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CLINES INDUCED BY VARIABLE SELECTION AND MIGRATION

P. C. Fife and L. A. Peletier

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ABSTRACT

Clines (nonuniform spatial distributions in the genetic composition of a population in equilibrium) are often modeled by nonconstant solutions $u(x) \in [0,1]$ of $(D(x)u')' + h(x,u) = 0$, $-\infty < x < \infty$, where h satisfies $h(x,0) = h(x,1) = 0$, and D is often taken to be identically 1. The functions D and h have interpretations in terms of mobility, carrying capacity and natural selection. We define clines as stable solutions satisfying $u(-\infty) = 0$, $u(\infty) = 1$. All past analyses of clines have considered the case when (say) 0 is the favored state for large negative x, and 1 for large positive x (i.e., $\int_0^1 h(x,u)du$ changes sign from negative to positive as x increases from $-\infty$ to ∞). In this paper, however, we assume that the state 0 is favored for all x, although both 0 and 1 are stable as uniform states. A number of conditions are given which ensure the existence of stable clines, or their analogs in the bounded habitat case. Conditions are also given which ensure the nonexistence of clines. The concept of stability is with reference to the corresponding nonlinear diffusion equation, and is used in a special technical sense.

AMS (MOS) Subject Classifications: 92A15, 92A10, 34B15, 35K55.

Key Words: Clines, stability, population genetics, ecology, subsolutions, selection.

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SIGNIFICANCE AND EXPLANATION

The problem studied is in the area of differential equations; it models the spatial distribution of the genetic composition of a population in a heterogeneous environment, account being taken of migration and natural selection effects. More generally, it models a distribution in the composition of an ecological community. A number of conditions are given which guarantee the existence or nonexistence of a stable nonuniform equilibrium distribution, which is known as a cline. Of special interest is the case when two stable homogeneous distributions are possible; there may or may not also exist a heterogeneous one.

The responsibility for the wording and views expressed in the descriptive summary lies with MRC, and not with the authors of this report.

CLINES INDUCED BY VARIABLE SELECTION AND MIGRATION

P. C. Fife and L. A. Peletier

1. Introduction.

Clines are nonuniform spatial distributions in the genetic composition of a population in equilibrium. They have been studied a great deal by population geneticists (see for example [7, 9, 15, 16, 19]), often within the context of the simple class of equations

$$\frac{d^2u}{dx^2} + s(x)f(u) = 0 \quad , \tag{1.1}$$

in which u is a scalar variable representing some gene frequency, f a selection pressure mechanism tending to drive the population to certain preferred states, s a measure of the selective intensity, and the second derivative of u a term designed to account for spatial migration.

Outside the context of population genetics, equation (1.1) has been used in models designed to describe certain phenomena in ecology [12].

We suppose that $f(0) = f(1) = 0$, so that $u = 0$ and $u = 1$ are solutions of (1.1). These solutions represent the situations where the gene in question is either entirely absent or everywhere present. We shall say that $u = 0$ $(u = 1)$ is <u>favored</u> at the location x if

$$s(x) \int_0^1 f(u)du < 0 \qquad (> 0) \quad .$$

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One reason for this terminology is the fact that in the case when s is constant, travelling waves of the corresponding nonlinear diffusion equation

$$u_t = u_{xx} + s\,f(u) \tag{1.2}$$

always move in a direction so that at each fixed x, $u(x,t)$ tends towards the favored state.

Another reason for this terminology is that it is consistent with the notion of relative fitness in population genetics. In that context, the derivation of (1.1) proceeds from a single-locus, two allele model (A and a), with u the frequency of the a-allele. In the special case when the fitnesses of the genotypes AA, Aa and aa are independent of population density and genotype-frequencies, and are denoted by $1 + s_1$, 1, $1 + s_2$ respectively ($s_1, s_2 \in R$), sf becomes

$$sf(u) = ru(1 - u)\{(s_1 + s_2)u - s_2\} \quad , \qquad r > 0$$

and it is easily verified that the state $u = 0$ is "favored" in the above sense if and only if $s_1 > s_2$. In this case, travelling waves tend to eliminate allele a, and drive u to 0.

We define clines to be stable nonconstant solutions $u(x)$ of (1.1). If the domain Ω - the habitat - is the entire real line, we shall for definiteness require that $u(-\infty) = 0$ and $u(+\infty) = 1$. On the other hand, if Ω is a bounded interval: $\Omega = (-1,1)$, we require Neumann ($u_x = 0$) conditions at the endpoints and $u(1) > u(-1)$. The notion of stability is here to be understood with regard to equation (1.2). The precise definition of stability to be used is critical, and we shall explain it at the end of this section. The reason for including stability in the definition of a cline stems from the fact that unstable solutions of (1.1) are not likely to reflect anything seen in the natural world.

Past analyses of clines [3, 6-9, 15, 16, 19] have all been devoted to the case when $u = 0$ is favored for large negative x and $u = 1$ is favored for large positive x. In this paper we shall suppose that $u = 0$ is favored <u>everywhere</u> in the habitat:

$$s > 0 \quad \text{in} \quad \Omega \quad \text{and} \quad \int_0^1 f(u)du < 0 \quad ,$$

and we ask whether it is still possible for clines to exist. If s is constant, the answer is no. For a bounded habitat this follows from [1], and if $\Omega = R$ it follows from results in [10] and elsewhere. However, we shall show that provided

(i) $s(x)$ is allowed to vary in certain ways, and

(ii) the selection mechanism is bistable, i.e.

$$f'(0) < 0 \quad \text{and} \quad f'(1) < 0 \quad ,$$

a cline can indeed exist. In terms of the example from population genetics, bistability means we are in the <u>underdominant</u> case, i.e., $s_1 > 0$ and $s_2 > 0$.

Again in the population genetic context, (1.1) is derived under the assumptions that the total population density is constant in space and time, that the migration rate is likewise constant, that no drift (i.e., no preferred direction of migration) is present in the latter, and that the relative fitnesses of the genotypes are constant. These restrictions, however, can be dropped and (1.1) replaced by a more general equation. These generalizations are examined in this paper. For example in sections 6 and 7, we extend our analysis to allow for variable total density and migration rate (but we continue to assume, for simplicity, that no drift is present), and find that spatial variation in the carrying capacity of the environment and in the migration rate may also be sufficient for the existence of a cline.

The biological picture we shall have in mind is the following. The individuals of the three genotypes AA, Aa, aa operate under the same migration rules: more specifically, there is an infinitesimal variance (mobility) $V(x)$ in the migration rate, common to all three types, and in all cases the drift is zero. [The effects of genotype-dependent migration were studied in [14].] The carrying capacity k of the environment is assume to be, to first order, independent of the population's genetic composition, and is a given function $k(x)$. When the relative fitnesses of the genotypes vary in space, the selection term $s(x)f(u)$ should be replaced by some function $h(x,u)$. Under all these conditions, the appropriate generalization of (1.2) is [5, p.64]

$$\frac{\partial u}{\partial t} = \frac{1}{V(x)k^2(x)} \frac{\partial}{\partial x} (V^2(x)k^2(x) \frac{\partial u}{\partial x}) + h(x,u) \quad . \tag{1.3}$$

Other migration rules, such as given in [5, (1.20)] could be handled by our technique; but the results obtained here suffice for the purpose of illustrating the effects of variable migration and carrying capacity.

We shall give various sufficient conditions for the existence of clines; typically they involve the statement that the function s, V, or k experiences a sufficient drop over some finite zone in the habitat. However, not only does the magnitude of the drop in this zone have to be large enough; but also the gradient of the function in question has to be steep enough over part of this zone. The function should remain relatively large over that part of the habitat lying to the right of the zone, whereas its values to the left are not so important. The intuitive role of this zone is that it separates two communities, which are more or less in states $u = 0$ and $u = 1$ respectively. In the case when the function experiencing the drop is the mobility V, the zone would clearly act as a barrier tending to isolate the two communities, and so providing for their coexistence in different states. Our results show that a similar variation in carrying capacity or strength of selection can function equally well as a barrier. Matano [13] has shown that in higher dimensions, the shape of the habitat Ω is relevant to the existence of clines, domains with narrow middle sections favoring their existence through a type of barrier action.

We shall give a brief description of the results of the paper. The function u will assume values only in the range $0 \leq u \leq 1$. The following hypotheses on f and s will be made throughout.

H_f: $f \in C^2([0,1])$; $f(0) = f(a) = f(1) = 0$ for some $a \in (0,1)$; $f'(0) < 0$, $f'(1) < 0$; $f(u) < 0$ on $(0,a)$, $f(u) > 0$ on $(a,1)$; and $\int_0^1 f(u)du < 0$.

Remark: This last inequality means (since $s > 0$) that the state $u = 0$ is favored for all x.

H_s: s is piecewise continuously differentiable on Ω where $\Omega = \mathbf{R}$ or $[-1,1]$;
$\inf\{s(x): x \in \Omega\} \equiv s_1 > 0$.

Conditions for nonexistence in the unbounded habitat. As mentioned before, it is well know that a cline cannot exist if s is constant. More generally the following holds. Let $\bar{\gamma} \in (0,1)$ be defined by

$$\bar{\gamma} \equiv \frac{\int_a^1 f(u)du}{-\int_0^a f(u)du} \quad .$$

Theorem 1. If $\frac{\inf[s(x)]}{\sup[s(x)]} > \bar{\gamma}$, then no cline exists. This condition is sharp. Moreover, not only must $(\inf s)/(\sup s)$ be large enough, but s must be an increasing function on some interval (Theorem 2), and the variation of s must be abrupt enough:

Theorem 3: Let $s^*(x) \in C^1(-\infty,\infty)$ and $s_\varepsilon(x) \equiv s^*(\varepsilon x)$. Then there exists an $\varepsilon_0 > 0$ such that if $0 < \varepsilon < \varepsilon_0$ and $s(x) = s_\varepsilon(x)$, no cline exists.

Conditions for existence in the unbounded habitat. Here we insert an extra positive parameter λ into (1.1):

$$\frac{d^2u}{dx^2} + \lambda\, s(x)f(u) = 0 \quad . \tag{1.4}$$

Let $\theta(x,\xi)$ be any nonnegative piecewise continuously differentiable function which vanishes for $|x| > \xi$ and is chosen so that $\sup \theta = 1$. For some positive μ and ξ, let

$$s(x) = [1 + \mu\theta(x,\xi)]^{-1} \quad .$$

Theorem 4: If $\lambda\xi^2 > \frac{\pi^2}{8}[\int_a^1 f(u)du]^{-1}$, then there is a number μ^* such that if $\mu > \mu^*$, (1.4) has a cline.

Of course, μ being large simply assures us that the "dip" in s will be low enough and abrupt enough.

Existence conditions can also be given for the more general equation

$$\frac{d^2u}{dx^2} + h(x,u) = 0 \quad ,$$

h satisfying

H_h: h is twice continuously differentiable in u and once in x; $h(x,0) = h(x,1) = 0$.

Theorem 5 and Corollary 5.1 give conditions on h, in the form of inequalities, which imply the existence of a cline. The principal requirements are that $h(x,u) \geq s(x)f(u)$, where H_f and H_s are satisfied, s is sufficiently small on some interval $(0,B)$, $s \geq 1$ on (A,∞) (where $A > B$), $s \leq 1$ on (B,A), B and A are sufficiently large, and $A-B$ is sufficiently small. The interpretation is that $(0,B)$ is a "barrier" region between the two "communities" $(-\infty,0)$ and (A,∞), and (B,A) is a "transition" zone.

Finally, in Theorem 6, it is shown that $s' > 0$ implies that the cline is strictly increasing.

Results for a bounded habitat and for variable V or k: An existence condition analogous to Theorem 4, but for a bounded habitat, is given in Theorem 7. Finally, conditions for nonexistence and for existence of clines are given, for cases in which $V(x)$ and $k(x)$ are variable, in Theorems 8 - 13. The conditions are similar to the conditions on s in the foregoing results.

Results of the type presented in this paper were conjectured to be true by S. Levin (personal communication and [12]). In [12], the interpretation is within the context of the spatial variation in composition of ecological communities, rather than the context described here.

We have assumed throughout that $\int_0^1 f(u)du < 0$ (or the analogous condition on h), so that 0 is the favored state for all x. As mentioned before, this is a major distinction from previous treatments of clines, where the favored state was assumed to change within the habitat. It goes without saying that if $\int f\,du = 0$, then a cline exists even in a homogeneous habitat; but it is structurally unstable, since a slight change in the function f will destroy it. To ensure that a cline exists when $\int f\,du = 0$ and that a cline continues to exist when f is perturbed by any small amount, it suffices to have s, V, and/or k vary in ways described by our theory; we shall not pursue the details. The idea is that existence conditions may be given which remain valid when these functions are altered slightly but arbitrarily.

Finally, let us explain the notion of stability which we shall use throughout the paper. It is designed so that the following statement is true.

Proposition. Let $\underline{\phi}$ be a stationary subsolution and $\bar{\phi}$ a stationary supersolution of (1.3) together with appropriate boundary conditions, such that $\underline{\phi} < \bar{\phi}$, and neither is an exact solution. Then there exists a stable equilibrium solution ϕ of (1.3) between $\underline{\phi}$ and $\bar{\phi}$.

This proposition is the basis for nearly all the existence theorems in the paper. A stationary subsolution $\underline{\phi}$ of (1.3) is defined to be a continuous function on [illegible] such that for some finite decomposition of [illegible] intervals, $\underline{\phi}$ is twice continuously differentiable in the interior [illegible] and it satisfies

$$N[\underline{\varphi}] \geq 0 \quad ,$$

$N[u]$ being the expression on the right of (1.3), whilst at each endpoint ξ in the interior of Ω, $\underline{\varphi}'(\xi + 0) \geq \underline{\varphi}'(\xi - 0)$. For Ω bounded, we also require $\underline{\varphi}' \leq 0$ at its left endpoint, the opposite inequality holding on the right. An analogous definition holds for supersolutions.

If the habitat Ω is bounded, we shall define stability in the usual C° sense. It was shown by Matano [13] that the proposition is true when stability is interpreted this way. If the habitat is unbounded, the proposition has only been proved for the following weaker notion of stability [2].

Let $\varphi: \mathbf{R} \to (0,1)$ be a solution of (1.1), and let T be a family of functions (defined below) with prescribed behavior for large $|x|$.

<u>Definition</u>. φ is said to be stable if, for every $\varphi_1, \varphi_2 \in T$ with $\varphi_1 \leq \varphi \leq \varphi_2$, there exist elements $\tilde{\varphi}_1, \tilde{\varphi}_2 \in T$ with $\tilde{\varphi}_1 \leq \varphi \leq \tilde{\varphi}_2$ such that if $\tilde{\varphi}_1 \leq u_0 \leq \tilde{\varphi}_2$, then the solution $u(t;u_0)$ of (1.1) which satisfies $u(0;u_0) = u_0$ has the property

$$\varphi_1 \leq \liminf_{t\to\infty} u(t,u_0) \leq \limsup_{t\to\infty} u(t,u_0) \leq \varphi_2 \quad .$$

Here all the inequalities are understood in the pointwise sense.

To complete our definition of stability, we need only say which functions belong to the family T.

<u>Definition</u>: A function $\psi \in C^1(\mathbf{R};[0,1])$ is said to belong to T if

(i) $\psi(x)$ is an exact solution of (1.3) for large $|x|$, and

(ii) $\psi(-\infty) = 0$, $\psi(\infty) = 1$.

Within our level of generality, it will not necessarily follow that the stable solution we obtain is asymptotically stable, in that small perturbations of it return to it as $t \to \infty$. In fact, in exceptional cases there may be many clines, and all we say is that when one is perturbed by a small amount, the subsequent evolution of $u(x,t)$ never leaves a neighborhood of the cline that was perturbed. A different cline in that same neighborhood may be approached. We are guaranteed, however, that $u(x,t)$ remains between $\underline{c}$ and $\bar{c}$ for all time, and so despite the possibility of many successive perturbations through the course of time, it will never evolve to a spatially constant distribution.

Clines can also be studied from the point of view of discrete, rather than continuous, selection-migration models. A result of Karlin and MacGregor [11], for example, implies that when the migration rate between colonies is small and each colony in isolation has two stable equilibrium states, then many clines exist. This is conceptually in accord with our results, which say, very roughly, that certain spatial heterogeneities favor the occurence of clines. Colonies with small interchange, when conceived in a geographical setting, form an inherently heterogeneous model.

The authors benefited greatly from discussions with T. Nagylaki and S. Levin.

2. Nonexistence Theorems.

We consider the problem

$$
\text{(I)} \quad \begin{cases} u'' + \lambda s(x) f(u) = 0 & x \in \mathbf{R}, \quad \lambda > 0, \\ u(-\infty) = 0, \quad u(+\infty) = 1 & , \end{cases} \tag{2.1}
$$

where f and s satisfy the hypotheses H_f and H_s listed in the Introduction.

It is well known that if $s \equiv$ constant, Problem I has no solution in view of the fact that $\int_0^1 f(u)du \neq 0$. Thus it is the variation of s which may give rise to the occurence of clines. In the following theorem we give a lower bound for the variation of s which is necessary to sustain a cline. We define

$$
s_1 = \inf_{\mathbf{R}} s(x) \quad , \quad s_2 = \sup_{\mathbf{R}} s(x)
$$

and we assume that $s_1 > 0$.

Theorem 1. Let

$$
\frac{s_1}{s_2} > \frac{\int_a^1 f(u)du}{-\int_0^a f(u)du} \quad . \tag{2.2}
$$

Then Problem I has no solution.

Proof. Suppose, to the contrary, that Problem I has a solution φ. Clearly $\varphi'(x) > 0$ for large negative values of x. Set

$$
x_0 = \sup\{x : \varphi'(\xi) > 0 \text{ on } (-\infty, x)\}
$$

Then either $x_0 = \infty$ or $x_0 < \infty$, in which case

$$\varphi'(x_0) = 0,\ \varphi''(x_0) < 0,\ \varphi(x_0) > a \quad .$$

Multiplying (2.1) by u' and integrating over $(-\infty, x_0)$ we obtain

$$\int_0^{\varphi(x_0)} s(x(\varphi))f(\varphi)d\varphi = 0 \quad , \tag{2.3}$$

where $x(\varphi)$ denotes the inverse function of $\varphi(x)$. Since $\varphi' > 0$ on $(-\infty, x_0)$ this function is well defined. Since $\varphi(x_0) \in (a,1)$ (2.3) implies that

$$\int_0^1 s(x(\varphi))f(\varphi)d\varphi > 0 \quad .$$

Thus, using the bounds for s we obtain

$$s_1 \int_0^a f(\varphi)d\varphi + s_2 \int_a^1 f(\varphi)d\varphi > 0$$

or

$$\frac{s_1}{s_2} < \frac{\int_a^1 f(\varphi)d\varphi}{-\int_0^a f(\varphi)d\varphi} \quad , \tag{2.4}$$

which contradicts our assumption about s_1/s_2.

Theorem 1 is optimal in the following sense: If positive numbers s_1 and s_2 are given which violate (2.2), there exists a function $s : R \to [s_1, s_2]$ such that Problem I has a solution. We shall demonstrate this in the following proposition: (see also [17]).

Proposition 1. Let $s : R \to R^+$ be defined by

$$s(x) = \begin{cases} s_1 & x < 0 \\ s_2 & x > 0 \end{cases}$$

where $0 < s_1 < s_2$ and s_1/s_2 satisfies (2.4). Then Problem I has a solution.

Proof. We construct a supersolution $\overline{u}$ and a subsolution $\underline{u}$ such that $\underline{u} \le \overline{u}$. Then the existence of a solution φ such that $\underline{u} \le \varphi \le \overline{u}$ is ensured by the standard theory [18].

We begin with the construction of a monotone subsolution. Let V_1 be the solution of the problem

$$\begin{cases} u'' + s_1 f(u) = 0 & -\infty < x < 0 \\ u(-\infty) = 0, \quad u(0) = a \end{cases} \tag{2.5}$$

and let V_2 be the monotone solution of the problem

$$\begin{cases} u'' + s_2 f(u) = 0 & 0 < x < \infty \\ u(0) = a, \quad u(\infty) = 1 \quad . \end{cases} \tag{2.6}$$

Both solutions exist, and can be constructed implicitly by quadrature. In fact, multiplying (2.5) by u' and integrating, we obtain

$$\frac{1}{2} \{u'(x)\}^2 + s_1 \int_0^u f(s)ds = 0 \quad ,$$

which gives u' in terms of u for $u \in (0,a]$, since the integral is negative in that range. Define

$$\underline{u}(x) = \begin{cases} V_1(x) & x < 0 \\ V_2(x) & x > 0 \end{cases} .$$

Then $\underline{u}$ will be a subsolution of Problem I if

$$\underline{u}'(0^-) \leq \underline{u}'(0^+) \quad . \tag{2.7}$$

It follows from (2.5) that

$$\{V_1'(0)\}^2 = -s_1 \int_0^a f(v)dv$$

and from (2.6) that

$$\{V_2'(0)\}^2 = +s_2 \int_a^1 f(v)dv \quad .$$

Thus, by (2.4)

$$\{V_1'(0)\}^2 \leq \{V_2'(0)\}^2 \quad ,$$

which establishes (2.7).

For a supersolution we take, for some $\xi \in \mathbf{R}$, the function

$$\underline{u}(x) = \begin{cases} 1 & x > \xi \\ w(x) & x < \xi \end{cases} ,$$

where w is the solution of the problem

$$w'' + s_1 f(w) = 0 \qquad x < \xi$$

$$w(-\infty) = 0, \quad w(\xi) = 1 \quad .$$

This problem has a unique monotone solution (use the method outlined above and H_f). By choosing $\xi < 0$, we make $\bar{u}$ a supersolution of Problem I, and by choosing $(-\xi)$ large enough we can ensure that $\bar{u} \geq \underline{u}$. This completes the proof.

In the next theorem we limit the class of functions s for which we can expect clines even further.

<u>Theorem</u> 2. Let s be a nonincreasing function of x. Then Problem I has no solution.

<u>Proof</u>. Suppose again that Problem I has a solution φ, and define x_0 as in the proof of Theorem 1. Then we obtain (2.3) which we now write as

$$-\int_0^a s(x(\varphi))f(\varphi)d\varphi = \int_a^{\varphi_0} s(x(\varphi))f(\varphi)d\varphi \tag{2.8}$$

with $\varphi_0 = \varphi(x_0)$. Since φ is monotone on $(-\infty,x_0)$ and $\varphi(x_0) > a$, there exists a unique point $\xi \in (-\infty,x_0)$ such that $\varphi(\xi) = a$. Now utilizing the monotonicity of s we deduce from (2.8) that

$$-s(\xi) \int_0^a f(\varphi)d\varphi \leq s(\xi) \int_a^{\varphi_0} f(\varphi)d\varphi$$

and hence

$$\int_0^1 f(\varphi)d\varphi \geq \int_0^{\varphi_0} f(\varphi)d\varphi \geq 0 \quad .$$

which contradicts our assumption about the sign of $\int_0^1 f$.

Thus for there to exist a cline, it is necessary that s be increasing at some point of the domain. In fact, as we shall see as a corollary of the following more general nonexistence theorem, this is still not enough: it needs to increase sufficiently fast.

To prove this we consider the problem

$$(\mathrm{II})\quad \begin{cases} u'' + h(\varepsilon x,u) = 0 \\ u(-\infty) = 0, \quad u(\infty) = 1 \end{cases}$$

where we make the following assumptions about h.

A1. $h \in C^1(\mathbf{R} \times [0,1])$, $h(x,\cdot) \in C^2([0,1])$

A2. $|h_x| \leq 1$, $|h_u| \leq M_1$, $|h_{uu}| \leq M_2$ uniformly on $\mathbf{R} \times [0,1]$.

A3. $h(x,0) = h(x,a(x)) = h(x,1) = 0$ for all $x \in \mathbf{R}$, $a \in C(\mathbf{R})$, $0 < a(x) < 1$ for all $x \in \mathbf{R}$; $h(x,\cdot) < 0$ on $(0,a(x))$ and $h(x,\cdot) > 0$ on $(a(x),1)$.

A4. $h_u(x,0) \leq -\alpha < 0$, $h_u(x,1) < -\alpha < 0$ for all $x \in \mathbf{R}$.

A5. $\int_0^1 h(x,u)\,du \leq -3\rho < 0$ for all $x \in \mathbf{R}$.

Note that Problem II is equivalent with the problem

$$(\mathrm{II}')\quad \begin{cases} u'' + \lambda\, h(x,u) = 0 & \lambda = 1/\varepsilon^2 \\ u(-\infty) = 0, \quad u(\infty) = 1 & . \end{cases} \tag{2.9}$$

Theorem 3. Let h satisfy the assumptions A1-5. Then there exists an $\varepsilon^* > 0$ ($\lambda^* > 0$) such that if $\varepsilon \leq \varepsilon^*$ ($\lambda \geq \lambda^*$) Problem (II) (II') has no solution.

Proof. Suppose $\varphi(x,\lambda)$ is a solution of Problem II', and let ξ be the smallest root of the equation

$$\varphi(x,\lambda) = a(x) \quad .$$

In view of the boundary conditions, and the assumptions on a, such a root will always exist. Note that ξ will depend on λ.

Before we proceed further, we introduce some notation. Choose $\delta > 0$ such that

$$\int_{\delta}^{1} h(x,u)\,du \leq -2\rho \quad \text{for all} \quad x \in R$$

and define

$$R(\xi) = \{(x,u) : |x-\xi| < \rho,\ \delta < u < 1\} \quad .$$

To begin with we shall show that there exists a $\lambda_1 > 0$ such that if $\lambda \geq \lambda_1$, the graph of φ can only enter R through the bottom, i.e.

$$\varphi(x,\lambda) \leq \delta \quad \text{on} \quad (-\infty,\xi-\rho] \quad . \tag{2.10}$$

Suppose to the contrary that φ enters R at a point $(\xi-\rho,u_1)$, where $u_1 \in (\delta,1)$. Then, because $\varphi'' > 0$ on $(\xi-\rho,\xi)$,

$$\varphi'(\xi-\rho) < (1-\delta)/\rho$$

and hence

$$\int_{-\infty}^{\xi-\rho} |h(x,\varphi(x,\lambda))|\,dx < (1-\delta)/(\rho\lambda) \quad . \tag{2.11}$$

Since

$$\left|\frac{d}{dx} h(x,\varphi(x,\lambda))\right| \leq |h_x(x,\varphi(x,\lambda))| + |h_u(x,\varphi(x,\lambda))|\ |\varphi'(x,\lambda)|$$

$$\leq 1 + M_1(1-\delta)/\rho$$

the inequality (2.11) implies that at each $x \in (-\infty,\xi-\rho]$,

$$h(x,\varphi(x,\lambda)) \to 0 \quad \text{as} \quad \lambda \to \infty$$

and in particular

$$h(\xi-\rho,\ \varphi(\xi-\rho,\lambda)) \to 0 \quad \text{and} \quad \lambda \to \infty \quad .$$

Thus, for λ large enough,

$$u_1 = \varphi(\xi-\rho,\lambda) \leq \delta$$

and we obtain a contradiction.

We shall now show that there exists a $\lambda_2 > 0$ such that if $\lambda > \lambda_2$, the graph of φ can only leave R through the top. This contradicts the boundary condition at $+\infty$ and thereby proves the theorem.

We multiply (2.9) by $2\varphi'$ and integrate over $(-\infty,\xi)$. This yields

$$\{\varphi'(\xi)\}^2 = 2\lambda \int_0^{a(\xi)} |h(x(\varphi),\varphi)|\, d\varphi > 2\lambda \int_\delta^{a(\xi)} |h(x(\varphi),\varphi)|\, d\varphi \quad ,$$

where $x(\varphi)$ is the inverse of $\varphi(x)$. Let $\lambda \geq \lambda_1$. Then $|x(\varphi) - \xi| < \rho$ on $[\xi, a]$ and it follows that

$$\{\varphi'(\xi)\}^2 > 2\lambda \int_\delta^{a(\xi)} |h(\xi,\varphi)| d\varphi - 2\lambda\rho a(\xi) \sup|h_x| \sup|x(\varphi) - \xi|$$

$$> 2\lambda \int_\delta^{a(\xi)} |h(\xi,\varphi)| d\varphi - 2\lambda\rho a(\xi) \quad .$$

For $x \in (\xi, \xi+\rho]$, we now get, as long as $\varphi'(x) > 0$

$$\{\varphi'(x)\}^2 = \{\varphi'(\xi)\}^2 - 2\lambda \int_a^{\varphi(x)} h(x(\varphi),\varphi) d\varphi$$

$$> -2\lambda \int_\delta^a h(\xi,\varphi) d\varphi - 2\lambda\rho a - 2\lambda \int_a^{\varphi(x)} h(\xi,\varphi) d\varphi - 2\lambda\rho(1-a)$$

$$\geq +2\lambda\{-\int_\delta^1 h(\xi,\varphi) d\varphi - \rho\}$$

$$> 2\lambda(2\rho-\rho)$$

$$= 2\lambda\rho \quad .$$

Thus, choosing $\lambda_2 = 1/2\rho\delta^2$, we achieve that

$$\varphi'(x) > 1/\delta \qquad x > \xi$$

and hence, that the graph of φ leaves R through the top.

Remark. Theorem 3 may be regarded as a partial converse to Theorem 6.1 of [4], in which the existence of a transition layer solution is established for the equation

$$\varepsilon^2 u'' + h(x,u) = 0 \qquad x \in R$$

in which $h(x,0) = h(x,1) = 0$, $h_u(x,0) \leq -\kappa$ $h_u(x,1) \leq -\kappa$ for some $\kappa > 0$ and in which it is assumed that for some $x_0 \in R$,

$$\int_0^1 h(x_0,u)\,du = 0 \quad .$$

In our terminology, a transition layer solution is a special type of cline, one on which the change is primarily concentrated in a small interval. It is the last condition which is violated here, and indeed we find that no cline exists for small enough ε.

We now return to our original problem. Consider

$$(I_\varepsilon) \quad \begin{cases} u'' + s(\varepsilon x)f(u) = 0 \\ u(-\infty) = 0, \qquad u(\infty) = 1 \end{cases} ,$$

where s and f satisfy, respectively, H_s and H_f. In addition we assume that $s \in C^1(\mathbf{R})$, and

$$|s'(x)| \leq m, \quad x \in R \quad .$$

<u>Corollary 2</u>. There exists an $\varepsilon^* > 0$ such that if $\varepsilon < \varepsilon^*$, Problem I_ε has no solution.

3. Existence Theorems.

Having established a number of necessary conditions on s for there to exist a cline, we shall now give two sets of sufficient conditions.

In the first theorem, we describe the effect of a localized inhomogeneity in an otherwise uniform habitat. Thus, we assume that s is given by

$$s(x,\mu;\xi) = \{1 + \mu\theta(x,\xi)\}^{-1} \quad \mu > 0,\ \xi > 0 \quad , \tag{3.1}$$

where $\theta \in C^1(\mathbf{R})$ has the following properties:

$H_\theta 1$ $\theta(x,\xi) = 0$ for $|x| \geq \xi$

$H_\theta 2$ $\theta(x,\xi) \geq 0$ for $|x| < \xi$ $(\not\equiv 0)$

$H_\theta 3$ $\text{Max}\{\theta(x) : |x| < \xi\} = 1$.

Thus, 2ξ denotes the width of the inhomogeneity, and μ is a measure of its "strength".

Theorem 4. Let f satisfy H_f and let s be of the form (3.1) in which θ satisfies the assumptions H_θ. Then, if

$$\lambda\xi^2 > \frac{a^2}{8}\left\{\int_a^1 f(r)dr\right\}^{-1} \quad , \tag{3.2}$$

there exists a number μ^* such that if $\mu > \mu^*$, Problem I has a solution. μ^* depends on λ and ξ and tends to infinity if either $\lambda \to \infty$ or $\xi \to \infty$.

Remark: We have normalized the function $s(x)$ so that its maximum is equal to one. This can be done by properly scaling the variable x. By (3.1), we are assuming that s is identically one for $|x| > \xi$ but experiences a drop in the center zone $|x| < \xi$. It will be clear, however, that the proof works as well if s is any other positive constant for $x \leq -\xi$. Thus, let $\chi(x)$ be a smooth monotone function with $\chi(x) \equiv \alpha > 0$ for $x < -\xi$ and $\chi(x) \equiv 1$ for $x > \xi$. Multiply the function on the right of (3.1) by $\chi(x)$ and use the resulting expression for s. Then Theorem 4 and its proof are still valid.

Proof of Theorem. We construct a sub- and a supersolution. The subsolution v we are going to construct will consist of three pieces: v_1, v_2, and v_3. For v_3 we take the solution of (2.1) on (ξ,∞) which satisfies the boundary conditions $v_3(\xi) = a$ and $v_3(\infty) = 1$. This solution clearly exists, and it is unique. For v_1 we choose $v_1(x) = 0$ on $(-\infty,p]$, where $p \in [-\xi,\xi)$ is still to be determined. Observe that

$$\{v_3'(\xi)\}^2 = 2\lambda \int_a^1 f(r)dr \quad .$$

Let $f(u) \geq -M$ on $[0,a]$. Then we choose for v_2 the solution of the problem

$$\begin{cases} u'' = \lambda s(x,\mu,\xi)M & \text{on } (p,\xi) \\ u(\xi) = a, \quad u'(\xi) = v_3'(\xi) & . \end{cases} \tag{3.3}$$

Then v_2 is a subsolution of (2.1) on (p,ξ). We shall show that if (3.2) is satisfied and μ large enough, $v_2' > 0$ on (p,ξ) and $v_2(p) = 0$.

Clearly, since $u'' > 0$ by (3.3) a necessary condition is

$$v_3'(\xi) > a/(2\xi) \quad ,$$

which implies (3.2). Moreover, integrating (3.3) we find

$$u'(\xi) - u'(x) \leq \lambda M \int_{-\xi}^{\xi} \frac{dx}{1 + \mu\theta(x,\xi)} \stackrel{\text{def}}{=} \varepsilon \quad . \tag{3.4}$$

Thus integrating once again, we obtain

$$a \geq \{v_3'(\xi) - \varepsilon\} (\xi - p)$$

whence $p \geq -\xi$ if

$$\varepsilon \leq v_3'(\xi) - \frac{a}{2\xi} \quad .$$

This can clearly be achieved by choosing $\mu \geq \mu^*$ for some large μ^*. It is clear however from (3.4) that as $\lambda \to \infty$ or $\xi \to \infty$, $\mu^* \to \infty$ as well.

The supersolution w is constructed out of two pieces w_1 and w_2. Here w_1 is the solution of (2.1) on $(-\infty,-\xi)$, which satisfies the boundary conditions $w_1(-\infty) = 0$, $w_1(-\xi) = 1$. In view of the integral condition on f this solution exists, and is unique. For w_2 we choose $w_2(x) = 1$ on $[-\xi,\infty)$.

By construction $v(x) < w(x)$ on **R**. Hence there exists a solution u of Problem I such that $v < u < w$.

To construct other sufficient conditions for the existence of a stable cline, we envisage a pair of piecewise continuous functions $\underline{H}(u)$ and $\overline{H}(u)$ satisfying

$$\overline{H}(0) = \underline{H}(1) = 0 \quad , \tag{3.5}$$

$$\int_0^b \overline{H}(u)\,du < 0 \quad \text{for all} \quad b \in (0,1] \quad , \tag{3.6a}$$

$$\int_b^1 \underline{H}(u)\,du > 0 \quad \text{for all} \quad b \in [0,1) \quad , \tag{3.6b}$$

together with solutions $\underline{U}(x)$, $\overline{U}(x)$ of

$$\underline{U}'' + \underline{H}(\underline{U}) = 0, \quad \underline{U}(\infty) = 1 \quad , \tag{3.7}$$

$$\overline{U}'' + \overline{H}(\overline{U}) = 0, \quad \overline{U}(-\infty) = 0 \quad . \tag{3.8}$$

Representing the solutions in the usual way, one can see that $\underline{U}$ must vanish at a finite value $\underline{x}$, which may be chosen arbitrarily, and $\overline{U} = 1$ at a finite value $\overline{x}$. We consider $\underline{U}$ to be defined only on $[\underline{x},\infty)$ and $\overline{U}$ only on $(-\infty,\overline{x}]$.

Theorem 5. Let $\underline{H}$, $\overline{H}$, $\underline{U}$, $\overline{U}$ be as above, with $\underline{U}(x) \leq \overline{U}(x)$ where they are both defined. Assume $h(x,u)$ satisfies H_h and

$$h(x,\underline{U}(x)) \geq \underline{H}(\underline{U}(x)) \quad \text{for} \quad \underline{U} \in [0,1] \quad , \tag{3.9a}$$

$$h(x,\overline{U}(x)) \leq \overline{H}(\overline{U}(x)), \quad \text{for} \quad \overline{U} \in [0,1] \quad . \tag{3.9b}$$

Then there exists a stable solution of Problem (II) with $\varepsilon = 1$.

<u>Proof:</u> The function $\underline{u}(x) = \mathrm{Max}\{0, \underline{U}(x)\}$ is a subsolution, and $\overline{u}(x) = \mathrm{Min}\{1, \overline{U}(x)\}$ is a supersolution. The conclusion follows immediately.

The following corollary treats the case when h can be compared, in a certain way, with functions of the form $s(x)f(u)$, where s and f satisfy H_s and H_f, respectively. We picture the habitat as being divided into four regions, the first two being (i) the interval $(-\infty, 0)$, where the population exists in a state near $u = 0$; and (ii) the interval (A, ∞) for some $A > 0$, where u is near 1. The interval $(0, A)$ between these two population states is divided into (iii) a "barrier" region $(0, B)$, wherein the selection strength is required to be small enough, and (iv) a "transition" interval (B, A) of length $T = A - B$, which is simply assumed to be short enough. In region (ii), the selection strength must be large enough but no strong requirements are imposed upon it in (i) and (iv).

The critical ratio

$$\overline{\gamma} = \frac{\int_a^1 f(u)\,du}{-\int_0^a f(u)\,du}, \tag{3.10}$$

will play a crucial role. Note that $0 < \overline{\gamma} < 1$.

<u>Corollary 5.1.</u> Let $\gamma < \overline{\gamma}$. Suppose $h(x,u) \geq s(x)f(u)$ where s and f satisfy H_s and H_f, respectively, and in addition for some nonnegative numbers B, T, and σ,

$$\begin{aligned}
s(x) &\leq \sigma, & x &\in (-\infty, 0) \\
s(x) &\leq \sigma, & x &\in (0, B) \\
s(x) &\geq 1, & x &\in (B, B+T) \\
s(x) &\geq 1, & x &\in (B+T, \infty)\,.
\end{aligned} \tag{3.11a-d}$$

Also for some negative number $-X$, we assume that

$$h(x,u) \leq s(x)f(x) \quad , \quad x \leq -X \quad ,$$

where s and f also satisfy H_s and H_f, $0 < s_1 \leq s(x) \leq s_2$ for $x \leq -X$, and

$$\frac{s_1}{s_2} > \gamma \quad , \tag{3.12}$$

γ being defined by (3.10) with f replaced by f. Then there are numbers $B^*(\gamma,\sigma)$, $T^*(\gamma,\sigma)$ such that if

$$B \geq \lambda^{-1/2}B^*, \; T \leq \lambda^{-1/2}T^*, \; B + T \geq \lambda^{-1/2}(B^* + T^*) \quad , \tag{3.13}$$

there exists a stable solution of Problem (II').

<u>Remark.</u> Formulas for suitable B and T will be given in Proposition 5.1. It clearly follows from the construction below that

$$\lim T^*(\gamma,\sigma) = 0 \quad \text{for} \quad \sigma \geq \gamma \quad .$$

It can also be shown that

$$\lim B^*(\gamma,\sigma) = \infty \quad .$$

<u>Proof.</u> It suffices to prove the theorem for the case $\lambda = 1$; the general case can be reduced to that by rescaling, $x = \lambda^{-1/2}y$.

For some $w \in [0,a/2]$, let

$$\underline{H}(u) = \begin{cases} \underline{\gamma} f(u), & u \in (0,w) \quad , \\ \gamma f(u), & u \in (w,a-w) \\ f(u) \; , & u \in (a-w,1) \quad . \end{cases}$$

For $w = 0$, $\int_0^1 \underline{H}(u)du = \gamma \int_0^a f du + \int_a^1 f du > 0$, since $\gamma < \bar{\gamma}$. Therefore there exists a value $w_1 \in (0,a/2)$ for which $\int_0^1 \underline{H}(u)du > 0$ as well. For $w = w_1$ let $\underline{U}(x)$ be the solution of (3.7) satisfying $\underline{U}(0) = w_1$. Let $(0,B^*)$ and $(B^*, B^* + T^*)$ be the intervals on which $\underline{U} \in (w_1, a - w_1)$ and $(a - w_1, a)$, respectively. Then (3.11) for $B = B^*$, $T = T^*$ implies (3.9a).

$$\text{Defining} \quad \bar{H}(u) = \begin{cases} s_1 f(u), & u \in (0,a) \quad , \\ s_2 f(u), & u \in (a,1) \quad , \end{cases}$$

we see that (3.12) implies (3.6a); and if $\bar{U}$ is the solution of (3.8) satisfying $\bar{U}(-X) = 1$, (3.9b) will be satisfied.

For $B = B^*$, $T = T^*$, the conclusion follows from Theorem 5. Now let B and T be any numbers satisfying (3.13) (λ still equal to 1). Then setting $x_0 = (B + T) - (B^* + T^*)$, we see that (3.11) still hold, with the four intervals mentioned there shifted to the right by the amount x_0. This proves the corollary.

[illegible] 5.1. Let w_1 be defined as in the proof of Corollary 5.1. [illegible] $\int_{a}^{1}$ [illegible] $]^{-1}$. Then the following expressions yield [illegible] B and T fulfilling the requirements of Corollary 1:

$$B = (a - 2w_2)(F(0,w_1)\sigma^{1/2})^{-1} + w_1(F(a,1))^{-1} ,$$

$$T = w_1(F(a,1))^{-1} ,$$

where $F(\alpha,\beta) \equiv (2\int_\alpha^\beta |f(u)|du)^{1/2}$.

Proof: Let $c < 0$ be such that $\underline{U}(c) = 0$. Multiply (3.7) by $\underline{U}'$ and integrate from c to 0, to obtain

$$\underline{U}'(0) > F(0,w_1)\sigma^{1/2} .$$

For $x \in (0,B^*)$, $\underline{U}'' \geq 0$, so $\underline{U}'(x) \geq \underline{U}'(0)$, and

$$\underline{U}(x) > w_1 + x\, F(0,w_1)\sigma^{1/2} .$$

Setting $x = B^*$, $\underline{U}(B^*) = a - w_1$, we obtain

$$B^* < (a - 2w_1)(F(0,w_1)\sigma^{1/2})^{-1} . \qquad (3.14)$$

Working from the other end, we find $\underline{U}'(B^* + T^*) = F(a,1)$, and for $x \in [B^*, B^* + T^*]$,

$$\underline{U}'(B^* + T^*) - M(B^* + T^* - x) \leq \underline{U}'(x) \leq \underline{U}'(B^* + T^*) ,$$

where $-M = \inf f$. Integrating from B^* to $B^* + T^*$ and using the facts that $\underline{U}(B^*) = a - w_1$, $\underline{U}(B^* + T^*) = a$, we get

$$F(a,1)T^* - \frac{1}{2} MT^{*2} \leq w_1 \leq F(a,1)T^* ,$$

hence

$$w_1 F(a,1)^{-1} \leq T^* \leq M^{-1} F(a,1) \; [1 - (1 - \frac{2Mw_1}{(F(a,1))^2})^{1/2}]$$

$$\leq 2w_1 (F(a,1))^{-1} . \qquad (3.15)$$

It is seen from (3.14) and (3.15) that the values of B and T given in the proposition satisfy (3.13).

4. Properties of solutions.

We begin with a monotonicity theorem.

Theorem 6. Let φ be a solution of Problem I in which s and f satisfy, respectively, H_s and H_f. Then if s is nondecreasing, φ is strictly increasing.

Proof. Without loss of generality we may set $x = 1$. Let

$$x_2 = \inf\{x \in R : \varphi' > 0 \text{ on } (x,\infty)\}$$

and let us assume that $x_2 > -\infty$. Set $\varphi_2 = \varphi(x_2)$. Since $\varphi'(x_2) = 0$, $\varphi''(x_2) \geq 0$, and $u \equiv a$ is a solution of equation (2.1), it follows that $\varphi_2 \in (0,a)$ and $\varphi''(x_2) > 0$. Let

$$x_1 = \inf\{x < x_2 : \varphi' < 0 \text{ on } (x,x_2)\} \quad .$$

In view of the boundary condition at $x = -\infty$, $x_1 > -\infty$. Set $\varphi_1 = \varphi(x_1)$. Then $\varphi_1 \in (a,1)$. Denote by $x_1(\varphi)$ the inverse of $\varphi(x)$ on (x_1,x_2) and by $x_2(\varphi)$ the inverse of $\varphi(x)$ on (x_2,∞).

If we multiply (2.1) by φ' and integrate over (x_1,x_2) we obtain

$$\int_{\varphi_2}^{\varphi_1} s(x_1(\varphi))f(\varphi)\,d\varphi = 0 \quad , \tag{4.1}$$

and if we integrate over (x_2,∞):

$$\int_{\varphi_2}^{1} s(x_2(\varphi))f(\varphi)\,d\varphi = 0 \quad . \tag{4.2}$$

Equation (4.1) yields

$$\int_{\varphi_2}^{a} s(x_1(\varphi))|f(\varphi)|d\varphi = \int_a^{\varphi_1} s(x_1(\varphi))|f(\varphi)|d\varphi$$

and hence, by the monotonicity of s

$$s(\xi) \int_{\varphi_2}^{a} |f(\varphi)|d\varphi \leqslant s(\xi) \int_a^{\varphi_1} |f(\varphi)|d\varphi$$

whence ξ is the (unique) zero of the equation

$$\varphi(x) - a = 0 \tag{4.3}$$

on (x_1, x_2). Thus, since $s > 0$

$$\int_{\varphi_2}^{a} |f(\varphi)|d\varphi \leqslant \int_a^{\varphi_1} |f(\varphi)|d\varphi \quad . \tag{4.4}$$

Similarly, (4.2) yields

$$\int_{\varphi_2}^{a} s(x_2(\varphi))|f(\varphi)|d\varphi = \int_a^{1} s(x_2(\varphi))|f(\varphi)|d\varphi$$

and hence

$$s(\eta) \int_{\varphi_2}^{a} |f(\varphi)|d\varphi \geqslant s(\eta) \int_a^{1} |f(\varphi)|d\varphi$$

where η is the (unique) zero of (4.3) on (x_2, ∞). Thus

$$\int_{\varphi_2}^{a} |f(\varphi)|d\varphi > \int_a^1 |f(\varphi)|d\varphi \quad . \tag{4.5}$$

Together (4.4) and (4.5) imply

$$\int_a^{\varphi_1} |f(\varphi)|d\varphi > \int_a^1 |f(\varphi)|d\varphi \quad ,$$

which would mean that $\varphi_1 > 1$. This is impossible.

Next, we turn to the question of uniqueness. We shall show by means of the example discussed in Problem 1, that we generally cannot expect a unique solution (see also [17]).

Proposition 2. Let $\lambda = 1$ and $s : R \to R^+$ be defined by

$$s(x) = \begin{cases} s_1 & x < 0 \\ s_2 & x > 0 \end{cases}$$

whence $0 < s_1 < s_2$. Then

(i) if $s_1/s_2 = \overline{\gamma}$, Problem I has precisely one solution

(ii) if $s_1/s_2 < \overline{\gamma}$, Problem I has precisely two solutions.

Proof. Let $v(x,\alpha)$ be the solution of equation (2.1) on $(-\infty,0)$ which satisfies the boundary conditions $v(-\infty,\alpha) = 0$, $v(0,\alpha) = \alpha$. Then for each $\alpha \in [0,1]$, $v(\cdot,\alpha)$ is well defined and

$$\{v'(0,\alpha)\}^2 = -2s_1 \int_0^\alpha f(r)dr, \quad 0 \leq \alpha \leq 1 \quad .$$

Similarly, let $w(x,\alpha)$ be the solution of equation (2.1) which satisfies the boundary conditions $v(0,\alpha) = \alpha$, $v(\infty,\alpha) = 1$. This solution is well defined for $\overline{\alpha} < \alpha \leq 1$, whence $\overline{\alpha}$ is determined by $\int_{\overline{\alpha}}^1 f(r)dr = 0$, and

$$\{w'(0,\alpha)\}^2 = 2s_2 \int_\alpha^1 f(r)dr \quad \bar{\alpha} < \alpha \leq 1 \quad .$$

Clearly the co..osite function

$$\varphi = \begin{cases} v & x < 0 \\ w & x > 0 \end{cases}$$

is a solution of Problem I if

$$v'(0,\alpha) = w'(0,\alpha). \quad \bar{\alpha} < \alpha \leq 1 \quad .$$

It is readily seen that this equation has one root $(\alpha = a)$ if $s_1/s_2 = \bar{\gamma}$, and two roots α_1, α_2 $(\bar{\alpha} < \alpha_1 < a < \alpha_2 < 1)$ of $s_1/s_2 < \bar{\gamma}$.

5. Bounded domains.

In this section we consider the problem

$$\text{(III)} \quad \begin{cases} u'' + \lambda s(x) f(u) = 0 & -1 < x < 1 \\ u'(-1) = u'(+1) = 0 & . \end{cases}$$

Clearly this problem has three trivial solutions $u_1 = 0$, $u_2 = a$ and $u_3 = 1$. u_1 and u_3 are stable and u_2 is unstable. We shall inquire into the existence of stable nontrivial solutions.

To begin with we shall generalize Theorem 4. However, before we can state it we need to introduce some notation. Consider the problem

$$\begin{cases} u'' + \lambda f(u) = 0 \\ u(0) = a, \quad u'(1) = 0 & . \end{cases}$$

This problem has a strictly increasing solution $u(x,\lambda)$ for $\lambda > \lambda_0 > 0$. Set

$$\omega(\lambda) = \int_a^{u(1,\lambda)} f(r)dr \qquad \lambda > \lambda_0 \quad .$$

Clearly $\omega(\lambda) \searrow 0$ as $\lambda \searrow \lambda_0$ and $\omega(\infty) = \int_a^1 f(r)dr$.

Next, consider the problem

$$u'' + \lambda f(u) = 0 \tag{5.1}$$

$$u(0) = 1, \quad u'(1) = 0 \quad . \tag{5.2}$$

In view of the integral condition on f there exists a $\lambda^* > 0$ such that if $\lambda > \lambda^*$, this problem has a strictly decreasing solution (which is not unique).

Theorem 7. Let f satisfy H_f and let s be of the form (3.1) in which $\xi \in (0,1)$ and θ satisfies assumptions H_θ.

Suppose λ and ξ satisfy the following inequalities

$$\lambda\xi^2\omega(\lambda(1-\xi)^2) > \frac{1}{8} a^2 \tag{5.3}$$

$$\lambda(1-\xi)^2 \geq \max\{\lambda_0, \lambda^*\} \quad . \tag{5.4}$$

Then there exists a constant μ^* such that if $\mu > \mu^*$, Problem III has a solution. If $\lambda \to \infty$, then $\mu^* \to \infty$.

Proof. We proceed as in the proof of Theorem 4 constructing a subsolution v and a supersolution w such that $v \leq w$.

For v_3 we now take the solutin of (2.1) on $(\xi,1)$ which satisfies the boundary conditions $v_3(\xi) = a$ and $v_3'(1) = 0$. This solution exists in view of (5.4) and it can be seen by a scaling argument that

$$\{v_3'(\xi)\}^2 = 2\lambda\omega(\lambda(1-\xi)^2) \quad . \tag{5.5}$$

As in the proof of Theorem 4 we require that

$$v_3'(\xi) > a/2\xi \quad ,$$

which, together with (5.5) yields (5.3).

The construction of the pieces v_1 and v_2 is the same as in the proof of Theorem 4.

The supersolution w consists again of two pieces w_1 and w_2. Again, $w_2 = 1$ on $[-\xi,1]$ but w_1 is now the solution of equation (2.1) on $(-1,-\xi)$ which satisfies the boundary conditions $w_1'(-1) = 0$ and $w_1(-\xi) = 1$. It is a simple matter to transform this problem to (5.1), (5.2). By a appropriate scaling we find that the function w_1 exists if the inequality (5.4) is satisfied.

In view of the construction $v < w$ on $[-1,1]$. This completes the proof.

6. Variable migration and/or carrying capacity.

We now consider the problem

$$\text{(IV)} \quad \begin{array}{l} (k^2(x)V^2(x)u')' + 2\lambda k^2(x)V(x)f(u) = 0, \quad x \in \mathbf{R},\ \lambda > 0 \\ u(-\infty) = 0, \quad u(\infty) = 1 \quad , \end{array} \tag{6.1}$$

where f satisfies H_f, k and V are in $C^1(-\infty,\infty)$, and $k(x)$ and $V(x)$ have positive lower bounds. As we shall see, many of the results about Problem IV can be deduced from the results obtained about Problem I.

Let

$$y = \tau(x) \overset{\text{def}}{=} \int_0^x \frac{dr}{k^2(r)V^2(r)} \quad .$$

Clearly τ maps $\mathbf{R}$ onto $\mathbf{R}$ and its inverse τ^{-1} is well defined. Introducting y as the independent variable into (6.1), we obtain

$$u'' + \lambda s(y)f(u) = 0, \quad y \in \mathbf{R}$$

where the primes now denote differentiation with respect to y, and

$$s(y) = 2k^4(\tau^{-1}(y))V^3(\tau^{-1}(y)) \quad . \tag{6.2}$$

Let

$$s_1^* = \inf_{\mathbf{R}} k^4(x)V^3(x) \quad \text{and} \quad s_2^* = \sup_{\mathbf{R}} k^4(x)V^3(x) \quad .$$

Then the following result is immediate from Theorem 2:

Theorem 8. Let

$$\frac{s_1^*}{s_2^*} > \frac{\int_a^1 f(u)\,du}{-\int_0^a f(u)\,du} .$$

Then Problem IV has no solution.

It is also obvious from Proposition 1 that Theorem 8 is optimal. Next, we observe that for any $x_1, x_2 \in R$.

$$k^4(x_1)V^3(x_1) - k^4(x_2)V^3(x_2) = s(y_1) - s(y_2) ,$$

where $y_i = \tau(x_i)$ $(i = 1,2)$. Thus if $k^4(x)V^3(x)$ is nonincreasing, so is s. Whence by Theorem 2, we have proved the following.

Theorem 9. Let $k^4(x)V^3(x)$ be a nonincreasing function of x. Then Problem IV has no solution.

Finally, we shall show that like s, k^4V^3 has to increase somewhere sufficiently fast for there to exist a solution. Consider the problem

$$(IV_\varepsilon) \quad \begin{cases} [k^2(\varepsilon x)V^2(\varepsilon x)u']' + 2k^2(\varepsilon x)V(\varepsilon x)f(u) = 0 , \\ u(-\infty) = 0, \qquad u(\infty) = 1 . \end{cases}$$

Then writing $x' = \varepsilon x$, we can reduce this problem to Problem IV with $\lambda = 1/\varepsilon^2$, and hence to Problem I with $y = \tau(x')$, and s defined by (6.2). Theorem 3 now yields the desired result.

Theorem 10. There exists an $\varepsilon^* > 0$ such that if $\varepsilon < \varepsilon^*$, Problem IV_ε has no solution.

Next, we turn to the question of existence. It is here that the results for Problem IV become somewhat different, and in fact stronger.

To begin with, we introduce the two-parameter family of functions

$$V(x,\mu,\xi) = \{1 + \mu\theta(x,\lambda)\}^{-1}, \ \mu > 0, \ \xi > 0 \quad , \tag{6.3}$$

where $\theta \in C^1(\mathbf{R})$ is as in section 3.

<u>Theorem</u> 11_V. Let f satisfy H_f, and let V be of the form (6.3) in which θ satisfies assumptions H_θ. Let $k \in C^1(\mathbf{R})$ satisfy $0 < k(x) \leq 1$, and $k(x) \equiv 1$ for $|x| \geq \xi$. Then for each $\lambda > 0$, $\xi > 0$, there exists a $\mu^* > 0$ such that if $\mu > \mu^*$, Problem IV possesses a cline.

<u>Theorem 11_k</u>. In the hypotheses of Theorem 11_V and in (6.3), replace the symbol V by k and k by V. Then under the new hypotheses, Problem IV possesses a cline.

<u>Proof.</u> We give the proof for Theorem 11_V only, as that for Theorem 11_k is the same. Throughout, we shall keep ξ fixed, and we shall write $V = V(x,\mu)$ and $\theta = \theta(x)$. Define

$$\eta^+(\mu) = \int_0^\xi \frac{dr}{k^2(r)V^2(r,\mu)} \geq \int_0^\xi \frac{dr}{V(r,\mu)} = \xi + \mu \int_0^\xi \theta(r)dr \quad ;$$

$$\eta^-(\mu) = \int_{-\xi}^0 \frac{dr}{k^2(r)V^2(r,\mu)} \geq \int_{-\xi}^0 \frac{dr}{V(r,\mu)} = \xi + \mu \int_{-\xi}^0 \theta(r)dr \quad .$$

Thus $\eta^\pm(\mu) \to \infty$ as $\mu \to \infty$.

As in the proof of Theorem 4, we construct a subsolution v which consists of three pieces: v_1, v_2, and v_3. The last piece, v_3, is the same as before, with η replaced by η^*.

Let $\mu_1 > 0$ be chosen so that

$$\lambda(\eta_1^+ + \eta_1^-)^2 > \frac{1}{2} a^2\left(\int_a^1 f(r)dr\right)^{-1} \quad , \tag{6.4}$$

where $\eta_1^{\pm} = \eta^{\pm}(\mu_1)$. Then for $\mu > \mu_1$,

$$v_3'(\eta^+) > a/(\eta^+ + \eta^-) \quad .$$

Next, we choose for v_2 the solution of the problem

$$\begin{cases} u'' = \lambda s(y,\mu)M & (y < \eta^+) \\ u(\eta^+) = a, \quad u'(\eta^+) = v_3'(\eta^+) & . \end{cases}$$

Then there exists a $\mu_2 > 0$ such that if $\mu > \mu_2$,

$$p = \inf\{y < \eta^+ : v_2 > 0 \text{ on } (y,\eta^+]\} > \eta^+ - (\eta_1^+ + \eta_1^-) \quad .$$

We now define $v_1(y) = 0$ for $-\infty < y \leq p$. The composite function v is the desired subsolution.

For the supersolution w, we can take the same function as in the proof of Theorem 4, with $-\xi$ replaced by $-\eta^-(\mu)$.

Thus if $\mu > \mu^* = \max\{\mu_1,\mu_2\}$, there exists a subsolution v and a supersolution w such that $v < w$ on $\mathbf{R}$. This implies the existence of a stable cline.

<u>Remarks</u>. 1. In the case $k \equiv 1$, it follows from Theorem 8 that the parameter μ in Theorem 11_V must satisfy

$$\frac{s_1^*}{s_2^*} = \frac{1}{(1+\mu)^3} < \bar{\gamma} \quad ,$$

and hence $\mu^* > (1/\bar{\gamma})^{1/3} - 1$.

2. It is clear from (6.4) that if $\lambda \to 0$, then $\mu_1 \to \infty$ and hence $\mu^* \to \infty$.

Next, we consider (6.1) on a bounded domain:

$$(V) \quad \begin{cases} (k^2(x)V^2(x)u')' + \lambda k^2(x)V(x)f(u) = 0, & -1 < x < 1 \quad , \\ u'(-1) = 0, \quad u'(+1) = 0 & . \end{cases}$$

Theorem 12. Let f satisfy H_f and let V be of the form (6.3) with $0 < \xi < 1$ in which θ satisfies assumptions H_θ. Let $k \in C^1(\mathbb{R})$ satisfy $0 < k(x) \leq 1$, and $k(x) \equiv 1$ for $|x| \geq \xi$. Then provided

$$\lambda(1-\xi)^2 > \max\{\lambda_0, \lambda^*\}$$

there exists a $\mu^* > 0$ such that if $\mu > \mu^*$. Problem V has a cline.

Recall that λ_0 and λ^* were defined in section 5.

Proof. Following the proof of Theorem 11, we transform equation (6.1) on (-1.1) to equation (2.1) on the interval $I = I_1 \cup I_2 \cup I_3$, where

$$I_1 = (-\eta^- - (1-\xi), -\eta^-), \; I_2 = [-\eta^-, \eta^+], \; I_3 = (\eta^+, \eta^+ + (1-\xi)) \quad .$$

On I_1 and I_3, we choose the same super, resp subsolution as in the proof of Theorem 7, and on I_2 we choose them as in the proof of Theorem 11.

7. Clines on a bounded habitat II.

In this section we prove the existence of clines in bounded habitats by a method which is different from the one used in the previous sections. There our main tool was the maximum principle; here it is a variational argument due to Matano [13]. He used it to prove that the problem

$$\begin{cases} \Delta u + f(u) = 0 & \text{in } \Omega \\ \dfrac{\partial u}{\partial n} = 0 & \text{on } \partial\Omega \end{cases},$$

where Ω is a bounded domain in $R^N (N > 1)$ with smooth boundary $\partial\Omega$, and $\partial/\partial n$ is the outward normal derivation on $\partial\Omega$, could have clines if Ω consisted of subdomains Ω_i which were connected by sufficiently narrow passages. The idea was that in this manner, the passages offered an obstruction to the migration of the individuals between the subdomains, thus allowing them to maintain different states.

The problem considered in section 6 is analogous to the one considered by Matano: the obstruction now being caused by a diminished mobility V or carrying capacity k.

We consider the general problem

$$\text{(VI)} \quad \begin{cases} (D(x)u')' + \lambda s(x)f(u) = 0 & x \in \Omega = (-1,1) \\ u'(-1) = 0, \quad u'(+1) = 0 \end{cases} \tag{7.1}$$

and we assume that the function f satisfies, in addition to the hypotheses H_f the normalization:

$$H_f^* \qquad (u-a)f(u) \le (u-a)^2 \quad \text{for} \quad 0 \le u \le 1 .$$

About D and s we make the assumptions:

A_1. $D, s \in C^{1+\nu}(\bar{\Omega})$ for some $\nu \in (0,1]$

A_2. $0 < \min\{D(x) : x \in \bar{\Omega}\}$ and $D(x) \leq 1$ on $\bar{\Omega}$

$0 \leq \min\{s(x) : x \in \bar{\Omega}\}$ and $s(x) \leq 1$ on $\bar{\Omega}$,

A_3. $D(x) = 1$ and $s(x) = 1$ on $\Omega_1 \quad \Omega_2$,

where $\Omega_1 = (-1,-\xi)$ and $\Omega_2 = (\xi,1)$ for some $\xi \in (0,1)$. Still following Matano, we define

$$R[-,+] = \{\zeta \in C^2(\Omega) \quad C^1(\bar{\Omega}) : \int_{\Omega_1} (\zeta-a)\,dx < 0,\ \int_{\Omega_2} (\zeta-a)\,dx > 0\}$$

and we introduce the functional $J : H'(\Omega) \to \mathbf{R}$:

$$J(\zeta) = \int_{\Omega}[\tfrac{1}{2} D(x)\{\zeta'(x)\}^2 - \lambda s(x)F(\zeta))]\,dx \quad ,$$

where

$$F(\zeta) = \int_a^{\zeta} f(r)\,dr \quad .$$

Recall that

$$\bar{\gamma} = \frac{\int_a^1 f(r)\,dr}{-\int_0^a f(r)\,dr} = \frac{F(1)}{F(0)} \quad .$$

Lemma. Let f satisfy the hypotheses H_f and H_f^*, and let D and s satisfy the assumptins A1 - 3. Suppose there exists a function $w \in H'(\Omega)$ such that

$$J(w) < \lambda F(0)\{(1-\xi)\min(1, \frac{\pi^2}{(1-\xi)^2\lambda}) - 2\} \quad .$$

Then Problem VI has a stable solution in the set $R[-,+]$. The proof of this result is nearly identical to that of Theorem 6.2 in [13], whence we omit it.

To obtain explicit conditions on ξ, λ, D and s, which ensure that (7.2) is satisfied, we consider the function

$$w(x) = \begin{cases} 0 & -1 \leq x \leq -\xi \\ \frac{1}{2}(1 + \frac{x}{\xi}) & -\xi < x < \xi \\ 1 & \xi \leq x \leq 1 \quad . \end{cases}$$

We find that $J(w)$ satisfies (7.2) if ξ, λ and D satisfy the inequality

$$\frac{1}{2\xi}\int_{-\xi}^{\xi} D(x)dx \leq 4\lambda\xi F(0)[(1-\xi)\min(\frac{\pi^2}{(1-\xi)^2\lambda}, 1) - 1 + \bar{\gamma} - (1+\bar{\gamma})\xi] \quad . \tag{7.3}$$

Thus we have proved the following existence theorem.

<u>Theorem 13.</u> Let f satisfy hypotheses H_f and H_f^*, and D and s assumptions A1 - 3. Then, if λ, ξ and D satisfy the inequality (7.3), Problem VI has a cline.

<u>Remarks.</u> 1. Note that beyond the assumptins A1 - 3, no conditions on s are required.

2. For the equation discussed in section 6, the condition for the existence of a cline becomes an upper bound for the integral

$$\int_{-\xi}^{\xi} V^2(x)k^2(x)dx \quad ,$$

which demonstrates again that in this context, the roles of V and k are interchangeable.

__Example.__ Let $\overline{\gamma} = 1$, and $\xi = 1/4$. Then (7.3) becomes

$$2 \int_{-1/4}^{1/4} D(x)\,dx \le \frac{1}{4} F(0)R(\lambda) \qquad 0 < \lambda < \frac{3}{2}\lambda_0 \quad ,$$

whence $\lambda_0 = (4\pi/3)^2$ and

$$R(\lambda) = \begin{cases} \lambda & \text{for } 0 < \lambda \le \lambda_0 \\ 3\lambda_0 - 2\lambda & \text{for } \lambda_0 \le \lambda < \frac{3}{2}\lambda_0 \end{cases} \quad .$$

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Clines (nonuniform spatial distributions in the genetic composition of a population in equilibrium) are often modeled by nonconstant solutions $u(x) \in [0,1]$ of $(D(x)u')' + h(x,u) = 0$, $-\infty < x < \infty$, where h satisfies $h(x,0) = h(x,1) = 0$, and D is often taken to be identically 1. The functions D and h have interpretations in terms of mobility, carrying capacity and natural selection. We define clines as stable solutions satisfying $u(-\infty) = 0$, $u(\infty) = 1$. All past analyses of clines have considered the case when (say) 0 is the favored state for large negative x, and 1 for large positive x (i.e.,

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ABSTRACT (continued)

$\int_0^1 h(x,u)du$ changes sign from negative to positive as x increases from $-\infty$ to ∞). In this paper, however, we assume that the state 0 is favored for all x, although both 0 and 1 are stable as uniform states. A number of conditions are given which ensure the existence of stable clines, or their analogs in the bounded habitat case. Conditions are also given which ensure the nonexistence of clines. The concept of stability is with reference to the corresponding nonlinear diffusion equation, and is used in a special technical sense.

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