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A NONLINEAR INTEGRAL OPERATOR ARISING FROM
A MODEL IN POPULATION GENETICS IV. CLINES*

ROGER LUI†

Abstract. We study the existence, uniqueness and stability properties of solutions to the integral equation
ϕ = Q[ϕ] with ϕ(−∞) = 1, ϕ(∞) = 0. Here Q[u](x) = ∫ K(x−y)g(y, u(y)) dy is defined on functions
bounded between 0 and 1, K is a probability density function and g(x, u) = s(x)u^2 + u / [1 + s(x)u^2 +
σ(x)(1−u)^2] according to a population genetics model. The hypotheses on g are based on the biological
assumption that the homozygotes, that is individuals with genotypes AA or aa, are best fit to survive near
opposite ends of the one-dimensional habitat.

1. Introduction. In the first section of [13] a population genetics model was for-
mulated that describes the change in gene fractions over successive generations of a
population living in a homogeneous one-dimensional habitat. The model took selection
and migration into account and resulted in a recursion of the form

(1.1) \[ u_{n+1} = Q[u_n], \]

where u_n(x) is the gene fraction of the population at location x in the nth generation.
The operator

(1.2) \[ Q[u](x) = \int K(x−y)g(y, u(y)) dy \]

is defined on the set of functions \( C = \{ u : 0 \leq u \leq 1, u \text{ piecewise continuous} \} \).

In the model, the selection process is described by a function g : \( \mathbb{R} \times [0, 1] \rightarrow [0, 1] \),
where

(1.3) \[ g(x, u) = \frac{s(x)u^2 + u}{1 + s(x)u^2 + \sigma(x)(1−u)^2}. \]

Migration on the other hand is described by a probability density function K.

The formula (1.3) was arrived at under several severe restrictions, among which is
the fact that fitnesses of the three genotypes AA, Aa and aa present in the population
have to be in the ratio \( 1 + s : 1 : 1 + \sigma \). In actual situations, the difference between these
fitnesses is usually small.

Equation (1.1) has so far been studied only when \( s \geq \sigma \) are constants (g independent
of x). The case \( s > 0 > \sigma \) and \( s \geq \sigma > 0 \) are considered in the papers [10], [11] and
[12], [13] respectively. The case \( 0 > s > \sigma \) is essentially the same as that of \( s > 0 > \sigma \). It
has also been mentioned in these papers that our model came as an improvement of a
similar model proposed by R. A. Fisher in 1937 [6].

Fisher came up with the nonlinear diffusion equation \( u_t = u_{xx} + f(u) \). This equation
has received a lot of attention lately (see references in [13]). Our results in [10] through [13]
agreed to a remarkable extent with those obtained for Fisher’s equation. Not surprisingly,
the results in this paper are in line with those in [4] and [18]. Judging from what is known,
it is clear that the qualitative picture of the solutions is independent of the details of the modelling and therefore has much biological interest.

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The purpose of this paper is to study (1.1) without assuming that \( s \) and \( \sigma \) are constants. We assume however that individuals of genotype \( AA \) are more fit to survive in the far left region of the habitat while the same is true for genotype \( aa \) in the far right. In terms of \( s \) and \( \sigma \), we assume

\[
\text{There exists } N > 0 \text{ such that } s(x) \geq \sigma(x), s(x) > 0 \text{ for } x \leq -N \text{ and } s(x) \leq \sigma(x), \sigma(x) > 0 \text{ for } x \geq N.
\]

We also assume that none of the homozygotes is lethal. That is to say,

\[
1 + s(x) > 0, \quad 1 + \sigma(x) > 0 \quad \text{in } \mathbb{R}.
\]

This implies that \( g(x,0) \equiv 0, g(x,1) \equiv 1 \) and \( \bar{g}(x,0) \equiv 0, \bar{g}(x,1) \equiv 1 \). Here

\[
\bar{g}(x,u) \equiv 1 - g(x,1-u) = \frac{\sigma(x)u^2 + u}{1 + \sigma(x)u^2 + s(x)(1-u)^2}.
\]

From (1.3)

\[
g_x(x,u) = \frac{[s'u + (\sigma s' - s\sigma')u(1-u) - \sigma'(1-u)]u(1-u)}{[1 + su^2 + \sigma(1-u)^2]^2}.
\]

According to (1.5), the denominator is always positive. If \( \sigma'(x) > 0, s'(x) < 0 \) and \( 0 < u < 1 \), then \( s'u[1 + \sigma(1-u)] < 0 < \sigma'(1-u)[1 + su] \) so that \( g_x(x,u) < 0 \). Therefore we assume, in addition to (1.4) and (1.5),

\[
\sigma'(x) \geq 0, \quad s'(x) \leq 0 \quad \text{for } |x| \geq N.
\]

This will imply that \( g_x(x,u) \leq 0 \) for \( |x| \geq N \).

Condition (1.7) is only enough to guarantee the existence of clines but not the uniqueness or stability. For these we need the more restrictive assumption

\[
\sigma'(x) \geq 0, \quad s'(s) \leq 0 \quad \text{in } \mathbb{R} \quad \text{and there exists an interval } \mathcal{J}
\]

where \( \sigma'(x) > 0, s'(x) < 0 \).

In terms of \( g \), (1.8) implies that, \( g_x(x,u) \leq 0 \) and \( g_x(x,u) < 0 \) in \( \mathcal{J} \times (0,1) \).

Again from (1.3)

\[
g_u(x,u) = \frac{-(s + 2s\sigma + \sigma)u^2 + (2s + 2s\sigma)u + 1 + \sigma}{[1 + su^2 + \sigma(1-u)^2]^2}.
\]

Let \( N(u) = -(s + 2s\sigma + \sigma)u^2 + (2s + 2s\sigma)u + 1 + \sigma \). Then \( N(0) = 1 + s > 0 \), \( N(1) = 1 + s > 0 \) so that \( N(u) > 0 \) in \([0,1]\) if \( s + 2s\sigma + \sigma \geq 0 \). When \( s + 2s\sigma + \sigma < 0 \), the minimum of \( N \) occurs at \( u^* = s(1 + \sigma)/(s + 2s\sigma + \sigma) \). In order for \( 0 \leq u^* \leq 1 \), we must have \( s \leq 0, \sigma \leq 0 \). But then

\[
N(u^*) = \frac{(1 + \sigma)(1 + s)[s + s\sigma + \sigma]}{s + 2s\sigma + \sigma} > 0,
\]

since \( s + s\sigma + \sigma \leq s + 2s\sigma + \sigma < 0 \). Thus \( g_u(x,u) > 0 \) in \( \mathbb{R} \times [0,1] \). Note that \( g_u(x,0) = 1/(1 + \sigma) \) and \( g_u(x,1) = 1/(1 + s) \).
To continue, consider
\[
g(-N,u) = \frac{s(-N)u^2 + u}{1 + s(-N)u^2 + s(-N)(1-u)^2}.
\]

From (1.4), \(s(-N)\) is positive so that the numerator and denominator are both nonnegative. Since \(s(-N) \geq \sigma(-N)\), (1.7) implies that
\[
(1.9) \quad g(x,u) \geq g(-N,u) \geq g_1(u) = \frac{s(-N)u^2 + u}{1 + s(-N)u^2 + s(-N)(1-u)^2} \quad \text{for} \quad x \leq -N.
\]

Similarly, \(\sigma(N) \geq \sigma(N)\) and (1.7) imply that
\[
(1.10) \quad g(x,u) \leq g(N,u) \leq g_0(u) = \frac{\sigma(N)u^2 + u}{1 + \sigma(N)u^2 + \sigma(N)(1-u)^2} \quad \text{for} \quad x \geq N.
\]

This last inequality is easy to verify if we look at \(\hat{g}(N,u)\).

We now summarize the hypotheses on \(K\) and \(g\) to be assumed throughout the entire paper except for condition (viii*) of (1.12). The hypotheses on \(K\) are identical to those assumed in [12]. We shall not assume \(g\) has the form (1.3) but only that it satisfies all the conditions listed in (1.12). Our discussion earlier made it clear what to assume of \(s\) and \(\sigma\) in order that (1.12) holds when \(g\) has the form (1.3).

(i) \(K(x) \geq 0\). If \(B_1 = \inf \{x : K(x) > 0\}, \ B_2 = \sup \{x : K(x) > 0\}\), then \(K(x) > 0\) in \((B_1, B_2)\). We allow \(B_1 = -\infty, \ B_2 = +\infty\) so that \(K\) need not have compact support.

(ii) \(K(x)\) is continuous in \(\mathbb{R}\), except possibly at \(B_1\) and \(B_2\) where
\[
\lim_{x \to B_1} K(x) = p_1, \quad \lim_{x \to B_2} K(x) = p_2.
\]

Also \(K\) may be written in the form
\[
(1.11) \quad K(x) = K_0(x) - p_1 \chi_{(-\infty, B_1)} - p_2 \chi_{[B_2, \infty)}
\]

where \(K_0\) is absolutely continuous and \(\chi_S\) is the indicator function of the set \(S\).

(iii) \(\int K(x) \, dx = 1\).

(iv) \(\int e^{\mu x} K(x) \, dx\) is finite for all real \(\mu\).

(v) \(\int_{-\infty}^x K(y) \, dy \leq \text{const} \ K(x)\) for large \(x\), \(\int_{-\infty}^x K(y) \, dy \leq \text{const} \ K(x)\) for small \(x\).

(vi) \(g(x,u) : \mathbb{R} \times [0,1] \to [0,1]\) has continuous derivative. \(g_x, g_u, g_{uu}\) are uniformly bounded.

(vii) \(g(x,0) \equiv 0, \ g(x,1) \equiv 1\).

(viii) There exists \(N > 0\) such that \(g_x(x,u) \leq 0\) for \(|x| \geq N\); or

(viii*) \(g_x(x,u) \leq 0\) in \(\mathbb{R} \times [0,1]\) and \(g_x(x,u) < 0\) in \(\mathcal{J} \times (0,1)\) for some interval \(\mathcal{J}\).

(ix) \(g_u(x,u) \geq 0\) in \(\mathbb{R} \times [0,1]\) and \(g_u \neq 0\) in any rectangle.

(1.12) \(g_u(x,0) \in (0,1)\) uniformly for \(x \geq N\), \(g_u(x,1) \in (0,1)\) uniformly for \(x \leq -N\).

(xi) There exist two functions \(g_+, g_-\) satisfying all the conditions in (1.13) such that \(g(-N,u) \geq g_-(u)\) and \(g(N,u) \leq g_+(u)\). Furthermore, \(e^*(g_) > 0\) and \(e^*(g_) > 0\).
At this point we must digress to explain the meaning of condition (xi). Consider first a function \( g : [0, 1] \to [0, 1] \) satisfying the conditions:

1. \( g \in C^1[0, 1] \).
2. \( g(0) = 0, g(1) = 1 \).
3. There exists a constant \( \alpha \in (0, 1) \) such that \( g(u) < u \) in \((0, \alpha)\) and \( g(u) > u \) in \((\alpha, 1)\).

(1.13)

4. \( g'(u) \geq 0 \) in \([0, 1] \).
5. \( g(0) < 1, g(1) < 1 \).
6. \( g(u) \geq g'(\alpha) (u - \alpha) + \alpha \) in \([0, \alpha] \) and \( g(u) \leq g'(\alpha) (u - \alpha) + \alpha \) in \([\alpha, 1] \).
7. \( g'(0)u \leq g(u) \leq g'(1)(u - 1) + 1 \) in \([0, 1] \).

**Remark 1.1.** Condition (vi) implies that \( \max_{[0,1]}g(u)/u < g'(\alpha) \) and \( \max_{[0,1]}((1-g(1-u))/u)<g'(\alpha) \). All the results in [12] are valid under conditions (1.11) and (1.13).

Let \( \mathcal{Q} : \mathcal{C} \to \mathcal{C} \) be the nonlinear convolution operator \( \mathcal{Q}[u] = K \ast g(u) \). Then associated with \( \mathcal{Q} \) is a real number \( c^*(g) \) such that the following holds.

**Theorem 1.1 (Existence of traveling waves).** There exists a nonincreasing function \( w, w(-\infty) = 1, w(\infty) = 0 \) and \( w(x) = Q[w(x + c^*(g)) \).**

**Theorem 1.2 (Uniqueness).** Suppose \( u \in \mathcal{C} \) satisfies \( u(-\infty) > \alpha, u(\infty) < \alpha \) and \( u(x) = Q[u](x + c) \). Then \( c = c^*(g) \) and \( u(x) = w(x - \tau) \) for some constant \( \tau \).

The above two theorems are [12, Thm. 5] and [2, Thm. 1.2] respectively. The function \( w \) is called a travelling wave solution of \( \mathcal{Q} \) facing right. They are unique up to translation.

The number \( c^*(g) \) is called the wave speed of \( \mathcal{Q} \) in the positive direction [13], [21]. It should be pointed out that \( c^*(g) \) is the asymptotic speed of propagation for certain class of initial data. For example, let \( u_0 \in \mathcal{C} \) be decreasing, \( u_0(-\infty) > \alpha, u_0(\infty) < \alpha \) and \( u_{n+1} = Q[u_n] \) for all \( n \). Then \( \lim_{n \to \infty}(u_n\gamma/n) = c^*(g) \) for every \( 0 < \gamma < 1 \).

There are of course nondecreasing travelling waves facing left with wave speed \( c^*(g) \) in the negative direction. The meaning of condition (xi) should now be clear.

**Remark 1.2.** If \( n(x) = 0 \) for \( x \geq 0 \), then \( u_{n+1}(x) = 0 \) for \( x \geq B_2 \). Thus the speed of propagation to the right, namely \( c^*(g) \), cannot exceed \( B_2 \). We can show that \( B_1 < c^*(g) < B_2 \) and \( B_1 < c^*(g) < B_2 \), so that condition (xi) implies \( B_1 < B_2 \).

**Remark 1.3.** The wave speed depends monotonically on \( \mathcal{Q} \). Given \( \mathcal{Q}_1 \) and \( \mathcal{Q}_2 \), with \( \mathcal{Q}_1[u] \geq \mathcal{Q}_2[u] \) for all \( u \in \mathcal{C} \), then \( c^*_1(\mathcal{Q}_1) \geq c^*_2(\mathcal{Q}_2) \). For example, if \( g_1(u) \geq g_2(u) \) in \([0, 1] \) and \( \mathcal{Q}_1[u] = K \ast g_1(u), \mathcal{Q}_2[u] = K \ast g_2(u) \), then \( c^*_1(g_1) \geq c^*_2(g_2) \). In fact, more is true. If \( g_1(u) > g_2(u) \) for \( (0, 1) \) and \( g_1(0) > g_2(0), g_1(1) > g_2(1) \), then \( c^*_1(g_1) > c^*_2(g_2) \).

**Remark 1.4.** Let \( g_1, g_0 \) be defined as in (1.9) and (1.10). Then all the conditions in (1.13) are satisfied. It is easy to check that \( \alpha = 1/2, \sigma_1 = 2, g_1(0) = g_0(1) = (1 + s(-N))^{-1}, g_1(0) = g_0(1) = (1 + o(N))^{-1} \) and \( g_1(u) \leq g_0(1/2) \) in \([0, 1] \). This last inequality obviously implies condition (vi) of (1.13). It may be proved by observing that \( g'(u) \) is a rational function in \( u \). The numerator has a maximum at \( u = 1/2 \) and the denominator has a minimum also at \( u = 1/2 \). The right-hand inequality in (vii) of (1.13) is straightforward. The right-hand inequality is equivalent to showing that \( \tilde{g}_1(u) = 1 - g_1(1 - u) \geq g_0'(1)u \). But then \( \tilde{g}_1 = g_1 \) and \( g_0'(0) = g_0'(1) \) from (1.6), and so it is the same as the left-hand inequality.

**Remark 1.5.** If \( g \) is given by (1.3), we cannot take \( g_+ = g_0 \) or \( g_- = g_0 \) in assumption (xi) of (1.12). In fact when \( K \) is even, \( c^*_1(g_1) = c^*_0(g_0) = 0 \) [2]. However, if \( s(-N) > \sigma(-N) \) in (1.4), we let \( g_-(u) = (s(-N)u^2 + u)/(1 + s(-N)u^2 + \sigma_1(1 - u)^2) \) for some
max\{\sigma(-N),0\} < \sigma_1 < s(-N). Then \( g(-N,u) \geq g_-(u) \) and if \( \sigma_1 \), is close enough to \( s(-N) \), (1.13) will be satisfied by \( c^\ast_s(g_-) > 0 \) (Remark 1.3). A similar arrangement can be made for \( g_0 \) when \( s(N) < \sigma(N) \).

Finally a few words about references. As mentioned earlier, results in this paper parallel those obtained in [4] which considered the differential equation \( u_t = u_{xx} + f(x, u) \). Almost identical results were obtained in [18] for the equation \( u_t = u_{xx} + mu_x + f(x, u) \). The term \( mu_x \) came from assuming nonsymmetric migration. In [5], one of the homozygotes was assumed favored in the entire habitat, and the differential equation allowed to have variable coefficients in some cases. This could happen in our model also if we do not assume the total population density \( \mu(x) \) is a constant. Then \( K \) in (1.2) is replaced by

\[
K(x,y) = \frac{K(x-y) \mu(y)}{\int K(x-y) \mu(y) dy},
\]

see [21]. It is not clear if any of the techniques developed so far are applicable to this case.

The paper by Felsenstein [3] contains 152 references on the subject of variable selection and migration. Some of the fairly standard ones are [7], [14]–[17], [20]. We must also mention the work of Conley [1], who proved the existence of clines for the above differential equation with \( f(x,u) = s(x)u(1-u) \), \( s(\pm \infty) \neq 0 \), using a topological argument. A radially symmetric problem with \( x \in \mathbb{R}^2 \) is also considered. The paper by Sawyer [19] contains more complete and recent information.

2. Statement of results.

**Theorem 2.1.** There exists a function \( \phi \in \mathcal{C} \) such that \( \phi(-\infty) = 1, \phi(\infty) = 0 \) and \( \phi = Q[\phi] \).

**Remark 2.1.** If \( \phi \) is nonincreasing, it is often referred to as a cline.

The rest of the results assume the stronger condition (viii*) of (1.12).

**Theorem 2.2.** There is at most one solution to the problem \( \phi \in \mathcal{C}, \phi(-\infty) = 1, \phi(\infty) = 0 \) and \( \phi = Q[\phi] \). Furthermore, such a solution is decreasing in \( \mathbb{R} \).

In the next two theorems, \( u_n \) is defined recursively by (1.1) for a given \( u_0 \). \( \phi \) is the unique monotone cline from Theorems 2.1 and 2.2.

From conditions (viii*) and (xi) of (1.12), we have \( g(x,u) \geq g_- (u) \) for \( x \leq -N \) and \( g(x,u) \leq g_+(u) \) for \( x \geq N \). Since \( g_- (u) > u \) near 1 and \( g_+ (u) < u \) near 0, we can define the functions \( a_1(x) = \inf\{u : g(x,u) > u\} \) for \( x \leq -N \) and \( a_0(x) = \sup\{u : g(x,u) < u\} \) for \( x \geq N \). Also, \( a_1(x) \) is nondecreasing in \( x \) and \( a_0(x) \) is nonincreasing in \( x \). We let \( a^- = \lim_{x \to -\infty} a_0(x) \) and \( a^+ = \lim_{x \to -\infty} a_1(x) \). Clearly \( a^+ < 1 \) and \( a^- > 0 \).

**Theorem 2.3.** Suppose \( u_0 \) satisfies the condition (i) \( \phi(h_1) \leq u_0(h_2) \) for some \( h_1 < 0 < h_2 \) or (ii) \( \liminf_{x \to -\infty} u_0(x) > a^+ \), \( \limsup_{x \to -\infty} u_0(x) < a^- \), then \( \lim_{n \to \infty} u_n - \phi = 0 \).

**Theorem 2.4.** There exist positive constants \( \delta, \mu \) and \( C \) such that if \( \|u_0 - \phi\|_\infty \leq \delta \), then \( \|u_n - \phi\|_\infty \leq Ce^{\mu n} \) for all \( n \). Consequently, the uniform convergence in Theorem 2.3 may be replaced by exponential convergence.

3. Proof of Theorem 2.1. We begin by proving left continuity of \( c^\ast_s(g) \) with respect to \( g \). It is a consequence of Theorem 1.2.

**Lemma 3.1.** Suppose \( g_\delta, 0 < \delta < \delta_0 \) is a family of functions each of which satisfies the conditions in (1.13) with some \( \alpha_\delta \in (0,1) \). Suppose further that \( g_\delta \) increases uniformly to \( g \) as \( \delta \downarrow 0 \). Then \( \lim_{\delta \downarrow 0} c^\ast_s(g_\delta) = c^\ast_s(g) \).
Proof. By Remark 1.3, \( c_\delta = c^*_\delta(g_\delta) \) increases as \( \delta \) decreases. Let \( \lim_{\delta \downarrow 0} c_\delta = c_0 \leq c^*_\delta(g) \). From Theorem 1.1, for each \( \delta > 0 \), there exists nonincreasing travelling waves \( w_\delta \) such that \( w_\delta(-\infty) = 1, w_\delta(\infty) = 0 \) and

\[
w_\delta(x) = \int K(x + c_\delta - y) g_\delta(w_\delta(y)) \, dy.
\]

Since \( w_\delta \) is determined only up to translation, we may choose \( w_\delta \) such that \( w_\delta(0) = \gamma \) for some fixed \( \gamma \in (0,1) \). From (ii) of (1.11), \( \| w_\delta' \|_\infty \leq \| K' \|_1 + p_1 + p_2 \). Arzela–Ascoli theorem implies that a subsequence, also denoted by \( w_\delta \), converges uniformly on compact sets to a nonincreasing function \( w^* \). Furthermore, \( w^*(0) = \gamma \) and \( w^*(x) = \int K(x + c_\delta - y) g(w^*(y)) \, dy \). Therefore \( w^*(-\infty) = 1 \) and \( w^*(\infty) = \alpha \) or \( 0 \). \( w^*(\infty) \) cannot be \( \alpha \) because \( g(u) > u \) in \( (\alpha, 1) \) and such a solution connecting \( 1 \) and \( \alpha \) exists if and only if \( c_0 \geq \rho^*_\delta > c^*_\delta(g) \). See [12, Prop. 3 and Lemma 2.2] for this fact and the definition of \( \rho^*_\delta \). Thus \( w^*(\infty) = 0 \) and by Theorem 1.2, \( c_0 = c^*_\delta(g) \). Q.E.D.

Lemma 3.2. There exist two nonincreasing functions \( \bar{u}, \tilde{u} \) in \( \mathcal{C} \) with the properties

\( \bar{u} \leq \tilde{u}, \bar{u} \leq Q[\bar{u}] \) and \( Q[\tilde{u}] \leq \tilde{u} \).

Proof. We first construct \( \bar{u} \). From condition (xi) of (1.12), there exists \( g^- \) satisfying (1.13) with \( c^*_\delta(g^-) > 0 \). Let \( \delta_0 > 0 \) be sufficiently small and for each \( 0 < \delta < \delta_0 \), construct \( g_\delta \in C^1[0,1] \) such that \( g_\delta = g^- \) on \( [\delta, 1] \), \( g_\delta = 0 \) on \( [0, \delta/2] \) and on the interval \( (\delta/2, \delta) \), \( g_\delta > 0 \) and \( g_\delta \) increases uniformly to \( g^- \) as \( \delta \downarrow 0 \). It is clear that (1.13) is satisfied for each \( g_\delta \).

From Lemma 3.1, for sufficiently small \( \delta > 0 \), \( c_\delta = c^*_\delta(g_\delta) > 0 \). Fix such a \( \delta \) and let \( w_\delta \) be the nonincreasing travelling wave of the operator \( K \ast g_\delta(u) \), translated so that \( w_\delta(-N) = \delta/2 \). We have

\[
w_\delta(x) = \int K(x + c_\delta - y) g_\delta(w_\delta(y)) \, dy = \int K(x - y) g_\delta(w_\delta(y + c_\delta)) \, dy
\]

\[
\leq \int K(x - y) g_\delta(w_\delta(y)) \, dy = \int_{-\infty}^{-N} K(x - y) g_\delta(w_\delta(y)) \, dy
\]

\[
\leq \int_{-\infty}^{-N} K(x - y) g_\delta(w_\delta(y)) \, dy.
\]

Let

\[
u(x) = \begin{cases} w_\delta(x) & \text{if} \ x \leq -N, \\ 0 & \text{if} \ x > -N. \end{cases}
\]

Then from (1.2) and (viii) of (1.12), we have

\[
Q[\nu](x) = \int_{-\infty}^{-N} K(x - y) g(y, u(y)) \, dy \geq \int_{-\infty}^{-N} K(x - y) g(-N, u(y)) \, dy
\]

\[
\geq \int_{-\infty}^{-N} K(x - y) g_\delta(u(y)) \, dy \geq w_\delta(x).
\]

Therefore, \( Q[\nu](x) \geq \nu(x) \) for \( x \leq -N \). Since \( Q[\nu] \geq 0 \), the inequality holds for all \( x \).

To construct \( \tilde{u} \), let \( K_\top(x) = K(-x), \tilde{g}_\top(u) = 1 - g_\top(1 - u) \) and \( \tilde{Q}[u] = K_\top \ast \tilde{g}_\top(u) \). The relation between this (dual) operator \( \tilde{Q} \) and \( \tilde{Q}[u] = K_\top \ast g_\top(u) \) is given in [12, §2]. It is shown there that \( \tilde{g}_\top \) satisfies the set of hypotheses (1.13) and that the wave speed of \( \tilde{Q} \) in the positive direction, hereby denoted by \( \tilde{c}_\top(g_\top) \), is equal to the wave speed of \( \tilde{Q} \) in the negative direction, \( c_\top(g_\top) \). This fact is a consequence of the symmetry between 0 and 1 in the graph of \( g_\top \).
As before, we construct \( \tilde{g}_\delta \) increasing uniformly to \( \tilde{g}_+ \) as \( \delta \downarrow 0 \), \( \tilde{g}_\delta(u)=0 \) in \([0,\delta/2] \), \( \tilde{g}_\delta=\tilde{g}_+ \) in \([\delta,1] \) and each \( \tilde{g}_\delta \) satisfies (1.13). Since \( c^*(g_+)>0 \), Lemma 3.1 and above implies that for sufficiently small \( \delta>0 \), \( \tilde{c}_\delta=c^*_\delta(\tilde{g}_\delta) \) is positive.

Now let \( \tilde{w}_\delta \) be the nonincreasing travelling wave of the operator \( K_1 \ast \tilde{g}_\delta(u) \) translated so that \( \tilde{w}_\delta(-N)=\delta/2 \). As before,

\[
\tilde{w}_\delta(x) = \int K_1(x-y) \tilde{g}_\delta(\tilde{w}_\delta(y+\tilde{c}_\delta)) \, dy \\
\leq \int_{-\infty}^{-N} K(-x+y) \tilde{g}_\delta(\tilde{w}_\delta(y)) \, dy \\
= \int_{-\infty}^{\infty} K(-x-y) \tilde{g}_\delta(\tilde{w}_\delta(-y)) \, dy.
\]

Define \( v(x)=1-\tilde{w}_\delta(-x) \). We have

\[
v(x) \leq 1 - \int_{-\infty}^{\infty} K(x-y) \tilde{g}_\delta(\tilde{w}_\delta(-y)) \, dy \\
= 1 - \int_{-\infty}^{\infty} K(x-y) \tilde{g}_\delta(1-v(y)) \, dy.
\]

Now let

\[
\bar{u}(x) = \begin{cases} 1 & \text{if } x \leq N, \\ v(x) & \text{if } x \geq N, \end{cases}
\]

\( \bar{g}(x,u)=1-g(x,1-u) \). Then

\[
Q[\bar{u}](x) = 1 - \int_{-\infty}^{\infty} K(x-y) \bar{g}(y,1-\bar{u}(y)) \, dy \\
= 1 - \int_{-\infty}^{\infty} K(x-y) \bar{g}(y,1-\bar{u}(y)) \, dy.
\]

From condition (xi) of (1.12), \( \tilde{g}(x,u) \geq \bar{g}_+(u) \) for \( x \geq N \) so that

\[
Q[\bar{u}](x) \leq 1 - \int_{-\infty}^{\infty} K(x-y) \bar{g}_+(1-\bar{u}(y)) \, dy \\
\leq 1 - \int_{-\infty}^{\infty} K(x-y) \tilde{g}_\delta(1-\tilde{u}(y)) \, dy \leq v(x).
\]

Since \( \bar{u}(x)=v(x) \) for \( x \geq N \) and \( Q[\bar{u}]=1 \), we have \( Q[\bar{u}] \leq \bar{u} \). It is also clear from the definitions of \( u \) and \( \bar{u} \) that they are nonincreasing and \( u \leq \bar{u} \). This completes the proof of Lemma 3.2.

To prove Theorem 2.1, we first observe that \( Q \) is order-preserving in the sense that \( u \leq v \) implies \( Q[u] \leq Q[v] \).

Let \( u_0=u \), \( \bar{u}_0=\bar{u} \) and define \( u_n, \bar{u}_n \) recursively as in (1.1). An inductive argument shows that \( u_0 \leq u_n \leq u_{n+1} \leq \bar{u}_n \leq \bar{u}_{n+1} \leq \bar{u}_0 \) for all \( n \). Therefore \( u_n, \bar{u}_n \) converge, as \( n \to \infty \), to \( \phi_1, \phi_2 \) respectively. Since \( u \preceq \phi_1 \preceq \phi_2 \preceq \bar{u} \), we have \( \phi_i(-\infty)=1, \phi_i(\infty)=0 \) and \( \phi_i=Q[\phi_i] \). The proof of Theorem 2.1 is complete if we take \( \phi_1=\phi_2 \).

Remark 3.1. It does not follow from the above construction that \( \phi_i \) is nonincreasing in \( \mathbb{R} \), even though \( u, \bar{u} \) are. This is true if we assume \( g_\times \leq 0 \). In this case there exists a cline.
Remark 3.2. The solution \( \phi \) we have constructed in Theorem 2.1 lies between \( y \) and \( \bar{y} \). Since \( w_\delta(x) \), \( \bar{w}_\delta(x) \) converge to 1 exponentially as \( x \to -\infty \) [12, Prop. 5], there exist \( \mu > 0 \), \( C > 0 \) such that \( |\phi(x)| \leq Ce^{-\mu x} \) as \( x \to -\infty \) and \( |1 - \phi(x)| \leq Ce^{\mu x} \) as \( x \to -\infty \).

Without further assumptions other than (viii) of (1.12), the solution \( \phi \) is not unique. For example, let \( h(x,u) \), defined on \( \mathbb{R} \times [0,1] \), be sufficiently smooth and satisfy the conditions (i) \( h(x,u) = 0 \) on \( (-\infty,N] \times [\frac{1}{2},1] \) and \( [-N,\infty) \times [0,\frac{1}{2}] \), (ii) \( h(x,0) = h(x,1) = 0 \), (iii) \( h(x,u) \leq 0 \) for \( |x| \geq N \) and (iv) \( -\frac{1}{2} \leq h(x,u) \leq \frac{1}{2} \) in \( \mathbb{R} \times [0,1] \). It is clear that such an \( h \) exists and if \( \gamma \in (0,1) \), \( \gamma h \) also satisfies conditions (i) to (iv).

Let \( K(x) = K(-x) \), \( g(x,u) = g_0(u) + \gamma h(x,u) \), where \( g_0 \) is given by (1.10). Choose \( \gamma \) so small that \( g_0(u) + \gamma h_u(x,u) > 0 \) in \( \mathbb{R} \times [0,1] \). This is possible since \( \min_{[0,1]} g_0(u) > 0 \). For small \( \gamma \), it is straightforward to verify that conditions (vi) to (x) of (1.12) are satisfied for \( g \). However, according to Theorem 1.1 and Remark 1.5, there exists a nonincreasing function \( w \), \( w(-\infty) = 1 \), \( w(0) = \frac{1}{2} \) and \( w(\infty) = 0 \) such that \( w(x) = \int K(x-y)g_0(w(y))dy \). From (i) above, it is easy to see that \( w(x+\tau) = \int K(x-y)g(y,w(y+\tau))dy \) for \( |\tau| \leq N \). Therefore we have nonuniqueness.

4. Proof of Theorem 2.2. For the rest of the paper we assume condition (viii*) of (1.12). Proposition 4.2 is the basis for much of the results that follow. The following lemma is the heart of its proof.

Lemma 4.1. Let \( \phi \) be nonincreasing, \( \phi(-\infty) = 1 \), \( \phi(\infty) = 0 \) and \( \phi = Q[\phi] \). There exist two decreasing sequences \( \{z_n\}, \{q_n\} \) such that if \( v_n(x) = \phi(x-z_n) - q_n \), then \( v_{n+1} \leq Q[v_n] \) for all \( n \).

Remark 4.1. We shall see from the proof that there are no restrictions on \( z_0, q_0 \) except that \( z_0 \leq 0 \) and \( q_0 > 0 \) be sufficiently small.

Proof. We begin by showing \( \phi'(x) < 0 \) in \( \mathbb{R} \). From \( g_\epsilon \leq 0 \) and our hypotheses, \( \phi'(x) \leq \int K(x-y)g_u(y,\phi(y))\phi'(y)dy \leq 0 \). Let \( \phi(x_0) = 0 \). Then \( g_u(y,\phi(y))\phi'(y) = 0 \) on the interval \( [x_0-B_2,x_0-B_1] \), which, according to Remark 1.2, contains \( x_0 \). Since \( g_u \) does not vanish on any rectangle, \( \phi'(x) = 0 \) on an open interval containing \( x_0 \). This means that the set \( S \) when \( \phi' = 0 \) is open. From the continuity of \( \phi' \), \( S \) is closed. Obviously \( \phi \) is not a constant, \( S \) is empty and so \( \phi'(x) < 0 \) in \( \mathbb{R} \).

Next we show that there exist constants \( q_0, \delta, \theta \) all in the interval \( (0,1) \) such that

\[
(4.1) \quad g(x,u-q) - g(x,u) \geq -\theta q \quad \text{for} \quad 0 \leq q \leq q_0,
\]

\[
\quad u \in [1-\delta,1] \quad \text{and} \quad x \leq -N \quad \text{or} \quad u \in [0,\delta] \quad \text{and} \quad x \geq N.
\]

To begin, consider the function

\[
\psi(x,u,q) = \begin{cases} \frac{g(x,u) - g(x,u-q)}{q} & \text{if } q > 0, \\ g_u(x,u) & \text{if } q = 0 \end{cases}
\]

in the set \( \mathcal{D} = \mathbb{R} \times [1-\delta,1] \times [0,q_0] \), where we shall define \( g(x,u) = 0 \) if \( u < 0 \). It is clear that \( \psi \) is uniformly continuous in \( \mathcal{D} \). Also

\[
\psi(x,1,q) = \frac{1 - g(x,1-q)}{q} = g_u(x,\theta) \quad \text{where} \quad 1 - q \leq \theta \leq 1.
\]

From (x) of (1.12) and the fact that \( g_u \) is uniformly continuous, there exists \( \theta_1 \in (0,1) \) such that \( \psi(x,1,q) < \theta_1 < 1 \) for \( q \) sufficiently small and \( x \leq -N \). Since \( \psi \) is uniformly continuous in \( \mathcal{D} \), \( \psi(x,u,q) < \theta_1 \) for \( u \) near 1. Therefore (4.1) holds when \( x \leq -N \) and \( 1 - \delta \leq u \leq 1 \).
Next consider \( g(x, u - q) - g(x, u) \) for \( 0 \leq u \leq \delta \) and \( x \geq N \). If \( u - q \geq 0 \), then
\[
g(x, u - q) - g(x, u) = -g_u(x, u)q,
\]
where \( u - q \leq u \). From (x) of (1.12) and uniformly continuity of \( g_u \), we may assume (by increasing \( \delta \) if necessary) that \( g_u(x, u) < \delta \) for \( x \geq N \) and \( \delta \) sufficiently small. Therefore (4.1) holds when \( x \geq N \) and \( u \) sufficiently small.

On the other hand, if \( u - q < 0 \), then \( g(x, u - q) - g(x, u) = g(x, u) \). From the mean value theorem and the fact that \( g_{uu} \) is bounded, \( \lim_{u \to 0} (g(x, u)/u) = g_u(x, 0) \) uniformly in \( \mathbb{R} \). Therefore for \( x \geq N \) and \( u \) small \( g(x, u)/u < \delta \) so that \( g(x, u - q) - g(x, u) \geq -\theta_1 u \geq -\delta \). Altogether (4.1) is valid. It should be pointed out that (4.1) continues to hold with the same \( \delta \) and \( N \) if we decrease \( q_0 \) and \( \delta \).

To continue, let \( M = \sup_{\mathbb{R} \times [0, 1]} g_u(x, u) \geq 1 \) and choose \( \epsilon > 0, \eta > 0 \) such that \( \theta = \epsilon M + \theta_1 < 1 \),
\[
\int_{-\infty}^{\infty} K(x) \, dx \leq \epsilon, \quad \int_{-\infty}^{-\eta} K(x) \, dx \leq \epsilon.
\]
Define \( \mu \) and \( q_n \) by \( \theta = e^{-\mu} \) and \( q_n = \phi e^{-\mu^n} = \phi \theta^n \) for all \( n \). Since \( \phi' < 0 \) in \( \mathbb{R} \), \( \phi(-\infty) = 1 \), \( \phi(\infty) = 0 \), we define \( E_\gamma = \phi^{-1}(\gamma) \) for every \( 0 < \gamma < 1 \).

Let \( \Gamma = [E_1 - \delta - 2\eta, E_\delta + 2\eta] \). We assume \( \delta > 0 \) is sufficiently small so that \( E_\delta \geq N \), \( E_1 - \delta \leq -N \). There exists \( \theta_2 > 0 \) such that
\[
\phi(\xi_1) - \phi(\xi_2) \leq \theta_2 (\xi_1 - \xi_2) \quad \text{if} \quad \xi_1 > \xi_2 \quad \text{are in} \quad \Gamma.
\]
Finally, let \( z_0 \) be arbitrary and define \( z_n \) recursively by
\[
z_{n+1} = \frac{(\theta - M) q_0 e^{-\mu^n}}{\theta_2} + z_n.
\]
Clearly \( z_n \)'s are nonpositive and decreasing and converge to the limit
\[
x_1 = \frac{(\theta - M) q_0}{\theta_2} \left( \frac{1}{1 - e^{-\mu}} \right) + z_0.
\]
We may assume that \( q_0 \) is sufficiently small so that \( (M - \theta) q_0 \theta^{-1} \leq \eta \).

Having defined all the constants, we proceed to prove the inequality \( v_{n+1} \leq Q[v_n] \), where \( v_n(x) = \phi(x - z_n) - q_n \). This is equivalent to showing
\[
\phi(x - z_{n+1}) - \phi(x - z_n) - \int K(x - y) [g(y, \phi(y - z_n) - q_n) - g(y - z_n, \phi(y - z_n))] \, dy \leq q_{n+1}.
\]
Let
\[
\Gamma_n = [E_1 - \delta + z_n, E_\delta + z_n], \quad \Gamma' = [E_1 - \delta + z_n - \eta, E_\delta + z_n + \eta]
\]
and
\[
h_n(x) = g(x, \phi(x - z_n) - q_n) - g(x - z_n, \phi(x - z_n)).
\]
Then
\[
\int K(x - y) h_n(y) \, dy = \int_{\Gamma_n} K(x - y) h_n(y) \, dy + \int_{y \geq E_\delta + z_n} K(x - y) h_n(y) \, dy
\]
\[
+ \int_{y \leq E_1 - \delta + z_n} K(x - y) h_n(y) \, dy,
\]
\[
\equiv I_1 + I_2 + I_3.
\]
Consider first the case \( x \in \Gamma_n' \). Since \( z_n \leq 0 \),

\[
I_1 \geq \int_{\Gamma_n} K(x-y) \left[ g(y, \phi(y-z_n) - q_n) - g(y, \phi(y-z_n)) \right] dy
\]

\[
= \int_{\Gamma_n} K(x-y) g_u(y, \theta)(-q_n) dy \geq -Mq_n \int_{\Gamma_n} K(x-y) dy \geq -Mq_n \varepsilon.
\]

The last inequality follows from (4.2).

If \( y \geq E_\delta + z_n \), then \( y - z_n \geq E_\delta \geq N \) and \( \phi(y-z_n) \leq \delta \). From (4.1),

\[
h_n(y) \geq g(y-z_n, \phi(y-z_n) - q_n) - g(y-z_n, \phi(y-z_n)) \geq -\theta_1 q_n.
\]

Therefore, \( I_2 \geq -\theta_1 q_n \int_{y \geq E_\delta + z_n} K(x-y) dy \). Similarly, if \( y \leq E_\delta + z_n \), then \( y - z_n \leq E_\delta - z_n \leq -N \) and \( \phi(y-z_n) \geq 1 - \delta \). Again from (4.1),

\[
h_n(y) \geq g(y, \phi(y-z_n) - q_n) - g(y, \phi(y-z_n)) \geq -\theta_1 q_n \text{ so that } I_3 \geq -\theta_1 q_n \int_{y \leq E_\delta - z_n} K(x-y) dy.
\]

Combining all three inequalities, we have, when \( x \in \Gamma_n' \),

\[
\int K(x-y) h_n(y) dy \geq -Mq_n \varepsilon - \theta_1 q_n = -\theta q_n = -q_{n+1}.
\]

Since \( z_{n+1} \leq z_n \) and \( \phi \) is nonincreasing, the difference between the first two terms in (4.5) is nonpositive. Therefore (4.5) is established when \( x \in \Gamma_n' \).

If \( x \in \Gamma_n' \), then \( E_\delta - \eta \leq x - z_n \leq E_\delta + \eta \) and

\[
h_n(y) \geq g(y, \phi(y-z_n) - q_n) - g(y, \phi(y-z_n)) = g_u(y, \theta)(-q_n) \geq -Mq_n.
\]

Therefore \( \int K(x-y) h_n(y) dy \geq -Mq_n \). From (4.4), \( z_n - z_{n+1} \leq (M - \theta) q_{n+1} \leq \eta \) and hence \( x - z_n \leq x - z_{n+1} \leq E_\delta + 2 \eta \). From (4.3) and (4.4), \( \phi(x - z_{n+1}) - \phi(x - z_n) \leq -\theta_2(z_n - z_{n+1}) = (\theta - M) q_{n+1} \). Hence (4.5) is valid if \( x \in \Gamma_n' \). This completes the proof of Lemma 4.1.

**Proposition 4.2.** Let \( u_0 \) satisfy the conditions

\[
\liminf_{x \to -\infty} u_0(x) > a^+ \quad \text{and} \quad \limsup_{x \to \infty} u_0(x) < a^-.
\]

Let \( \phi \) be a nonincreasing function satisfying \( \phi(-\infty) = 1, \phi(\infty) = 0 \) and \( \phi = Q[\phi] \). Then there exist constants \( x_1, x_2, q_0, \mu, \) the last two positive, such that

\[
\phi(x - x_1) - q_0 e^{-\mu x} \leq u_n(x) \leq \phi(x - x_2) + q_0 e^{-\mu x} \quad \text{for all } n.
\]

**Proof.** We only prove the left-hand inequality. The right-hand inequality is the same but requires a result like Lemma 4.1 with \( v_n \geq Q[v_n] \). We begin by showing that \( u_n(\infty) \) increases to 1 as \( n \to \infty \).

Since \( a_1(x) \) decreases to \( a^+ \) as \( x \to -\infty \) (see §2), there exist \( \varepsilon > 0, N_\varepsilon > N \) such that

\[
a^+ \leq a_1(x) \leq a_1(-N_\varepsilon) < a^+ + \varepsilon \leq u_0(x)
\]

and

\[
g(x, u_0(x)) \geq g(-N_\varepsilon, u_0(x)) \geq g(-N_\varepsilon, a^+ + \varepsilon) \quad \text{for } x \leq -N_\varepsilon.
\]

From Fatou’s lemma,

\[
\liminf_{x \to -\infty} u_1(x) \geq \int K(y) \liminf_{y \to -\infty} g(x-y, u_0(x-y)) dy \geq g(-N_\varepsilon, a^+ + \varepsilon).
\]

Now suppose \( \liminf_{x \to -\infty} u_n(x) \geq g(-N_\varepsilon, a^+ + \varepsilon) \). Then for any \( \delta > 0, \) \( u_n(x) \geq q^n(-N_\varepsilon, a^+ + \varepsilon) - \delta \) and \( g(x, u_n(x)) \geq g(-N_\varepsilon, u_n(x)) \geq g(-N_\varepsilon, q^n(-N_\varepsilon, a^+ + \varepsilon) - \delta) \) for \( x \).
near $-\infty$. Hence \( \liminf_{x \to -\infty} u_{n+1}(x) \geq \int K(y) \liminf_{x \to -\infty} g(x-y, u_n(x-y)) \, dy \geq g(-N, g^n(-N, a^+ + \epsilon) - \delta) \). Since \( \delta > 0 \) is arbitrary, we have

\[
(4.6) \quad \liminf_{x \to -\infty} u_n(x) \geq g^n(-N, a^+ + \epsilon) \quad \text{for all } n.
\]

From the definition of \( a_1(x) \), we have \( g(-N, u) > u \) for \( a_1(-N) < u < 1 \). This implies that \( g^n(-N, a^+ + \epsilon) \) increases to 1 as \( n \to \infty \). Therefore, let \( q_0 > 0 \) be as defined in Lemma 4.1. There exist, by (4.6) positive integers \( k \) and \( N_0 \) such that \( u_k(x) > 1 - q_0 \) for \( x \leq -N_0 \). Hence \( v_0(x) = \phi(x - z_0) - q_0 \leq 1 - q_0 \leq u_k(x) \) for \( x \leq -N_0 \). From Remark 4.1, \( z_0 \leq 0 \) is arbitrary and we now choose it sufficiently negative so that \( \phi(-N_0 - z_0) - q_0 \leq 0 \). Therefore, \( v_0(x) \leq u_k(x) \) for all \( x \).

Since \( v_{n+1} \leq Q[v_n] \) and \( Q \) is order-preserving, an inductive argument shows that \( v_n \leq u_{k+n} \) for all \( n \geq 0 \). Explicitly,

\[
\phi(x - z_n) - q_0 e^{-\mu n} \leq u_{k+n}(x) \quad \text{for all } n \geq 0.
\]

Since \( z_n \) is decreasing, we may replace \( z_n \) by its limit \( x_1 \) in the above inequality. Doing so and writing \( n \) for \( k + n \), we have

\[
\phi(x - x_1) - q_0' e^{-\mu n} \leq u_n(x) \quad \text{for all } n \geq k, \quad \text{where } q_0' = q_0 e^{\mu k}.
\]

The first \( k \) terms are then taken care of by increasing \( q_0' \) until \( 1 - q_0' e^{-\mu k} \leq 0 \). This completes the proof of Proposition 4.2.

Remark 4.2. The condition \( \limsup_{x \to -\infty} u_0(x) < a^- \) is needed to prove the right-hand inequality.

Lemma 4.3. Let \( \phi \) satisfy \( \phi = Q[\phi] \) and let \( u_0(x) = \phi(x - h) \). Then \( u_n \), defined recursively by (1.1), is nonincreasing (nondecreasing) in \( n \) if \( h > 0 \) (\( h < 0 \)).

Proof. We only prove the case \( h > 0 \). Proceeding by induction,

\[
u_1(x) = \int K(x - y) g(y, \phi(y - h)) \, dy = \int K(x - h - y) g(y + h, \phi(y)) \, dy \leq \int K(x - h - y) g(y, \phi(y)) \, dy = u_0(x).
\]

Assume that \( u_n \leq u_{n-1} \). Then since \( Q \) is order-preserving, we have \( u_{n+1} = Q[u_n] \leq Q[u_{n-1}] = u_n \). Therefore \( u_{n+1} \leq u_n \) for all \( n \) and the lemma is proved.

To show uniqueness of clines, we first recall from Remark 3.1 that \( g_1 \leq 0 \) implies the existence of at least one cline \( \phi \). Suppose \( u \) is another solution of \( u = Q[u] \) with \( u(-\infty) > a^+ \), \( u(\infty) < a^- \). Proposition 4.2 with \( u_0 = u \) implies that \( \phi(x - x_1) - q_0' e^{-\mu n} \leq u(x) \leq \phi(x - x_1) + q_0' e^{-\mu n} \) for all \( n \). Letting \( n \to \infty \), we have \( \phi(x - x_1) \leq u(x) \leq \phi(x - x_2) \). Since \( \phi \) is nonincreasing, we may assume that \( x_1 < 0 \) and \( x_2 > 0 \).

Let \( u_0(x) = \phi(x - x_1), \bar{u}_0(x) = \phi(x - x_2) \) and define \( u_n, \bar{u}_n \) recursively by \( u_{n+1} = Q[u_n], \bar{u}_{n+1} = Q[\bar{u}_n] \). Clearly, \( u_n \leq u \leq \bar{u}_n \) and \( u_n \leq \phi \leq \bar{u}_n \) for all \( n \). From Lemma 4.3, \( u_n \) increases to a nonincreasing function \( u \) with the properties \( u \leq u, \phi \leq \phi, u(\infty) = 1, u_0(\infty) = 0 \) and \( u = Q[u] \). Similarly, \( \bar{u}_n \) decreases to a nonincreasing function \( \bar{u} \) with the properties \( u \leq \bar{u}, \phi \leq \bar{u}, \bar{u}(\infty) = 1, \bar{u}(\infty) = 0 \) and \( \bar{u} = Q[\bar{u}] \). In order to show that \( u = \phi \), it suffices to show that \( u = \bar{u} \). This follows from Remark 3.2 and the next lemma.

Lemma 4.4. Let \( \phi_1, \phi_2 \) be two nonincreasing solutions of \( \phi = Q[\phi] \), \( \phi_1 \leq \phi_2 \) which both converge to 1 and 0 exponentially as \( x \to \mp \infty \). Then \( \phi_1 \equiv \phi_2 \).
Before we can prove Lemma 4.4, we must establish two lemmas.

From Proposition 4.2, \( \phi_2(x + h) \leq \phi_1(x) \) for some \( h > 0 \). Let \( h \) be the infimum of such \( h \). We assume that \( h > 0 \) and derive from it a contradiction. Note that from \((\text{viii}^*)\) of (1.12), the function \( \int K(x-y)\left( g(y+h, \phi(y+h)) - g(y, \phi(y+h)) \right) dy \) is not identically zero if \( h \neq 0 \). Therefore translation of \( \phi_1 \) is not a solution of \( q = Q[\phi] \).

Let \( u_\epsilon(x) = \phi_2(x + h - \epsilon) \) for \( 0 \leq \epsilon \leq h/2 \). According to the definition of \( h \), we have \( u_\epsilon(x) > \phi(x) \) on some interval for sufficiently small \( \epsilon > 0 \). Write

\[
u(x) = \int K(x-y)g(y, u_\epsilon(y)) dy + n_\epsilon(x),
\]

where \( n_\epsilon(x) = \int K(x-y)\left[ g(y+h-\epsilon, u(y))-g(y, u_\epsilon(y)) \right] dy \) is nonpositive but not identically zero. Let \( \psi_\epsilon(x) = u_\epsilon(x) - \phi_1(x) \). Then

\[
(4.7) \quad \psi_\epsilon(x) = \int K(x-y)h_\epsilon(y)\psi_\epsilon(y) dy + n_\epsilon(x),
\]

where we set

\[
h_\epsilon(x) = \frac{g(x, u_\epsilon(x)) - g(x, \phi_1(x))}{u_\epsilon(x) - \phi_1(x)} \geq 0.
\]

We shall employ the following notation: \( \mathcal{H} = L^2(\mathbb{R}) \) with inner product \((\cdot, \cdot)\), \( \psi^+ = \max\{\psi, 0\}, K_\epsilon : \mathcal{H} \to \mathcal{H} \) is the linear operator

\[
K_\epsilon\psi(x) = \int K(x-y)h_\epsilon(y)\psi(y) dy.
\]

From Young's inequality, \( K \) is bounded. Observe that \( \psi^+_\epsilon \neq 0 \) for every \( \epsilon > 0 \) sufficiently small but \( \psi^+_0 \equiv 0 \). Finally for an operator \( A : \mathcal{H} \to \mathcal{H} \), the symbols \( \sigma(A), r(A), A^* \) and \( ||A|| \) will denote respectively the spectrum of \( A \), spectral radius of \( A \), adjoint of \( A \) and operator norm of \( A \).

We state two lemmas and defer their proofs until after we have proved Lemma 4.4.

**Lemma 4.5.** For \( \epsilon > 0 \) sufficiently small (i) \( K_\epsilon \) is a positive operator in the sense that \( \psi \geq 0 \) implies that \( K_\epsilon\psi \geq 0 \); (ii) \( K_\epsilon \) is quasi-compact, i.e., there exist operators \( V_\epsilon \) and \( C_\epsilon \) such that \( ||C_\epsilon|| < 1 \), \( V_\epsilon \) is compact and \( K_\epsilon = C_\epsilon + V_\epsilon \); (iii) \( \lim_{\epsilon \to 0} ||K_\epsilon - K_0|| = 0 \).

**Lemma 4.6.** \( r(K_0) < 1 \).

**Proof of Lemma 4.4.** From (4.7), \( \psi_\epsilon \leq K_\epsilon\psi \) so that \( \psi^+_\epsilon \leq [K_\epsilon\psi]^+ \leq K_\epsilon\psi^+_\epsilon \). Since the operator \( K \) is order-preserving, an inductive argument shows that \( K^n\psi^+_\epsilon \geq \psi^+_\epsilon \) for all \( n \). From our hypotheses, \( \psi_\epsilon \in \mathcal{H} \). Therefore \( ||K^n\psi^+_\epsilon||_2 \geq ||\psi^+_\epsilon||_2 \) which implies that \( ||K^n\psi^+_\epsilon||^{1/n} \geq 1 \) for all \( n \). Now if we fix \( n \) and let \( \epsilon \downarrow 0 \), we have from Lemma 4.5, \( ||K^n||^{1/n} \geq 1 \). Hence \( \lim_{n \to \infty} ||K^n||^{1/n} = r(K_0) \geq 1 \) which contradicts Lemma 4.6. Therefore \( h = 0 \) and \( \phi_1 \equiv \phi_2 \). The proof of Lemma 4.4 is complete.

**Proof of Lemma 4.5.** \( K_\epsilon \) is positive because \( K_\epsilon(x) \geq 0 \) and \( h_\epsilon(x) \geq 0 \) in \( \mathbb{R} \). To show that \( K_\epsilon \) is quasi-compact, recall from the definition of \( h_\epsilon \) that \( h_\epsilon(x) = g_\epsilon(x, \theta) \), where \( \theta_\epsilon \) is between \( u_\epsilon \) and \( \phi_1 \). From hypothesis \((x)\) of (1.12), there exist \( \delta > 0 \), \( \theta_1 \in (0,1) \) such that

\[
g_\epsilon(x, u) \leq \theta_1 < 1 \quad \text{for} \quad u \in [0, \delta], \quad x \geq N \quad \text{or} \quad u \in [1-\delta, 1], \quad x \leq -N.\]

Since \( u_\epsilon(-\infty) = \phi_1(-\infty) = 1, u_\epsilon(\infty) = \phi_1(\infty) = 0 \). We can choose \( a_\epsilon > N \) such that \( |h_\epsilon(x)| \leq \theta_1 < 1, \) when \( x \in [-a_\epsilon, a_\epsilon] \).

Define \( C_\epsilon \), \( V_\epsilon : \mathcal{H} \to \mathcal{H} \) by

\[
C_\epsilon\psi(x) = \int K(x-y)\chi_{[-a_\epsilon, a_\epsilon]}(y)h_\epsilon(y)\psi(y) dy
\]
and
\[ V_\epsilon \psi(x) = \int K(x-y) \chi_{[-a_\epsilon, a_\epsilon]}(y) h_\epsilon(y) \psi(y) dy. \]

Then \( K_\epsilon = C_\epsilon + V_\epsilon \) and \( V_\epsilon \) is compact because \( \int K^2(x-y) \chi_{[-a_\epsilon, a_\epsilon]}(y) h_\epsilon^2(y) dy \) is finite. For \( C_\epsilon \), we have \( \|C_\epsilon \psi\|_2 = \|K^* \chi_{[-a_\epsilon, a_\epsilon]} h_\epsilon \psi\|_2 \leq \theta_1 \|K\|_1 \|\psi\|_2 \). Therefore \( \|C_\epsilon\| \leq \theta_1 < 1 \) and \( K_\epsilon \) is quasi-compact.

Finally it is elementary to show that \( h_\epsilon \) converges to \( h_0 \) pointwise as \( \epsilon \downarrow 0 \) and \( \| (K_\epsilon - K) \psi \|_2 = \| K^* [h_\epsilon - h_0] \psi \|_2 \leq \| K^* \| \| h_\epsilon - h_0 \| \| \psi \|_1 \leq \| K^* \| \| h_\epsilon - h_0 \| \| \psi \|_2 \). From the fact that \( h_\epsilon(x) = g_{\epsilon u}(x, \xi) \), where \( \theta_\epsilon \) is between \( u_\epsilon \) and \( \phi_1 \), we have
\[ |h_\epsilon(x) - h_0(x)| = |g_{\epsilon u}(x, \xi)||\theta_\epsilon - \theta_0| \leq \text{const.} |\theta_\epsilon - \theta_0|. \]

But then \( \phi_1, \phi_2 \) converge to 1 and 0 exponentially as \( x \to \mp \infty \). Thus \( |\theta_\epsilon - \theta| \) is dominated by a square integrable function independently of \( \epsilon \). From the dominated convergence theorem, \( \lim_{\epsilon \downarrow 0} \|h_\epsilon - h_0\|_2 = 0 \). This establishes (iii) and completes the proof of Lemma 4.5.

**Proof of Lemma 4.6.** From (4.7), we have
\[ \psi_0(x) = K_0^* \psi_0(x) + n_0(x), \]
where \( \psi_0 \) and \( n_0 \) are both nonpositive and not identically zero.

From Lemma 4.5, \( K_0^* = C_0^* + V_0^* \). As is well known, \( \|C_0^*\| = \|C_0\| \) and \( V_0^* \) is compact if and only if \( V_0 \) is compact. Therefore \( K_0^* \) is also quasi-compact. In fact, \( K_0^* \) is the operator \( K_0^* \psi(x) = h_0(x) \int K(y-x) \psi(y) dy \). Therefore \( K_0^* \) is a positive operator.

According to [9, Thm. 4], since \( K_0^* \) is a positive operator \( r(K_0^*) \in \sigma(K_0^*) \). If \( r(K_0^*) < 1 \), then \( r(K_0) = r(K_0^*) < 1 \) and the lemma is proved. We cannot have \( r(K_0^*) \geq 1 \). For if so, \( r(K_0^*) \not\in \sigma(C_\epsilon) \) since \( \|C_\epsilon\| < 1 \). However, \( K_\epsilon \) is a perturbation of \( C_\epsilon \) by a compact operator. Weyl's lemma says that perturbation by a compact operator can only change the spectrum of an operator by eigenvalues, [8]. Therefore, \( r(K_0^*) \) is an eigenvalue of \( K_0^* \) and clearly has the largest modulus among the eigenvalues of \( K_0^* \). By [9, Thm. 5, Cor. 1] applied to \( r(K_0^*) \), there exists a nonnegative eigenfunction \( e_\epsilon \) corresponding to \( r(K_0^*) \). That is to say, \( r(K_0^*) e_\epsilon(x) = h_0(x) \int K(y-x) e_\epsilon(y) dy \geq 0 \).

Using the same idea we used to show \( \psi < 0 \) at the beginning of the proof of Lemma 4.1, we see that \( e_\epsilon(x) > 0 \) in \( \mathbb{R} \).

From (4.8), we have \( (\psi_0, e_0) = (K_0^* \psi_0, e_0) + (n_0, e_0) < (K_0^* \psi_0, e_0) = (\psi_0, K_0^* e_0) = r(K_0^*) (\psi_0, e_0) \). Since \( \psi_0 \leq 0 \), we have \( r(K_0^*) < 1 \) which is a contradiction to our assumption. Lemma 4.6 is therefore established and so is Theorem 2.2.

**5. Proof of Theorem 2.3.** The argument given after Lemma 4.3 actually provides a proof for part (i) of Theorem 2.3. Letting \( u_0(x) = \phi(x - h_1) \) and \( \bar{u}(x) = \phi(x - h_2) \), we have \( u_n \leq u_n \leq \bar{u}_n \) for all \( n \), and \( u_n, \bar{u}_n \) converge monotonically to the (unique) cline \( \phi \). With all the properties \( u_n, \bar{u}_n \) and \( \phi \) have, it is an elementary exercise to show that the convergence is uniform in \( \mathbb{R} \).

To prove part (ii) of Theorem 2.3, we first observe that \( \|u_n\|_\infty \leq \|K\|_1 + p_1 + p_2 \) so that \( \{u_n\} \) is an equicontinuous sequence of functions. By the Arzela–Ascoli theorem, a subsequence \( \{u_{n_k}\} \) will converge uniformly on compact subsets of \( \mathbb{R} \) to some continuous function \( U \). From Proposition 4.2, \( \phi(x - x_1) \leq U(x) \leq \phi(x - x_2) \). We may assume that \( x_1 < 0 \) and \( x_2 > 0 \). Apply part (i) of Theorem 2.3 with \( U \) as the initial data. Then
U_n \equiv Q^n[U] converges uniformly to \phi as n \to \infty. The convergence of u_{n_k} to U is also uniform in \mathbb{R}, since u_{n_k, \phi} are uniformly close to 1 and 0 near \pm \infty respectively.

We now state a lemma and use it to prove part (ii) of Theorem 2.3. The proof of the lemma will be given at the end of this section.

**Lemma 5.1.** Given \( \epsilon > 0 \), there exists \( \delta' > 0 \) such that if \( \|v_0 - \phi\|_{\infty} \leq \delta' \), then \( \|v_n - \phi\|_{\infty} \leq \epsilon \) for all \( n \).

Let \( M = \sup_{x \in [0,1]} g_u(x,u) \). We have \( \|Q^n[u] - Q^n[v]\|_{\infty} \leq M^n\|u - v\|_{\infty} \) for all \( n \) and \( u, v \in \mathcal{U} \). For any \( \epsilon > 0 \), let \( \delta' \) be chosen as in Lemma 5.1 and let \( k_1, k_2 \) be positive integers such that

\[
\frac{\|u_{n_k} - U\|_{\infty}}{2M_k} \leq \frac{\delta'}{2} \quad \text{if} \quad k \geq k_1,
\]

\[
\frac{\|u_{n_k} - U\|_{\infty}}{2M_{k_1}} \leq \frac{\delta'}{2} \quad \text{if} \quad k \geq k_2.
\]

Then

\[
\|Q^{k_1}[u_{n_k}] - Q^{k_1}[U]\|_{\infty} \leq M^{k_1}\|u_{n_k} - U\|_{\infty} \leq \frac{\delta'}{2} \quad \text{if} \quad k \geq k_2.
\]

Furthermore,

\[
\|u_{n_k + k_1} - \phi\|_{\infty} \leq \|Q^{k_1}[u_{n_k}] - Q^{k_1}[U]\|_{\infty} + \|Q^{k_1}[U] - \phi\|_{\infty} \leq \delta' \quad \text{if} \quad k \geq k_2.
\]

Now set \( k = k_2 \) and \( v_0 = u_{n_k + k_1} \). From Lemma 5.1, we have \( \limsup_{n \to \infty} \|u_n - \phi\| \leq \epsilon \). Since \( \epsilon > 0 \) is arbitrary, Theorem 2.3 is proved.

**Proof of Lemma 5.1.** We have to look carefully into the proofs of Proposition 4.2 and Lemma 4.1. Recall from Remark 4.1 that the only requirements on \( z_0 \) and \( q_0 \) for Lemma 4.1 to hold are \( z_0 \leq 0 \) and that \( q_0 > 0 \) be sufficiently small. Also, in the proof of the left-hand inequality in Proposition 4.2, \( k, z_0, q_0 \) have to satisfy the condition \( \phi(x - z_0) - q_0 \leq u_k(x) \) in \( \mathbb{R} \). From our hypothesis, \( \phi(x) - \delta' \leq v_0(x) \) in \( \mathbb{R} \). Therefore, we set \( z_0 = 0 \) and \( \delta' = q_0 \) small enough to obtain the inequality \( \phi(x - z_0) - q_0 \leq u_k(x) \) for all \( n \). Again from the proof of Lemma 4.1, \( \lim_{n \to \infty} z_n = x_1 = (\theta - M)q_0\theta^{-1}(1 - e^{-\mu})^{-1} \). Now (4.1) is valid with the same \( \theta_1, \delta, N \) if we decrease \( q_0 > 0 \). Consequently, \( \theta, M, \theta_2, \mu \) above are independent of \( \delta' (= q_0) \) if \( \delta' \) is sufficiently small. Hence let \( \delta' \) be so small that \( |x_1| \leq \epsilon/2\|\phi\|_{\infty} \) and \( q_0 \leq \epsilon/2 \). Then

\[
\phi(x) - q_0e^{-\mu} = \phi(x - x_1) - q_0e^{-\mu} + \phi(x) - \phi(x - x_1) \leq u_n(x) + \frac{\epsilon}{2}.
\]

This implies that \( \phi(x) - \epsilon \leq u_n(x) \) for all \( n \) which is half of Lemma 5.1. The other half may be proved similarly.

**6. Proof of Theorem 2.4.** Let \( T : \mathcal{X} \to \mathcal{X} \) be the bounded linear operator

\[
T\phi(x) = \int K(x-y)g_u(y,\phi(y))\psi(y)dy.
\]

It is easy to see that \( T \) is positive and quasi-compact. Furthermore, the proof of Lemma 4.6 can be used to show that \( r(T) < 1 \). In place of (4.8), we use

\[
\phi'(x) = \int K(x-y)g_u(y,\phi(y))\phi'(y)dy + \int K(x-y)g_y(y,\phi(y))\psi(y)dy,
\]

where the last term is nonpositive and not identically zero.
Choose \( \lambda \in (r(T), 1) \) and \( \eta \in \mathcal{H} \) such that \( \eta(x) > 0 \) in \( \mathbb{R} \). Then \( \lambda w - Tw = \eta \) has a unique solution \( w \in \mathcal{H} \). Since \( (\lambda - T)^{-1} = \sum_{j=0}^{\infty} T^j / \lambda^{j+1} \), we see that \( w \geq 0 \). In fact \( \eta > 0 \) implies that \( w(x) > 0 \) in \( \mathbb{R} \). By adjusting \( \eta \), we may assume that \( \|w\|_{\infty} = 1 \) and that \( w \) is sufficiently regular.

Consider the following inequality:

\[
\int K(x-y)g_u(y, \phi(y)) \, dy \leq \int_{|y| \leq N_1} K(x-y)g_u(y, \phi(y)) \, dy + \text{const.} \int_{|y| \leq N_1} K(x-y) \, dy.
\]

From condition (xi) of (1.12), \( g_u(x, \phi(x)) < \theta_1 < 1 \) if \( |x| \geq N_1 \) for some large \( N_1 \). Therefore, \( \int K(x-y)g_u(y, \phi(y)) \, dy \leq \theta_1 < 1 \) if \( |x| \geq N_2 \). We extend \( g \) to \( \mathbb{R} \times \mathbb{R} \) so that \( g_u(x, u) \geq 0 \) and \( M = \frac{1}{2} \sup_{\mathbb{R} \times \mathbb{R}} g_{uu}(x, u) \) is finite.

Choose \( \mu > 0 \) such that \( \lambda < e^{-\mu} < 1 \). On the interval \( |x| \leq N_2 \), let \( w(x) \geq m > 0 \). Define \( m_1 = \sup_{\mathbb{R}} \int K(x-y)g_u(y, \phi(y)) \, dy \), \( \gamma = (e^{-\mu} - \lambda)m/(m_1 - \theta_1) \), \( \beta = \gamma(e^{-\mu} - \theta_1)/M(1 + \gamma)^2 \) and \( z_n(x) = \beta(w(x) + \gamma)e^{-\mu n} \) for all \( n \).

We claim that \( N[z_n] \leq z_{n+1} \) for all \( n \) where

\[
N[z_n](x) = \int K(x-y)[g(y, \phi(y) + z(y)) - g(y, \phi(y))] \, dy.
\]

Write

\[
N[z](x) = \int K(x-y)g_u(y, \phi(y))z(y) \, dy + \int K(x-y)h(y, z(y))z(y) \, dy,
\]

where

\[
h(x, z) = \frac{g(x, \phi(x) + z) - g(x, \phi(x))}{z} - g_u(x, \phi(x)).
\]

By the mean value theorem, \( |h(x, z)z| \leq M|z|^2 \).

To begin we have \( Tz_n(x) = \beta e^{-\mu}[\lambda w(x) - \eta(x) + \gamma \int K(x-y)g_u(y, \phi(y)) \, dy] \) and \( N_1[z_n](x) = \int K(x-y)h(y, z_n(y))z_n(y) \, dy \) satisfies the inequality

\[
|N_1[z_n](x)| \leq M \int |K(x-y)|z_n(y)|^2 \, dy \leq M\beta^2 e^{-\mu n}(1 + \gamma)^2.
\]

Hence \( N[z_n](x) \leq \beta e^{-\mu}[\lambda w(x) + \gamma \int K(x-y)g_u(y, \phi(y)) \, dy + \beta M(1 + \gamma)^2] \).

If \( |x| \geq N_2 \), the term inside the square bracket is bounded above by \( e^{-\mu}w(x) + \gamma \theta_1 + \beta M(1 + \gamma)^2 \) which by the definition of \( \beta \) is equal to \( (w(x) + \gamma)e^{-\mu} \). Therefore, \( N[z_n](x) \leq z_{n+1}(x) \) if \( |x| \geq N_2 \). On the other hand if \( |x| \leq N_2 \), we have

\[
(\lambda - e^{-\mu})w(x) + \gamma \int K(x-y)g_u(y, \phi(y)) \, dy + \beta M(1 + \gamma)^2 - \gamma e^{-\mu}
\]

\[
\leq (\lambda - e^{-\mu})m + \gamma(m_1 - e^{-\mu}) + \beta M(1 + \gamma)^2
\]

\[
= (\lambda - e^{-\mu})m + \gamma(m_1 - \theta_1) = 0,
\]

and so the term inside the square bracket is bounded above by \( e^{-\mu}(w(x) + \gamma) \). Therefore, \( N[z_n](x) \leq z_{n+1}(x) \) if \( |x| \leq N_2 \) and our claim is proved.
Finally let $\delta = \beta\gamma$ in the statement of Theorem 2.4 and $v_0 = u_n - \phi$ for all $n$. If $v_0 \leq \delta$, then $v_0 \leq z_0$ since $w > 0$. Proceeding inductively, suppose $v_n \leq z_n$, then

$$v_{n+1}(x) = u_{n+1}(x) - \phi(x) = \int K(x-y)[g(y, \phi(y) + v_n(y)) - g(y, \phi(y))] \, dy$$

$$\leq \int K(x-y)[g(y, \phi(y) + z_n(y)) - g(y, \phi(y))] \, dy$$

$$= N[z_n](x) \leq z_{n+1}(x).$$

Hence, $u_n(x) - \phi(x) \leq Ce^{-\mu n}$ for all $n$ where $C = \beta(1 + \gamma)$. This proves half of Theorem 2.4.

To show the other half, we first observe that the proof of $N[z_n] \leq z_{n+1}$ also shows that $N[-z_n] \geq -z_{n+1}$ for all $n$. This part involves no more than changing the sign of some of the terms in the proof of $N[z_n] \leq z_{n+1}$.

Now suppose $v_0 \geq -\delta \geq -z_0$. Proceeding inductively as before, assuming that $v_n \geq -z_n$, we have

$$u_{n+1}(x) - \phi(x) = \int K(x-y)[g(y, \phi(y) + v_n(y)) - g(y, \phi(y))] \, dy$$

$$\geq \int K(x-y)[g(y, \phi(y) - z_n(y)) - g(y, \phi(y))] \, dy$$

$$= N[-z_n](x) \geq -z_{n+1}(x).$$

Therefore, $\phi(x) - u_n(x) \leq Ce^{-\mu n}$ for all $n$. The proof of Theorem 2.4 is now complete.

Note added in proof. Since this paper was accepted, Dr. Odo Diekmann in Amsterdam has informed the author that some of the results in this paper overlap with his paper, Clines in a discrete time model in population genetics, Proc. Conference on Models of Biological Growth and Spread, W. Jäger, ed., Lecture Notes in Biomathematics, 38, Springer-Verlag, New York, 1981.

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