large λ, the difference is small except near the endpoints of the finite habitat.

Appendix

Let us first review briefly some background from the Hilbert space approach to parabolic partial differential equations. Then we verify that $I(u)$ defined by (3.1) is a nonincreasing function of t, and obtain the instability criterion in Lemma 3.1.

Consider the parabolic equation

$$\begin{aligned} &u_t = \Delta u + h(x,u), \quad x \in R,\ t \geq 0 \\ &\frac{\partial u}{\partial n} = 0 \text{ on } \partial R, \quad u(0,x) = \phi(x),\ x \in R. \end{aligned} \tag{A.1}$$

Let R be bounded with ∂R smooth, and h of class C^1 in u with h and h_u bounded. Suppose that $\phi \in V$, where $V = H^1(R)$. By a compactness method [13, chapter 1] and a regularity result about solutions of linear parabolic equations [14, II, p. 36], there is a unique solution $u(t,x)$ such that $u(t,\cdot)$, $u_{x_i}(t,\cdot) \in L^2(R)$ for each $t \geq 0$ and $u_t, u_{x_i x_j} \in L^2(Q_{0T})$ for each $T > 0$, $i, j = 1, \ldots, r$. Here $Q_{0T} = (0, T) \times R$. For almost all $t > 0$, $u(t,\cdot)$ is in the Sobolev space $H^2(R)$; for such t, $\partial u / \partial n$ (which is defined almost everywhere on ∂R) is 0. Moreover, if $h(x,0) = 0$ and $u(0,x) \geq 0$, then $u \geq 0$ (a maximum principle).

The time derivative $w = u_t$ satisfies, in the sense of the Hilbert space theory, the linear equation

$$w_t = \Delta w + h_u w \tag{A.2}$$

with $\partial w / \partial n = 0$ on ∂R. For almost all $s > 0$, $w(s,\cdot) \in L^2(R)$. If we consider (A.2) for $t \geq s$ with initial data $w(s,\cdot)$, then [12, p. 46] $u_t(t,\cdot) \in L^2(R)$, $u_{tx_i} \in L^2(Q_{sT})$, $t > 0$, $0 < s < T$ $i = 1, \ldots, r$. For almost all $t > 0$, $u(t,\cdot) \in H^2(R)$, $u_t(t,\cdot) \in H^1(R)$. For such t,

$$\int_R (\Delta u)\, u_t\, dx = -\int_R \nabla u \cdot \nabla u_t\, dx = -\frac{d}{dt} \frac{1}{2} \int_R |\nabla u|^2\, dx. \tag{A.3}$$

Let us now take $h(x,u) = \lambda g(x) f(u)$ as in section 2. For $I(u)$ defined by (3.1) and $0 \leq t_1 < t_2$, we get from (2.1), (A.3)

$$I[u(t_2,\cdot)] - I[u(t_1,\cdot)] = -\int_{Q_{t_1 t_2}} u_t^2\, dx\, dt \leq 0. \tag{A.4}$$

Hence $I[u(t,\cdot)]$ is nonincreasing. We take $\phi \in X$, with X as defined in section 3. By the maximum principle, $0 \leq u(t,x) \leq 1$; thus $u(t,\cdot) \in X$ for all $t \geq 0$.

The following argument was suggested by C. Dafermos. By (A.4) and the fact that $g(x) F[u(t,x)]$ is bounded, $I[u(t,\cdot)]$ is bounded. Thus

$$\lim_{T \to \infty} \int_{Q_{T,\infty}} u_t^2\, dx\, dt = 0.$$

Take a sequence t_n such that $u_t(t_n,\cdot)$ tends to 0 in $L^2(R)$. By (2.1), $\Delta u(t_n,\cdot)$ is bounded in $L^2(R)$. It follows that a subsequence of $u(t_n,\cdot)$ tends to a limit $u^\infty(\cdot)$ strongly in $H^1(R)$ and weakly in $H^2(R)$. Now (2.1) with the zero Neumann boundary condition $\partial u / \partial n = 0$ imply, for any $v \in V$,

$$\int_R u_t v\, dx = -\int_R \nabla u \cdot \nabla v\, dx + \lambda \int_R g(x) f[u(t,x)]\, v(x)\, dx.$$

Let t tend to ∞ through this subsequence. We get

$$0 = -\int_R \nabla u^\infty \cdot \nabla v\, dx + \lambda \int_R g(x) f[u^\infty(x)]\, v(x)\, dx. \tag{A.5}$$

But (A.5), for all $v \in V$, implies that u^∞ is an equilibrium. Moreover, if $u(0,x)=\phi(x)$, then by (A.4)

$$I(\phi) \geq I[u(t_n, \cdot)] \geq I(u^\infty). \tag{A.6}$$

Proof of Lemma 3.1 (b): Let $\eta > 0$ be such that any equilibrium u^∞ distinct from u satisfies $\| u^\infty - u \| \geq \eta$. Suppose that $Q(v) < 0$ for some $v \in V$. We may assume that v is a bounded function. Since $Q(\pm |v|) = Q(v)$ we may also suppose that $v \geq 0$ if $u = u_0$, and $v \leq 0$ if $u = u_1$. For an equilibrium $u \neq u_0, u_1$, a version of the maximum principle and (1.3) imply $c \leq u(x) \leq 1 - c$ for some $c > 0$. Then $u + \varepsilon v \in X$ for small $\varepsilon \geq 0$. Since

$$I(u+\varepsilon v) = I(u) + \frac{\varepsilon^2}{2} Q(v) + o(\varepsilon^2),$$

for ε small enough $I(u+\varepsilon v) < I(u)$. Take $\phi = u + \varepsilon v$. By the discussion above there exists a sequence t_n and equilibrium u^∞ such that $T(t_n)\phi = u(t_n, \cdot)$ tends to u^∞ in H^1 norm. Since $I(\phi) < I(u)$ we have $u^\infty \neq u$ by (A.6), and hence $\| u^\infty - u \| \geq \eta$. This proves instability of the equilibrium u. ■

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Dr. Wendell H. Fleming
Lefschetz Center for Dynamical Systems
Division of Applied Mathematics
Brown University
Providence, RI 02912, U.S.A.