Periodic Traveling Waves in an Integro-Difference Equation With a Nonmonotone Growth Function and Strong Allee Effect

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Abstract

We derive sufficient conditions for the existence of periodic traveling wave solutions for a class of integro-difference equation with piecewise constant growth function exhibiting a period two cycle and a strong Allee effect. We also prove the convergence of solutions with compactly supported initial data to translations of the traveling wave under appropriate conditions.

Key words: Integro-difference equation, period two cycle, Allee effect, periodic traveling wave.

Todo: Double check Gaussian kernel proof.

AMS Subject Classification: 92D40, 92D25.

1 Introduction

Integro-difference equations are of great interest in the studies of invasions of populations with discrete generations and separate growth and dispersal stages. They have been used to predict changes in gene frequency [8, 9, 10, 14, 17], and applied to ecological problems [2, 3, 4, 5, 7, 11, 12, 13]. Previous rigrous studies on integro-difference equations have assumed that the growth function is nondecreasing [17, 18], or is nonmonotone without strong Allee

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effect [10, 16]. The results show existence of constant spreading speeds and travelng waves with fixed shapes and speeds. Sullivan et al. [15] demonstrated numerically that an integro-difference equation with a nonmonotone growth function exhibiting a strong Allee effect can generate traveling waves with fluctuating speeds. In this paper we give a sufficient condition for the existence of periodic traveling waves with a periodic speed for such an equation with a specific growth function.

We consider the following integro-difference equation

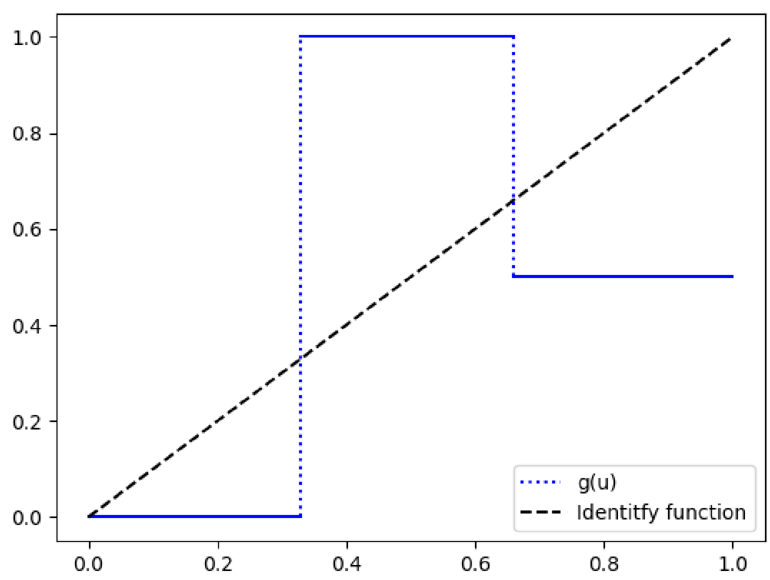
$$u_{n+1}(x) \;=\; Q[u_n](x) \;:= (k * (g \circ u_n))(x) \;=\; \int_{-\infty}^{\infty} k(x-y)\, g\big(u_n(y)\big)\, \mathrm{d}y, \qquad (1.1)$$

where

$$g(u) = \begin{cases} 0, & \text{if } u < a, \\ n_2, & \text{if } a \le u \le b, \\ n_1, & \text{if } u > b, \end{cases} \qquad (1.2)$$

with $0 < a < n_1 < b < 1$. $g(u)$ is a piecewise constant nonmonotone growth function exhibiting a strong Allee effect [1]. Specifically, it has a stable fixed point at zero and a stable period two cycle $(1, n_1)$ with a the Allee threshold value.

Figure 1: Plot of the growth function $g(u)$ compared to the identity function with growth parameters $a = 0.33$, $b = 0.66$, and $n_1 = 0.5$, and $n_2 = 1.0$.



Piecewise constant growth functions have been used in the studies of integro-difference equations; see for example [6, 11, 13, 15]. We rigorously construct periodic traveling waves with periodic speeds for (1.1). To the best of our knowledge, this is the first time that traveling waves with oscillating speeds have been analytically established for scalar spatiotemporal equations with constant parameters. We also show the convergence of solutions with compactly supported initial data to translations of the traveling wave under appropriate conditions. Equation (1.1) may be viewed as a symbolic model for integro-difference equations with a growth function exhibiting a strong Allee effect and a period two cycle. The results obtained this paper provide important insights into integro-difference equations with general growth functions.

2 Periodic traveling waves

In this section, we construct a periodic traveling wave solution to the recurrence (1.1). We will assume the dispersal kernel k satisfies the following hypotheses:

(H1) k is a non-negative, Lebesgue-integrable function with $\int_{-\infty}^{\infty} k(x)\,dx = 1$;

(H2) $k(x) = k(-x)$ for all $x \in \mathbb{R}$;

(H3) the support of k is connected;

(H4) for all $\lambda \in (0,1)$, for all $a \in \mathbb{R}$, the equation $k(x) = \lambda k(x-a)$ has at most one real solution.

Let w_1 and w_2 be two functions defined by

$$w_1(x) := \int_x^{\infty} n_2 k(y)\,dy \tag{2.1}$$

and

$$w_2(x) = \int_x^{\infty} \left(n_2 k(y - x_a) - (n_2 - n_1)k(y - x_b)\right)\,dy \tag{2.2}$$

where x_a and x_b constants constants given by

$$x_a = \sup\left\{x \in \mathbb{R} \mid \int_{-\infty}^{x} k(y)\,dy \leq \frac{a}{n_2}\right\}, \quad x_b = \sup\left\{x \in \mathbb{R} \mid \int_{-\infty}^{x} k(y)\,dy \leq \frac{b}{n_2}\right\} \tag{2.3}$$

Lemma 2.1. *If $||w_2||_\infty \leq b$, then w_1 and w_2 satisfy*

$$Q[w_1](x) = w_2(x) \tag{2.4}$$

and

$$Q[w_2](x) = w_1(x - 2c^*) \tag{2.5}$$

for all $x \in \mathbb{R}$, where c^* is a constant given by

$$c^* = \frac{1}{2} \sup\{x \in \mathbb{R} \mid w_2(x) \geq a\} \tag{2.6}$$

Proof. w_1 is monotonically decreasing with $w_1(-\infty) = n_2$ and $w_1(\infty) = 0$. It follows that $w_1(x) > b$ for $x < x_b$, $a \leq w_1(x) \leq b$ for $x_b \leq x \leq x_a$, and $w_1(x) < a$ for $x > x_a$. This yields

$$g(w_1(x)) = \begin{cases} n_1 & x < x_b \\ n_2 & x_b \leq x \leq x_a \\ 0 & x > x_a \end{cases} \tag{2.7}$$

Applying the integro-difference operator yields

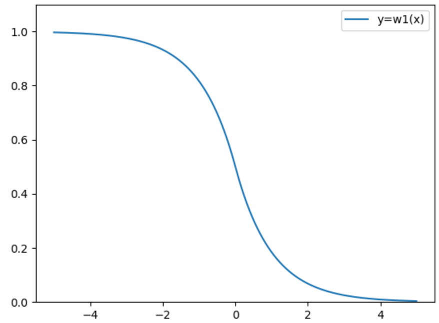
$$\begin{aligned} Q[w_1](x) &= \int_{-\infty}^{\infty} k(x-y) g(w_1(y))\, dy \\ &= n_1 \int_{-\infty}^{x_b} k(x-y)\, dy + n_2 \int_{x_b}^{x_a} k(x-y)\, dy \\ &= n_2 \int_{x-x_a}^{\infty} k(y)\, dy - (n_2 - n_1) \int_{x-x_b}^{\infty} k(y)\, dy \\ &= \int_{x}^{\infty} \left(n_2 k(y-x_a) - (n_2-n_1) k(y-x_b)\right)\, dy \end{aligned} \tag{2.8}$$

By Hypothesis (H4), we have assumed that the integrand on the right hand side has at most one zero. We can now proceed in cases. $w_2(x)$ has either zero or one turning point(s). In the first case, $w_2(x)$ is monotonically decreasing and satisfies $w_2(x) \geq a$ for $x \leq 2c^*$ and $w_2(x) < a$ for $x > 2c^*$. In the second case, $w_2(x)$ has a unique turning point $x_0 \in \mathbb{R}$; it follows that $w_2(x)$ is monotonically increasing on $(-\infty, x_0)$ and monotonically decreasing on (x_0, ∞), and x_0 is a global maximum. By the assumption $w_2(x) \leq \beta$ for all x, we have $w_2(x_0) \leq \beta$. It follows that $c^* \in (\frac{x_0}{2}, \infty)$, and $w_2(x)$ satisfies $g(w_2(x)) = 1$ for $x < 2c^*$ and $g(w_2(x)) = 0$ for $x > 2c^*$. In both cases, we have

$$g(w_2(x)) = \begin{cases} 1 & x \leq 2c^* \\ 0 & x > 2c^* \end{cases} \tag{2.9}$$

Thus,

$$\begin{aligned} Q[w_2](x) &= \int_{-\infty}^{\infty} k(x-y) g(w_2(y))\, dy \\ &= \int_{-\infty}^{2c^*} k(x-y)\, dy \\ &= \int_{x-2c^*}^{\infty} k(y)\, dy \\ &= w_1(x - 2c^*). \end{aligned} \tag{2.10}$$



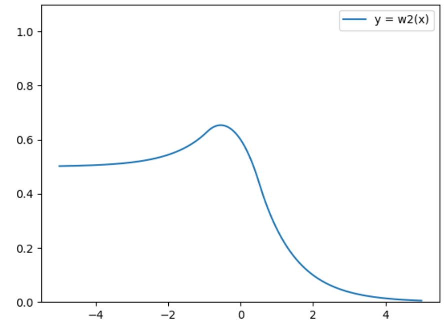


Figure 2: The shape of the two periodic traveling wave profiles with Laplace dispersal kernel and growth parameters $a = 0.3$, $n_1 = 0.5$, and $b = 0.8$.

$\square$

By Lemma 2.1, the wave functions $w_1(x)$ and $w_2(x)$ satisfy $Q^2[w_1](x) = w_1(x - 2c^*)$ and $Q^2[w_2](x) = w_2(x - 2c^*)$. As a result, they can be used to construct a solution to the integral recurrence which spreads in space with a mean speed of c^* and alternates in shape every two time steps. This is formalized in the following theorem:

Theorem 2.2. *If* $\sup_{x\in\mathbb{R}} w_2(x) \leq b$, *then equation* (1.1) *has a periodic traveling wave solution given by*

$$u_n(x) = \begin{cases} w_1(x - nc^*) & n \text{ even} \\ w_2(x - nc^* + c^*) & n \text{ odd} \end{cases} \tag{2.11}$$

for all $n \geq 0$.

Proof. It suffices to show that equation (2.11) satisfies $u_{n+1} = Q[u_n]$ for all $n \geq 0$. If n is even, then $n + 1$ is odd, so $u_n(x) = w_1(x - nc^*)$ and $u_{n+1}(x) = w_2(x - nc^*)$. Applying the integro-difference operator, we obtain

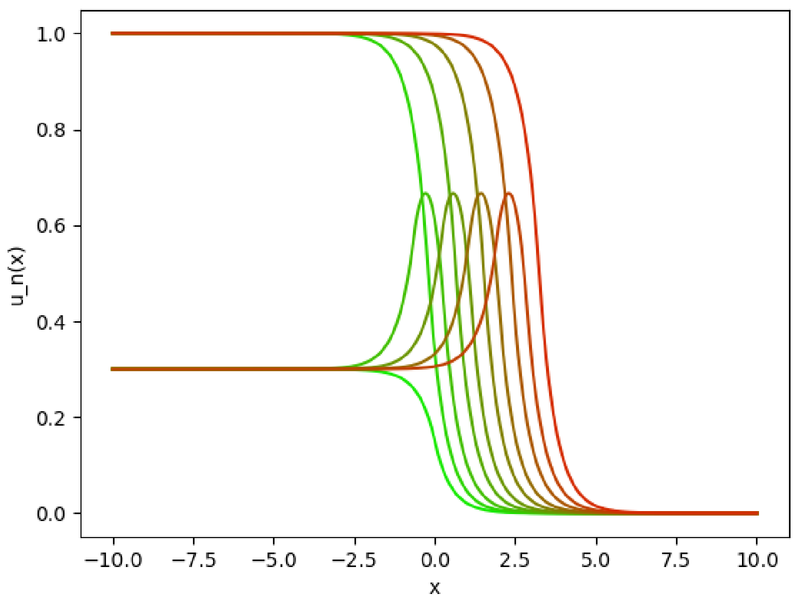
$$\begin{aligned} Q[u_n](x) &= Q[w_1](x - nc^*) \\ &= w_2(x - nc^*) \\ &= u_{n+1}(x) \end{aligned} \tag{2.12}$$

by (2.2). On the other hand, if n is odd, then $n + 1$ is even, so $u_n(x) = w_2(x - nc^* + c^*)$ and $u_{n+1}(x) = w_1(x - nc^* - c^*)$. Applying the operator, we get

$$\begin{aligned} Q[u_n](x) &= Q[w_2](x - nc^* + c^*) \\ &= w_1(x - nc^* - c^*) \\ &= u_{n+1}(x) \end{aligned} \tag{2.13}$$

by Lemma 2.1. □

Figure 3: Numerical simulation of our model using the Laplace dispersal kernel. The parameters chosen for this simulation were $a = 0.2$, $n_1 = 0.3$, and $b = 0.8$, and $n_2 = 1.0$. Later timepoints are colored in red, with earlier timepoints colored in green.



The previous theorem shows that our model can exhibit a periodic traveling wave solution with alternating wave profiles. Furthermore, we derived a constant wave speed at which the oscillating pair of waves travels. We now turn our attention to the magnitude of the oscillation in the wave speed. For a sufficiently small $\ell > 0$, we may label the point of intersection of the curve $u = u_n(x)$ with the horizontal line $u = \ell$ by $\xi_{n,\ell}$, or simply ξ_n. It follows that $\xi_1, \xi_2, \xi_3, \cdots \to \infty$ as $n \to \infty$; furthermore, the previous theorem implies that for any ℓ, we have $\xi_{n+2} - \xi_n = 2c^*$ for every $n \geq 1$.

For every $n \geq 1$, let $c_n = \xi_n - \xi_{n-1}$.

Theorem 2.3. *If* $\sup_{x\in\mathbb{R}} w_2(x) \leq b$*, then for all* $\epsilon > 0$*, the sequence 2.11 satisfies*

$$\lim_{n\to\infty} \inf_{x<2n(c^*-\epsilon)} u_{2n}(x) = 1 \tag{2.14}$$

and

$$\lim_{n\to\infty} \inf_{x<2n(c^*-\epsilon)} u_{2n+1}(x) = n_1 \tag{2.15}$$

and

$$\lim_{n\to\infty} \sup_{x>n(c^*+\epsilon)} u_n(x) = 0. \tag{2.16}$$

Proof.

$$\begin{aligned}
\lim_{n\to\infty} \inf_{x<2n(c^*-\epsilon)} u_{2n}(x) &= \lim_{n\to\infty} \inf_{x<2n(c^*-\epsilon)} w_1(x-2nc^*) \\
&= \lim_{n\to\infty} \inf_{x<-2n\epsilon} w_1(x) \\
&= \liminf_{x\to-\infty} w_1(x) \\
&= 1.
\end{aligned} \tag{2.17}$$

$$\begin{aligned}
\lim_{n\to\infty} \inf_{x<2n(c^*-\epsilon)} u_{2n+1}(x) &= \lim_{n\to\infty} \inf_{x<2n(c^*-\epsilon)} w_2(x-2nc^*) \\
&= \lim_{n\to\infty} \inf_{x<-2n\epsilon} w_2(x) \\
&= \liminf_{x\to-\infty} w_2(x) \\
&= n_1.
\end{aligned} \tag{2.18}$$

$$\begin{aligned}
\lim_{n\to\infty} \sup_{x>n(c^*+\epsilon)} u_n(x) &\le \lim_{n\to\infty} \sup_{x>n(c^*+\epsilon)} \sup\{w_1(x-nc^*), w_2(x-nc^*)\} \\
&= \lim_{n\to\infty} \sup_{x>n\epsilon} \sup\{w_1(x), w_2(x)\} \\
&= \limsup_{x\to\infty} \sup\{w_1(x), w_2(x)\} \\
&= \sup\{\limsup_{x\to\infty} w_1(x), \limsup_{x\to\infty} w_2(x)\} \\
&= 0.
\end{aligned} \tag{2.19}$$

In the last calculation, the left hand side is known to be non-negative; therefore the limit is exactly equal to zero. □

2.1 Compactly supported kernels

The next theorem concerns the spreading behavior of solutions to the IDE (1.1) with compactly supported initial data. We also assume the disperal kernel is compactly supported.

Lemma 2.4. *Suppose $k(x)$ has support $[-\sigma, \sigma]$ and $c^* \ge 0$.*

1. *If $r \ge \sigma - x_b$, then $Q[w_1](|x| - r) = w_2(|x| - r - c^*)$.*
2.

Proof. 1. Let $u(x) = w_1(|x| - r)$. Assuming $r + x_b \ge 0$, i.e. $r \ge -x_b$, we have $g(u(x)) = n_1$ for $|x| < r + x_b$, $g(u(x)) = 1$ for $r + x_b \le x \le r + x_a$, and $g(u(x)) = 0$ for

$x > r + x_a$. Note that $g(u(x)) = g(w_1(x-r))$ for $x \geq -r - x_b$. Applying the convolution operator, $Q[u](x) = Q[w_1](x-r)$ for $x \geq -r - x_b + \sigma$. Assuming $r \geq \sigma - x_b$, this shows $Q[u](x) = w_2(x - r - c^*)$ for $x \geq 0$. By the symmetry of $k(x)$, we have $Q[u](x) = w_2(|x| - r - c^*)$.

2. Let $u(x) = w_2(|x| - r)$. Assuming $r + x_b \geq 0$, i.e. $r \geq -x_b$, we have $g(u(x)) = n_1$ for $|x| < r + x_b$, $g(u(x)) = 1$ for $r + x_b \leq x \leq r + x_a$, and $g(u(x)) = 0$ for $x > r + x_a$. Note that $g(u(x)) = g(w_1(x-r))$ for $x \geq -r - x_b$. Applying the convolution operator, $Q[u](x) = Q[w_1](x-r)$ for $x \geq -r - x_b + \sigma$. Assuming $r \geq \sigma - x_b$, this shows $Q[u](x) = w_2(x - r - c^*)$ for $x \geq 0$. By the symmetry of $k(x)$, we have $Q[u](x) = w_2(|x| - r - c^*)$.

□

Theorem 2.5. *Suppose $k(x)$ has compact support and $\sup_{x\in\mathbb{R}} w_2(x) \leq b$. Let $u_0(x)$ be non-negative and continuous function, and suppose $a \leq u_0(x) \leq b$ for $|x| \leq r$ and $u_0(x) < a$ otherwise, for some $r > 0$. If r is sufficiently large and $c^* \geq 0$, then the sequence $(u_n)_{n=0}^{\infty}$ defined by $u_{n+1} = Q[u_n]$, $n \geq 0$ spreads with speed c^*, i.e.*

$$\lim_{n\to\infty} \inf_{|x|<n(c^*-\epsilon)} u_n(x) > 0, \tag{2.20}$$

and

$$\lim_{n\to\infty} \sup_{|x|>n(c^*+\epsilon)} u_n(x) = 0. \tag{2.21}$$

for all $\epsilon > 0$.

Theorem 2.6. *Suppose $k(x)$ has compact support and $||w_2||_\infty \leq b$. If $c^* \geq 0$ and r is sufficiently large, then equation (1.1) has a periodic spreading solution given by*

$$u_n(x) = \begin{cases} w_1(|x| - r - nc^*) & n \text{ even} \\ w_2(|x| - r - nc^*) & n \text{ odd} \end{cases} \tag{2.22}$$

for all $n \geq 0$.

Proof. As in the proof of Theorem 2.2, it suffices to show $u_{n+1} = Q[u_n]$ for all $n \geq 0$. If n is even, we have $u_n(x) = w_1(|x| - r - nc^*)$. Assuming $r \geq \sigma$ and $c^* \geq 0$, this implies $g(u_n(x)) = 0$ for $|x| > r + nc^* + x_a$, $g(u_n(x)) = 1$ for $r + nc^* + x_b \leq |x| \leq r + nc^* + x_a$, and $g(u_n(x)) = n_1$ for $|x| < r + nc^* + x_b$. Note that $g(u_n(x)) = g(w_1(x - r - nc^*))$ for $x \geq -r - nc^* - x_b$. Applying the convolution operator, we have $Q[u_n](x) = Q[w_1](x - r - nc^*)$ for $x \geq -r - nc^* - x_b + \sigma$. Assuming $r \geq \sigma - x_b$, it follows that $Q[u_n](x) = Q[w_1](x - r - nc^*)$ for $x \geq 0$. By hypothesis (H2), $k(x)$ is an even function, thus $Q[u_n](-x) = Q[u_n](x)$, hence $Q[u_n](x) = Q[w_1](|x| - r - nc^*)$ for all $x \in \mathbb{R}$, i.e. $u_{n+1}(x) = w_2(|x| - r - nc^* - c^*)$. Note that the preceding calculation requires $r \geq \max\{\sigma, \sigma - x_b\}$; a sufficient condition is $r \geq 2\sigma$.

If n is odd, then $u_n(x) = w_2(|x| - r - nc^*)$, and for $r \geq 0$ and $c^* \geq 0$ it follows that $g(u_n(x)) = 0$ for $|x| > r + nc^* + c^*$ and $g(u_n(x)) = 1$ for $|x| \leq r + nc^* + c^*$.

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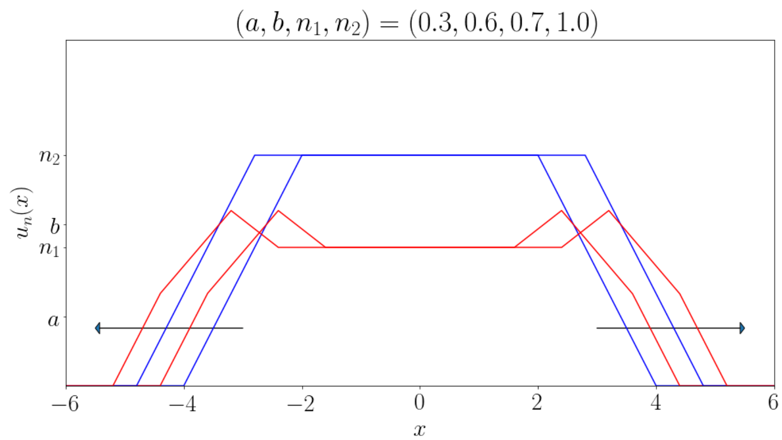
Figure 4: Spreading behavior for a uniform dispersal kernel with $\alpha = 0.3$, $\mu = 0.6$, and $\beta = 0.7$. The time steps corresponding to $w_1(x)$ are colored in blue, while time steps corresponding to $w_2(x)$ are colored in red.



Remark 2.7. This theorem indicates that a solution with proper compactly supported initial data coverges to translations of periodic traveling waves with profiles $w_1(x)$ and $w_2(x)$ in the positive direction and profiles $w_1(-x)$ and $w_2(-x)$ in the negative direction.

2.2 Variability in wave speed

3 Examples

In this section, we construct the periodic traveling wave solution for several well-known disperal kernels in population biology, namely the uniform, Laplace, and normal distributions. For the uniform and Laplace kernels, we were able to construct a piecewise expression for the mean wave speed in terms of the model parameters.

Example 3.1. The Laplace kernel,

$$k(x) = \frac{1}{2}e^{-|x|} \tag{3.1}$$

The reader can easily verify that the Laplace kernel satisfies hypotheses (H1) - (H3); the proof of (H4) is left in the appendix A.1.

The periodic traveling wave profiles are given by

$$w_1(x) = \begin{cases} 1 - \frac{1}{2}e^x & x \le 0 \\ \frac{1}{2}e^{-x} & x > 0 \end{cases} \tag{3.2}$$

and

$$w_2(x) = \begin{cases} m + \left(\frac{1-n_1}{2}e^{-x_b} - \frac{1}{2}e^{-x_a}\right)e^x & x < x_b \\ 1 - \left(\frac{1}{2}e^{-x_a}\right)e^x - \left(\frac{1-n_1}{2}e^{x_b}\right)e^{-x} & x_b \le x \le x_a \\ \left(\frac{1}{2}e^{x_a} - \frac{1-n_1}{2}e^{x_b}\right)e^{-x} & x_a < x \end{cases} \tag{3.3}$$

where

$$x_a = \begin{cases} -\ln(2a) & a \le \frac{1}{2} \\ \ln(2-2a) & a > \frac{1}{2} \end{cases}, \quad x_b = \begin{cases} -\ln(2b) & b \le \frac{1}{2} \\ \ln(2-2b) & b > \frac{1}{2} \end{cases} \tag{3.4}$$

A necessary condition for formulas (3.2) and (3.3) to generate a periodic traveling wave solution are given in Lemma A.2. This leads to an equation for the mean wave speed

$$c^* = \begin{cases} \frac{1}{2}x_a + \frac{1}{2}\log\left(\frac{1-(1-n_1)e^{x_b-x_a}}{2a}\right) & a \le w_2(x_a) \\ \frac{1}{2}x_a + \frac{1}{2}\log\left(1 - a + \sqrt{(1-a)^2 - (1-\mu)e^{x_b-x_a}}\right) & w_2(x_a) < a < w_2(x_b) \\ \frac{1}{2}x_a + \frac{1}{2}\log\left(\frac{2(a-n_1)}{(1-n_1)e^{x_a-x_b}-1}\right) & a \ge w_2(x_b) \end{cases} \tag{3.5}$$

Our formula can be written more explicitly based on the values of a and b:

Case 1. $a \le \frac{1}{2}$, $b \le \frac{1}{2}$.

$$w_2(x) = \begin{cases} n_1 + (b(1-n_1) - a)e^x & x < -\ln(2b) \\ 1 - ae^x - \frac{1-n_1}{4b}e^{-x} & -\ln(2b) < x < -\ln(2a) \\ \frac{b-a(1-m)}{4ab}e^{-x} & x > -\ln(2a) \end{cases} \tag{3.6}$$

We have $w_2(x_a) = \frac{b-a(1-n_1)}{2b}$ and $w_2(x_b) = n_1 + \frac{b(1-n_1)-a}{2b}$. Thus,

$$c^* = \begin{cases} \frac{1}{2}\ln\left(\frac{b-a(1-n_1)}{4a^2b}\right) & a < \frac{b-a(1-n_1)}{2b} \\ \frac{1}{2}\ln\left(\frac{1-a+\sqrt{(1-a)^2-\frac{a(1-n_1)}{b}}}{2a}\right) & \frac{b-a(1-n_1)}{2b} \le a \le \frac{b(1+n_1)-a}{2b} \\ \frac{1}{2}\ln\left(\frac{a-n_1}{b(1-n_1)-a}\right) & a > \frac{b(1+n_1)-a}{2b} \end{cases} \tag{3.7}$$

Case 2. $a \le \frac{1}{2}$, $b > \frac{1}{2}$.

$$w_2(x) = \begin{cases} n_1 + \frac{1-n_1-4a(1-b)}{4(1-b)} e^x & x < \ln(2-2b) \\ 1 - ae^x - (1-n_1)(1-b)e^{-x} & \ln(2-2b) < x < -\ln(2a) \\ \frac{1-4a(1-n_1)(1-b)}{4a} e^{-x} & x > -\ln(2a) \end{cases} \tag{3.8}$$

We have $w_2(x_a) = \frac{1-4a(1-n_1)(1-b)}{2}$ and $w_2(x_b) = \frac{1+n_1-4a(1-b)}{2}$. Thus,

$$c^* = \begin{cases} \frac{1}{2}\ln\left(\frac{1-4a(1-n_1)(1-b)}{4a^2}\right) & a < \frac{1-4a(1-n_1)(1-b)}{2} \\ \frac{1}{2}\ln\left(\frac{1-a+\sqrt{(1-a)^2-4a(1-n_1)(1-b)}}{2a}\right) & \frac{1-4a(1-n_1)(1-b)}{2} \le a \le \frac{1+n_1-4a(1-b)}{2} \\ \frac{1}{2}\ln\left(\frac{4(a-n_1)(1-b)}{1-n_1-4a(1-b)}\right) & a > \frac{1+n_1-4a(1-b)}{2} \end{cases} \tag{3.9}$$

Case 3. $a > \frac{1}{2}$, $b > \frac{1}{2}$.

$$w_2(x) = \begin{cases} n_1 - \frac{1-b+n_1(1-a)}{4(1-a)(1-b)} e^x & x < \ln(2-2b) \\ 1 - \frac{1}{4(1-a)} e^x - (1-n_1)(1-b)e^{-x} & \ln(2-2b) < x < \ln(2-2a) \\ (1-a-(1-n_1)(1-b))e^{-x} & x > \ln(2-2a) \end{cases} \tag{3.10}$$

Thus, $w_2(x_a) = \frac{1-a-(1-n_1)(1-b)}{2(1-a)}$ and $w_2(x_b) = n_1 - \frac{1-b+n_1(1-a)}{2(1-a)}$

$$c^* = \begin{cases} \frac{1}{2}\ln\left(\frac{1-a-(1-n_1)(1-b)}{a}\right) & a < \frac{1-a-(1-n_1)(1-b)}{2(1-a)} \\ \frac{1}{2}\ln\left(2(1-a)\left[1-a+\sqrt{\frac{(1-a)^3-(1-n_1)(1-b)}{1-a}}\right]\right) & \frac{1-a-(1-n_1)(1-b)}{2(1-a)} \le a \le \frac{b-1+n_1(1-a)}{2(1-a)} \\ \frac{1}{2}\ln\left(\frac{4(n_1-a)(1-a)(1-b)}{1-b+n_1(1-a)}\right) & a > \frac{b-1+n_1(1-a)}{2(1-a)} \end{cases} \tag{3.11}$$

Example 3.2. Consider the Gaussian kernel with zero mean and unit variance given by

$$k(x) = \frac{1}{\sqrt{2\pi}} e^{-\frac{x^2}{2}}$$

The kernel is symmetric and has connected support, hence it satisfies hypotheses (H1)-(H3); the proof for hypothesis (H4) is left in the appendix.

Let $\Phi(x) = \int_{-\infty}^{x} k(y)\, dy$ denote the cumulative density function of the standard normal distribution, and Φ^{-1} be its inverse. The periodic traveling wave solutions $w_1(x)$ and $w_2(x)$ are given by

$$w_1(x) = \Phi(-x) \tag{3.12}$$

and

$$w_2(x) = n_1 - \Phi(x - \Phi^{-1}(a)) + (1 - n_1)\Phi(x - \Phi^{-1}(b)) \tag{3.13}$$

w_2 has a unique global maximum at $x^* = \frac{x_a + x_b}{2} + \frac{1}{x_a - x_b} \ln(1 - n_1)$. Thus, by Theorem 2.2, w_1 and w_2 are a periodic traveling wave solution if $w_2(x^*) \leq b$.

Example 3.3. Consider the uniform dispersal kernel given by

$$k(x) = \begin{cases} \frac{1}{2} & |x| \leq 1 \\ 0 & |x| > 1 \end{cases} \tag{3.14}$$

Then w_1 is given by

$$w_1(x) = \begin{cases} 1, & x \in (-\infty, -1), \\ \frac{1}{2} - \frac{1}{2}x, & x \in [-1, 1], \\ 0, & x \in (1, \infty), \end{cases} \tag{3.15}$$

with inverse $w_1^{-1}(p) = 1 - 2p$ for $0 < p < 1$. Let $\alpha = 1 - 2a$ and $\beta = 1 - 2b$. Then

$$w_2(x) = \begin{cases} m, & x \in (-\infty, \beta - 1), \\ \frac{1-m}{2}x + m + b - mb, & x \in [\beta - 1, \alpha - 1), \\ -\frac{m}{2}x + m + b - mb - a, & x \in [\alpha - 1, \beta + 1), \\ -\frac{1}{2}x - a + 1, & x \in [\beta + 1, \alpha + 1], \\ 0, & x \in (\alpha + 1, \infty). \end{cases} \tag{3.16}$$

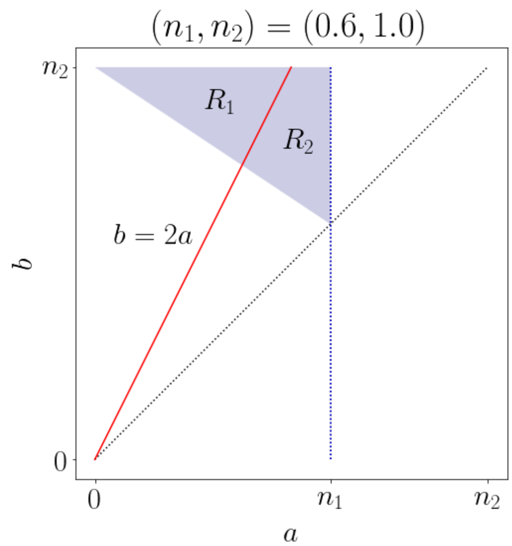
Observe that w_2 has a global maximum at $x = \alpha - 1$ so that $||w_2||_\infty = w_2(\alpha - 1) = m + (b - a)(1 - m)$. By Theorem 2.3, the pair w_1 and w_2 are a solution to equation (2.11) if $m - a < m(b - a)$.

We can also explicitly calculate the speed of the wave given by

$$c^* = \begin{cases} 1 - 2a & \text{if } a \leq b/2, \\ 1 - b + \frac{b-2a}{m} & \text{if } a > b/2. \end{cases} \tag{3.17}$$

Remark 3.4. $w_1(x)$ is positive for $x < 1$ and zero for $x \geq 1$, and $w_2(x)$ is positive for $x < 2 - 2a$ and zero for $x \geq 2 - 2a$. Thus, (1.1) has a traveling wave with wave profiles $w_1(x)$ and $w_2(x)$, intermediate wave speeds $c_1 = 1 - 2a$ and $c_2 = 2c^* - c_1$, and average wave speed c^*. It is easily seen that $c_1 = c_2$ if $a \leq b/2$, and $|c_1 - c_2| = (2\alpha - \beta)(1 - \frac{1}{m}) > 0$ if $a > b/2$. So for $a > b/2$, the traveling wave is periodic with two different intermediate wave speeds. Furthermore, the difference between these two intermediate speeds is increasing in a, decreasing in b, and increasing in m. This behavior is illustrated with two difference choices of parameters in Figure **??**.

Figure 5: The shaded region R indicates all pairs (a, b) such that the condition in Theorem 2.1 holds for $n_1 = 0.6$, and the line $b = 2a$ is drawn in red. The region R_1 contains all pairs (a, b) such that the traveling wave has constant speed, and R_2 contains all pairs such that the traveling wave has oscillating speed.



The regions in the parameter space where oscillating spreading speed exists can be determined as follows: for any fixed choice of (n_1, n_2), with $0 < n_1 < n_2$, let R be the set of pairs $(a, b) \in \mathbf{R}^2$ such that the hypothesis of Theorem 2.1 holds. Then R is a triangle in the a-b plane with endpoints at $(0, n_2)$, (n_1, n_1), and (n_1, n_2), depicted in Figure **??**. The line $b = 2a$ partitions R into two non-empty sets $R_1 = \{(a, b) \in R : a \leq b/2\}$ and $R_2 = \{(a, b) \in R : a > b/2\}$ such that the traveling has constant speed if $(a, b) \in R_1$ and oscillating speed if $(a, b) \in R_2$.

References

[1] W. C. Allee. 1931. Animal Aggregations. A Study on General Sociology. University of Chicago Press, Chicago, IL.

[2] A. Hastings and K. Higgins. 1994. Persistence of transients in spatially structured ecological models. Science **263**: 1133-1136.

[3] M. Kot and W. M. Schaffer. 1986. Discrete-time growth-dispersal models. Math. Biosci. **80**: 109-136.

[4] M. Kot. 1989. Diffusion-driven period doubling bifurcations. Biosystems **22**: 279-287.

[5] M. Kot. 1992. Discrete-time traveling waves: Ecological examples. J. Math. Biol. **30**: 413-436.

[6] M. Kot, M. A. Lewis, and P. van den Driessche. 1996. Dispersal data and the spread of invading organisms. Ecology **77**: 2027-2042.

[7] M. Kot. 2001. Elements of Mathematical Ecology. Cambridge University Press. Cambridge, United Kingdom.

[8] R. Lui. 1982. A nonlinear integral operator arising from a model in population genetics. I. Monotone initial data. SIAM. J. Math. Anal. **13**: 913-937.

[9] R. Lui. 1982. A nonlinear integral operator arising from a model in population genetics. II. Initial data with compact support. SIAM. J. Math. Anal. **13**: 938-953.

[10] R. Lui. 1983. Existence and stability of traveling wave solutions of a nonlinear integral operator. J. Math. Biol. **16**:199-220.

[11] F. Lutscher. 2019. Integrodifference Equations in Spatial Ecology. Springer.

[12] M. Neubert, M. Kot, and M. A. Lewis. 1995. Dispersal and pattern formation in a discrete-time predator-prey model. Theor. Pop. Biol. **48** : 7-43.

[13] G. Otto. 2017. Non-spreading Solutiona in a Integro-Difference Model Incorporating Allee and Overcompensation Effects. Ph. D thesis, University of Louisville.

[14] M. Slatkin. 1973. Gene flow and selection in a cline. Genetice **75**: 733-756.

[15] L. L. Sullivan, B. Li, T. E. X. Miller, M. G. Neubert, and A. K. Shaw. 2017. Density dependence in demography and dispersal generates fluctuating invasion speeds. Proc. Natl. Acad. Sci. USA **114**: 5053-5058.

[16] M. H. Wang, M. Kot, and M. G. Neubert. 2002. Integrodifference equations, Allee effects, and invasions. J. Math. Biol. **44**: 150-168.

[17] H. F. Weinberger. 1978. Asymptotic behavior of a model in population genetics, in Nonlinear Partial Differential Equations and Applications, ed. J. M. Chadam. Lecture Notes in Mathematics **648**: 47-96. Springer-Verlag, Berlin.

[18] H. F. Weinberger. 1982. Long-time beahvior of a class of biological models. SIAM. J. Math. Anal. **13**: 353-396.

A Appendix

Lemma A.1. *The Laplace kernel* (3.1) *satisfies hypothesis (H4).*

Proof. Let $k(x) = \frac{1}{2}e^{-|x|}$. For $a \in \mathbb{R}$ and $\lambda \in (0,1)$, define

$$f_{a,\lambda}(x) = \frac{1}{2}e^{-|x|} - \frac{\lambda}{2}e^{-|x-a|}. \tag{A.1}$$

If $a = 0$, then f has no zero-crossings, since $f_{0,\lambda}(x) = \frac{1-\lambda}{2}e^{-|x|}$ is strictly positive. If a is nonzero, then one can easily check the symmetry relation $f_{-a,\lambda}(x) = f_{\lambda,a}(-x)$. Since the number of zero-crossings are invariant with respect to a reflection about the vertical axis, we can assume without loss of generality $a > 0$.

Under this assumption, f is strictly increasing on $(-\infty, 0)$, and strictly decreasing on $(0, a)$. The behavior on (a, ∞) can be determined in three cases:

Case 1.) if $a < \ln \frac{1}{\lambda}$, then f is decreasing on $(0, \infty)$, hence has no zero-crossings;

Case 2.) if $a > \ln \frac{1}{\lambda}$, then f has a unique zero-crossing at $x = \frac{1}{2}(a - \ln \lambda)$;

Case 3.) if $a = \ln \frac{1}{\lambda}$, then f vanishes on (a, ∞), hence it has no zero-crossings.

In each case, the number of zero-crossings does not exceed one. □

Lemma A.2. *If $k(x)$ is given by the Laplace kernel, then w_1 and w_2 form a periodic traveling wave solution if $C_1 \le 0$, or if $C_1 > 0$ and $w_2\left(\ln\sqrt{\frac{C_3}{C_2}}\right) \le b$.*

Proof. We can proceed in cases. If $C_1 \le 0$, then $w_2(x)$ is monotone decreasing, hence $w_2(x) < w_2(-\infty) = m < b$ everywhere. Otherwise, if $C_1 > 0$, then $w_2(x)$ is increasing on $(-\infty, \beta)$ and decreasing on (α, ∞). Since $w_2(x)$ is concave-down on (β, α), this implies there is a unique global maximum somewhere in this interval. To find it, we can differentiate:

$$\left.\frac{dw_2}{dx}\right|_{\beta<x<\alpha} = C_3e^{-x} - C_2e^{x}$$

Setting this expression equal to zero and multiplying by e^x, we obtain $C_3 - C_2e^{2x} = 0$, which has a unique solution at $x = \ln\sqrt{\frac{C_3}{C_2}}$. □

Lemma A.3. *The Gaussian kernel satisfies hypothesis H4.*

Proof. Let $a \in \mathbb{R}$ and $\mu \in (0,1)$. Then

$$\begin{aligned} k(x) - \mu k(x-a) &= \frac{1}{\sqrt{2\pi}}\left(e^{-\frac{x^2}{2}} - \mu e^{-\frac{-(x-a)^2}{2}}\right) \\ &= \frac{1}{\sqrt{2\pi}}e^{-\frac{x^2}{2}}\left(1 - \mu e^{\frac{2ax-a^2}{2}}\right) \end{aligned} \tag{A.2}$$

This expression has a unique zero at $x = \frac{y^2 - 2\ln(\mu)}{2a}$, so the number of zero-crossings is at most one. $\square$

Lemma A.4. *For the Gaussian kernel, $w_2(x)$ has a unique local extrema which is a global maxium at $x = \frac{2\ln(1-m)}{\alpha-\beta} + \alpha + \beta$.*

Proof. The derivative of $w_2(x)$ is given by

$$\frac{dw_2}{dx} = -\frac{1}{\sqrt{2\pi}} e^{-\frac{(x-\alpha)^2}{2}} + \frac{1-m}{\sqrt{2\pi}} e^{-\frac{(x-\beta)^2}{2}}$$

Setting this quantity equal to zero, we obtain the equation

$$e^{-\frac{(x-\alpha)^2}{2}} = (1-m) e^{-\frac{(x-\beta)^2}{2}}$$

Taking logarithm on both sides, and rearrange terms,

$$(x-\beta)^2 = 2\ln(1-m) + (x-\alpha)^2$$

Distributing both sides and cancelling the quadratic term, we get the solution

$$x = \frac{2\ln(1-m)}{\alpha - \beta} + \alpha + \beta$$

$\square$