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

Michael Nestor, Bingtuan Li *

Department of Mathematics, University of Louisville,
Louisville, KY 40292.

June 20, 2021

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

*M. Nestor's email is mdnest01@louisville.edu. B. Li was partially supported by the National Science Foundation under Grant DMS-1515875 and Grant DMS-1951482.

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

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

where

$$g(u) = \begin{cases} 0, & \text{if } u < \alpha, \\ 1, & \text{if } \alpha \le u \le \beta, \\ \mu, & \text{if } u > \beta, \end{cases} \tag{1.2}$$

with $0 < \alpha < \mu < \beta < 1$. $g(u)$ 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 $(1, \mu)$ with α the Allee threshold value.

Piecewise constant growth functions and uniform distributions 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:

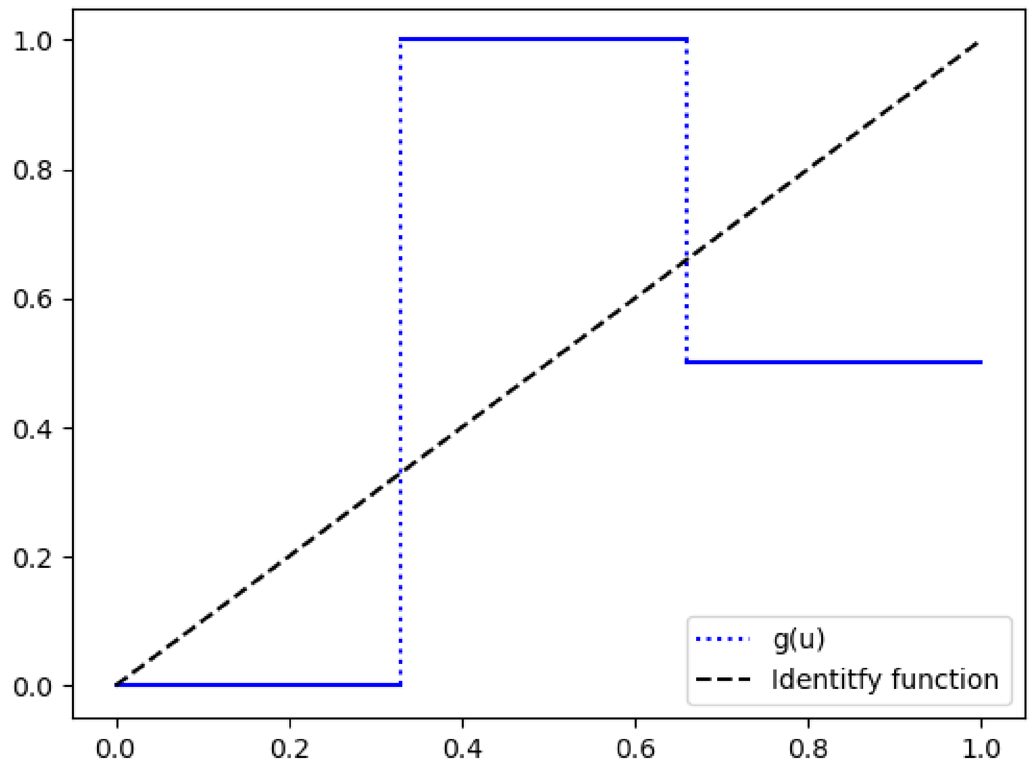
(H1) k is a non-negative Lebesgue-integrable function with $\int_{-\infty}^{\infty} k(x)\, dx = 1$;

(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 $y \in \mathbb{R}$, the function $x \mapsto k(x) - \lambda k(x - y)$ has at most one zero-crossing in $\mathbb{R}$.

Figure 1: Plot of the growth function $g(u)$ compared to the identity function with growth parameters $\alpha = 0.33$, $\beta = 0.66$, and $\mu = 0.5$.



Proposition 2.1. *The operator Q satisfies the following properties for all bounded continuous functions $u : \mathbb{R} \to \mathbb{R}_{\geq 0}$:*

(i.) (Translation invariance) $Q[T^t[u]] = T^t[Q[u]]$ for any translation operator $T^t[u](x) = u(x+t)$.

(ii.) (Symmetric) If $u(x) = u(-x)$ then $Q[u](x) = Q[u](-x)$.

(iii.) (Limit-preserving) If $u(x) \to \ell$ as $x \to \infty$, then $Q[u](x) \to g(\ell)$ as $x \to \infty$; likewise as $x \to -\infty$.

Let w_1 and w_2 be two functions defined by

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

and

$$w_2(x) := Q[w_1](x) = \int_{-\infty}^{\infty} k(y)g(w_1(x-y))\,dy \tag{2.2}$$

Hypothesis (H1) implies w_1 and w_2 have well-defined limits at $\pm\infty$ given by $w_1(\infty) = w_2(\infty) = 0$, $w_1(-\infty) = 1$, and $w_2(-\infty) = \mu$. Furthermore, w_1 is monotonically decreasing, while w_2 may be non-monotonic.

Lemma 2.2. *If $\max_{x\in\mathbb{R}} w_2(x) \leq \beta$, then there exists unique $c^* \in \mathbb{R}$ such that $Q[w_2](x) = w_1(x - 2c^*)$ for all $x \in \mathbb{R}$.*

Proof. Let $x_\alpha = \max\{x \in \mathbb{R} \mid w_1(x) \geq \alpha\}$ and $x_\beta = \max\{x \in \mathbb{R} \mid w_1(x) \geq \beta\}$. Since w_1 is monotone, it follows that $w_1(x) > \beta$ for $x < x_\beta$, $\alpha \leq w_1(x) \leq \beta$ for $x_\beta \leq x \leq x_\alpha$, and $w_1(x) < \alpha$ for $x > x_\alpha$. Applying the integro-difference operator to w_1 yields

$$\begin{aligned} Q[w_1](x) &= \int_{-\infty}^{\infty} k(x-y)g(w_1(y))\,dy \\ &= \mu \int_{-\infty}^{x_\beta} k(x-y)\,dy + \int_{x_\beta}^{x_\alpha} k(x-y)\,dy \\ &= \mu \int_{x-x_\beta}^{\infty} k(y)\,dy + \int_{x-x_\alpha}^{x-x_\beta} k(y)\,dy \\ &= \int_{x-x_\alpha}^{\infty} k(y)\,dy - (1-\mu)\int_{x-x_\beta}^{\infty} k(y)\,dy \end{aligned} \tag{2.3}$$

Taking the derivative with respect to x, we find

$$\frac{dw_2}{dx} = -k(x - x_\alpha) + (1-\mu)k(x - x_\beta) \tag{2.4}$$

From hypothesis (H4), we can conclude that (2.4) has at most one zero-crossing, hence $w_2(x)$ has at most one turning point. This leaves two cases:

Case 1. If w_2 has no turning points, it must be monotonically decreasing.

Case 2. If w_2 has a single turning point x^*, then $w_2(x)$ is increasing on $(-\infty, x^*)$ and decreasing on (x^*, ∞), with $\mu \leq w_2(x^*) \leq \beta$.

In both cases, $w_2(x)$ has a well-defined right inverse on the open interval $(0, \mu)$. Since $0 < \alpha < \mu$, let

$$c^* = \frac{1}{2}\max\{x \in \mathbb{R} \mid w_2(x) \geq \alpha\} \tag{2.5}$$

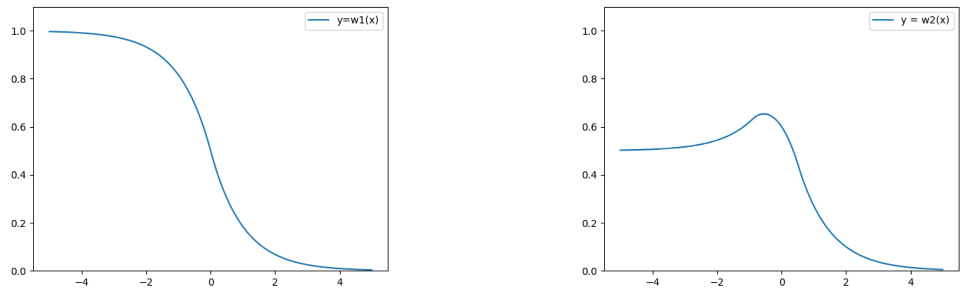


Figure 2: Plots of $w_1(x)$ (left) and $w_2(x)$ (right) with the Laplace dispersal kernel and growth parameters $\alpha = 0.3$, $\mu = 0.5$, and $\beta = 0.8$

It follows that $w_2(x) \geq \alpha$ for $x \leq 2c^*$ and $w_2(x) < \alpha$ for $x > 2c^*$. Along with the assumption that $\max_{x\in\mathbb{R}} w_2(x) \leq \beta$, we can apply the integro-difference operator once more:

$$\begin{aligned} Q[w_2](x) &= \int_{-\infty}^{2c^*} k(x-y)\,dy \\ &= \int_{x-2c^*}^{\infty} k(y)\,dy \qquad = w_1(x-2c^*). \end{aligned} \tag{2.6}$$

□

By Lemma 2.2, 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:

The condition that $\max_{x\in\mathbb{R}} w_2(x) \leq \beta$ may be difficult to verify for some choices of dispersal kernel. Thus, we provide a sufficient condition for this assumption:

Lemma 2.3. *Let x_α and x_β be as defined in Lemma 2.2. If $k(x)$ is unimodal and*

$$\mu + (1-\mu)\int_{-(x_\alpha - x_\beta)/2}^{(x_\alpha - x_\beta)/2} k(y)\,dy \leq \beta$$

then $\max_{x\in\mathbb{R}} w_2(x) \leq \beta$.

Proof. We have

$$\begin{aligned} w_2(x) &= (k * (g \circ w_1))(x) \\ &\leq (k * (m + (1-m)\mathbf{1}_{[x_\beta, x_a]}))(x) \\ &= m + (1-m)(k * \mathbf{1}_{[x_\beta, x_a]})(x) \\ &= \mu + (1-\mu)\int_{x_\beta}^{x_\alpha} k(x-y)\,dy. \end{aligned} \tag{2.7}$$

Taking the maximum over all x, we may shift the function horizontally so that the bounds of integration are symmetric. Since $k(x)$ is unimodal, the integral is then maximized for $x = 0$.

$$\begin{aligned}\max_{x\in\mathbb{R}} w_2(x) &\leq \max_{x\in\mathbb{R}} \left(\mu + (1-\mu)\int_{x_\beta}^{x_\alpha} k(x-y)\,dy\right)\\ &= \max_{x\in\mathbb{R}} \left(\mu + (1-\mu)\int_{-(x_\alpha-x_\beta)/2}^{(x_\alpha-x_\beta)/2} k(x-y)\,dy\right)\\ &= \mu + (1-\mu)\int_{-(x_\alpha-x_\beta)/2}^{(x_\alpha-x_\beta)/2} k(y)\,dy.\end{aligned} \tag{2.8}$$

□

Theorem 2.4. *If* $\max_{x\in\mathbb{R}} w_2(x) \leq \beta$, *then the recurrence* (1.1) *has a periodic traveling wave solution* $(u_n)_{n=0}^{\infty}$ *satisfying*

$$\begin{aligned}u_{2n}(x) &= w_1(x - 2nc^*)\\ u_{2n+1}(x) &= w_2(x - 2nc^*)\end{aligned} \tag{2.9}$$

for all $n \geq 0$.

Proof. It suffices to show that equation (2.9) satisfies $u_{n+1} = Q[u_n]$ for all $n \geq 0$. For convenience, we will switch the index and consider the cases u_{2n} and u_{2n+1} separately. The basic case, $u_1 = Q[u_0]$, follows immediately from definition 2.2. This proves the first half. Next, we have $u_2(x) = w_1(x - 2c^*)$, which follows by Lemma 2.2.

For the inductive step, suppose $u_{2n+1} = Q[u_{2n}]$ and $u_{2n+2} = Q[u_{2n+1}]$ for some $n \geq 0$. We only need to show $u_{2n+3} = Q[u_{2n+2}]$. We have

$$\begin{aligned}u_{2n+3}(x) &= w_2(x - 2nc^* - 2c^*)\\ &= Q^2[w_2](x - 2nc^*)\\ &= Q^2[u_{2n+1}](x)\\ &= Q[u_{2n+2}](x)\end{aligned} \tag{2.10}$$

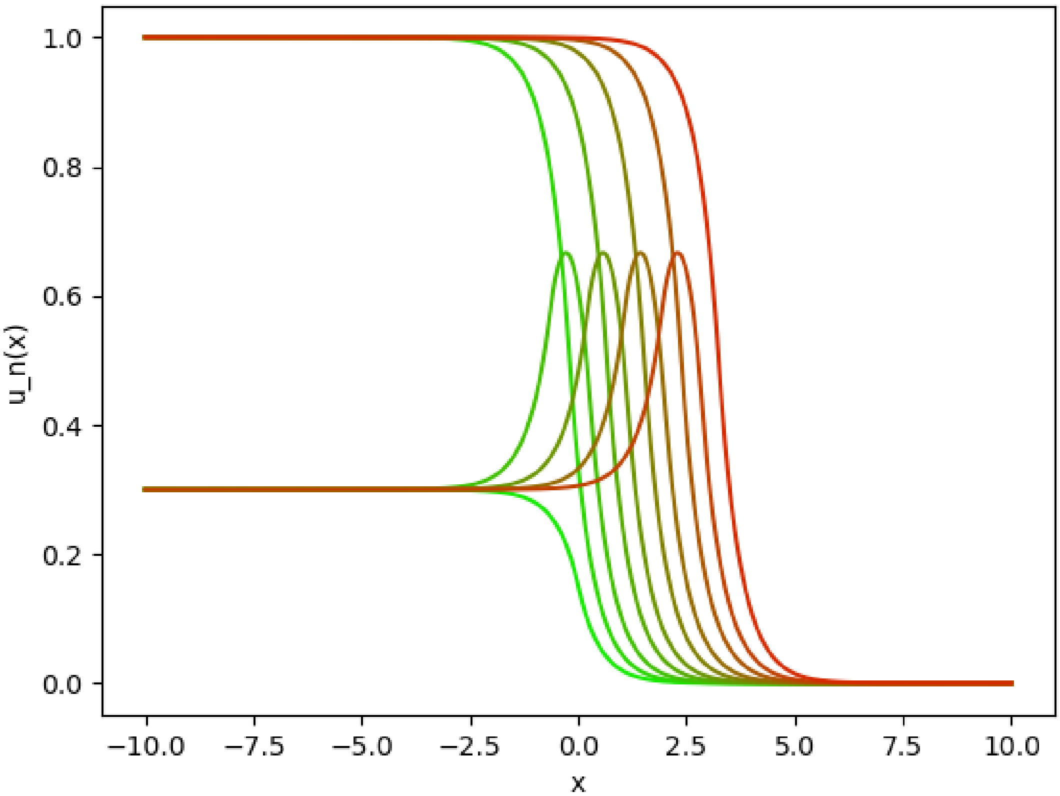
□

Figure 3 shows the propagation of the periodic traveling wave solution for a particular choice of dispersal kernel and growth parameters.

Theorem 2.5. *If* $\max_{x\in\mathbb{R}} w_2(x) \leq \beta$, *then for all* $\epsilon > 0$, *the sequence 2.9 satisfies*

$$\lim_{n\to\infty} \inf_{x<2n(c^*-\epsilon)} u_{2n}(x) = 1 \tag{2.11}$$

Figure 3: The periodic traveling wave solution (2.9) with a monotone initial condition for times $1 \leq n \leq 11$ using the Laplace dispersal kernel, $\alpha = 0.2$, $\mu = 0.3$, and $\beta = 0.8$. Later timepoints are colored in red, with earlier timepoints colored in green.



and

$$\lim_{n\to\infty} \inf_{x<2n(c^*-\epsilon)} u_{2n+1}(x) = m \tag{2.12}$$

and

$$\lim_{n\to\infty} \max_{x>n(c^*+\epsilon)} u_n(x) = 0. \tag{2.13}$$

Proof.

$$\begin{aligned}
\lim_{n\to\infty} \inf_{x<2n(c^*-\epsilon)} u_{2n}(x) &= \lim_{n\to\infty} \inf_{x<2n(c^*-\epsilon)} w_1(x-2nc^*) \\
&= \lim_{n\to\infty} \inf_{x<-2n\epsilon} w_1(x) \\
&= \liminf_{x\to-\infty} w_1(x) \\
&= 1.
\end{aligned} \tag{2.14}$$

$$\begin{aligned}
\lim_{n\to\infty} \inf_{x<2n(c^*-\epsilon)} u_{2n+1}(x) &= \lim_{n\to\infty} \inf_{x<2n(c^*-\epsilon)} w_2(x-2nc^*) \\
&= \lim_{n\to\infty} \inf_{x<-2n\epsilon} w_2(x) \\
&= \liminf_{x\to-\infty} w_2(x) \\
&= m.
\end{aligned} \tag{2.15}$$

$$\begin{aligned}
\lim_{n\to\infty} \max_{x>n(c^*+\epsilon)} u_n(x) &\leq \lim_{n\to\infty} \max_{x>n(c^*+\epsilon)} \max\{w_1(x-nc^*), w_2(x-nc^*)\} \\
&= \lim_{n\to\infty} \max_{x>n\epsilon} \max\{w_1(x), w_2(x)\} \\
&= \limsup_{x\to\infty} \max\{w_1(x), w_2(x)\} \\
&= \max\{\limsup_{x\to\infty} w_1(x), \limsup_{x\to\infty} w_2(x)\} \\
&= 0.
\end{aligned} \tag{2.16}$$

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

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. First, we introduce a useful lemma for compactly supported kernels.

Lemma 2.6. *Suppose $k(x)$ is compactly supported on $[-\sigma, \sigma]$ for some $\sigma > 0$, and let $u \in C(\mathbb{R})$. If $u(x) = 0$ for $x \in \Omega \subseteq \mathbb{R}$, then $(k * u)(x) = 0$ if $d(x, \mathbb{R} \setminus \Omega) := \inf\{d(x,y) \mid y \in \mathbb{R} \setminus \Omega\}$.*

Proof. Let $x \in \Omega$ such that $d(x, \mathbb{R} \setminus \Omega) \geq \sigma$. Then $(x-\sigma, x+\sigma)$ is a subset of Ω on which u vanishes; thus $(k * u)(x) = \int_{x-\sigma}^{x+\sigma} k(x-y)u(y)\,dy = 0$. $\square$

Theorem 2.7. *Let $u_0(x)$ be a non-negative continuous function with compact support such that the set $A = \{x \in \mathbb{R} : \alpha \leq u_0(x) \leq \beta\}$ is connected. Suppose $k(x)$ has compact support, $\max_{x\in\mathbb{R}} w_2(x) \leq \beta$, and $c^* > 0$. For A sufficiently large, the sequence $(u_n)_{n=0}^{\infty}$ defined by $u_{n+1} = Q[u_n]$, $n \geq 0$ spreads with speed c^*, i.e.*

$$\lim_{n\to\infty} \inf_{|x|<n(c^*-\epsilon)} u_n(x) > 0, \tag{2.17}$$

and

$$\lim_{n\to\infty} \max_{|x|>n(c^*+\epsilon)} u_n(x) = 0. \tag{2.18}$$

for all $\epsilon > 0$.

Proof. By the translation invariance property of Q, we may assume without loss of generality $A = [-r, r]$, for some $r > 0$. It follows that $u_0(x) < \alpha$ for $|x| > r$ and $\alpha \le u_0(x) \le \beta$ for $|x| \le r$. Furthermore, there exists $\sigma > 0$ such that $k(x) > 0$ if and only if $|x| < \sigma$.

Assuming $r \ge \frac{\sigma}{2}$, we have

$$\begin{aligned} u_1(x) = Q[u_0](x) &= \int_{-r}^{r} k(x-y)\,dy \\ &= \begin{cases} w_1(x-r) & x \ge 0 \\ w_1(-x+r) & x < 0 \end{cases} \end{aligned} \tag{2.19}$$

Let x_α and x_β be as defined in Lemma 2.2. Then, applying the growth function, we have

$$g(u_1(x)) = \begin{cases} 0 & x < -r - x_\alpha \\ 1 & -r - x_\alpha \le x \le -r - x_\beta \\ m & -r - x_\beta < x < r + x_\beta \\ 1 & r + x_\beta \le x \le r + x_\alpha \\ 0 & x > r + x_\alpha \end{cases} \tag{2.20}$$

Note that $g(u_1(x)) = g(w_1(x))$ for all $x > -r - x_\beta$. Thus, by Lemma 2.6, $Q[u_1](x) = (k * (g \circ u_1))(x) = (k * (g \circ w_1))(x) = Q[w_1](x)$ for all $x > -r - x_\beta + \sigma$. If we assume $r \ge x_\beta + \sigma$, then $u_2(x) = Q[u_1](x) = Q[w_1](x - r) = w_2(x - r)$ for $x > 0$.

By symmetry of the integro-difference operator, $Q[u_1](x) = Q[w_1](-x + r)$ for $x < 0$. Thus,

$$u_2(x) = Q[u_1](x) \begin{cases} w_2(x-r) & x \ge 0 \\ w_2(-x+r) & x < 0 \end{cases} \tag{2.21}$$

Since $c^* \ge 0$, we have

$$g(u_2(x)) = \begin{cases} 0 & x < -r - 2c^* \\ 1 & -r - 2c^* \le x \le r + 2c^* \\ 0 & x > r + 2c^* \end{cases} \tag{2.22}$$

Thus,

$$u_3(x) = Q[u_2](x) = \begin{cases} w_1(x - r - 2c^*) & x \ge 0 \\ w_1(-x + r + 2c^*) & x < 0 \end{cases} \tag{2.23}$$

The preceding argument can be repeated inductively to obtain

$$u_{2n+1}(x) = w_1(|x| - r - 2nc^*) \tag{2.24}$$

and

$$u_{2n+2}(x) = w_2(|x| - r - 2nc^*) \tag{2.25}$$

for all $n \geq 0$. $\square$

Remark 2.8. 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.

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 that is also satisfies (H4) is left in the appendix. The periodic traveling waves are given by

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

and

$$w_2(x) = \begin{cases} m + C_1 e^{x} & x < x_\beta \\ 1 - C_2 e^{x} - C_3 e^{-x} & x_\beta \leq x \leq x_\alpha \\ C_4 e^{-x} & x_\alpha < x \end{cases} \tag{3.3}$$

where

$$x_\alpha = \begin{cases} -\ln(2\alpha) & \alpha \leq \frac{1}{2} \\ \ln(2 - 2\alpha) & \alpha > \frac{1}{2} \end{cases} \qquad x_\beta = \begin{cases} -\ln(2\beta) & \beta \leq \frac{1}{2} \\ \ln(2 - 2\beta) & \beta > \frac{1}{2} \end{cases} \tag{3.4}$$

The constants C_1, C_2, C_3, and C_4 are continuous functions of the growth parameters α, β, and μ, with $C_2, C_3, C_4 \geq 0$. They can be expressed as piecewise expressions:

$$C_1 = \begin{cases} \beta(1-\mu) - \alpha & \alpha, \beta \leq \frac{1}{2} \\ \frac{1-\mu-4\alpha(1-\beta)}{4(1-\beta)} & \alpha \leq \frac{1}{2} < \beta \\ -\frac{1-\beta+\mu(1-\alpha)}{4(1-\alpha)(1-\beta)} & \frac{1}{2} < \alpha, \beta \end{cases} \tag{3.5}$$

$$C_2 = \begin{cases} \alpha & \alpha \leq \frac{1}{2} \\ \frac{1}{4(1-\alpha)} & \alpha > \frac{1}{2} \end{cases} \tag{3.6}$$

$$C_3 = \begin{cases} \frac{1-\mu}{4\beta} & \beta \leq \frac{1}{2} \\ (1-\mu)(1-\beta) & \beta > \frac{1}{2} \end{cases} \tag{3.7}$$

$$C_4 = \begin{cases} \frac{\beta-\alpha(1-m)}{4\alpha\beta} & \alpha, \beta \leq \frac{1}{2} \\ \frac{1-4\alpha(1-\mu)(1-\beta)}{4\alpha} & \alpha \leq \frac{1}{2} < \beta \\ 1-\alpha-(1-\mu)(1-\beta) & \frac{1}{2} < \alpha, \beta \end{cases} \tag{3.8}$$

To find c^*, we can now condition on the values of $w_2(x_\alpha)$ and $w_2(x_\beta)$.

Case 1. If $w_2(x_\alpha) = C_4 e^{-x_\alpha} > \alpha$, then $2c^*$ lies on the third piece of (3.3). Hence the mean wave speed is given by $c^* = \frac{1}{2}\ln(\frac{C_4}{\alpha})$.

Case 2. If $w_2(x_\alpha) = C_4 e^{-x_\alpha} \leq \alpha$ and $w_2(x_\beta) = \mu + C_1 e^{x_\beta} \geq \alpha$, then we solve the equation

$$1 - C_2 e^{2c^*} - C_3 e^{-2c^*} = \alpha$$

Multiplying through by e^{2c^*} yields a quadratic in e^{2c^*}:

$$C_2 e^{4c^*} + (a-1)e^{2c^*} + C_3 = 0$$

Using the quadratic formula, we get two solutions to this equation. To determine which is correct, note that $w_2'(2c^*)$ must be negative. Since C_2, C_3 are negative, $w_2(x)$ is concave down on $[x_\beta, x_\alpha]$, thus w_2 is increasing through the first solution and decreasing through the second. Clearly we must take the greater solution. Thus,

$$c^* = \frac{1}{2}\ln\left(\frac{1-\alpha+\sqrt{(1-\alpha)^2 - 4C_2C_3}}{2C_2}\right)$$

Case 3. If $w_2(x_\beta) = \mu + C_1 e^{x_\beta} < \alpha$, we have

$$\mu + C_1 e^{2c^*} = \alpha$$

implies

$$c^* = \frac{1}{2}\ln\frac{\alpha-\mu}{C_1}$$

Our general formula is thus

$$c^* = \begin{cases} \frac{1}{2}\ln\left(\frac{C_4}{\alpha}\right) & \alpha < C_4 e^{-x_\alpha} \\ \frac{1}{2}\ln\left(\frac{1-\alpha+\sqrt{(1-\alpha)^2-4C_2C_3}}{2C_2}\right) & C_4 e^{-x_\alpha} < \alpha < \mu + C_1 e^{x_\beta} \\ \frac{1}{2}\ln\left(\frac{\alpha-\mu}{C_1}\right) & \alpha > \mu + C_1 e^{x_\beta} \end{cases} \tag{3.9}$$

We can write this formula more explicitly depending on the signs of $\alpha - \frac{1}{2}$ and $\beta - \frac{1}{2}$ respectively.

Case 1. $\alpha \leq \frac{1}{2}$, $\beta \leq \frac{1}{2}$.

$$w_2(x) = \begin{cases} \mu + (\beta(1-\mu) - \alpha)e^x & x < -\ln(2\beta) \\ 1 - \alpha e^x - \frac{1-\mu}{4\beta}e^{-x} & -\ln(2\beta) < x < -\ln(2\alpha) \\ \frac{\beta-\alpha(1-m)}{4\alpha\beta}e^{-x} & x > -\ln(2\alpha) \end{cases} \tag{3.10}$$

We have $w_2(x_\alpha) = \frac{\beta-\alpha(1-\mu)}{2\beta}$ and $w_2(x_\beta) = \mu + \frac{\beta(1-\mu)-\alpha}{2\beta}$. Thus,

$$c^* = \begin{cases} \frac{1}{2}\ln\left(\frac{\beta-\alpha(1-\mu)}{4\alpha^2\beta}\right) & \alpha < \frac{\beta-\alpha(1-\mu)}{2\beta} \\ \frac{1}{2}\ln\left(\frac{1-\alpha+\sqrt{(1-\alpha)^2-\frac{\alpha(1-\mu)}{\beta}}}{2\alpha}\right) & \frac{\beta-\alpha(1-\mu)}{2\beta} \leq \alpha \leq \frac{\beta(1+\mu)-\alpha}{2\beta} \\ \frac{1}{2}\ln\left(\frac{\alpha-\mu}{\beta(1-\mu)-\alpha}\right) & \alpha > \frac{\beta(1+\mu)-\alpha}{2\beta} \end{cases} \tag{3.11}$$

Case 2. $\alpha \leq \frac{1}{2}$, $\beta > \frac{1}{2}$.

$$w_2(x) = \begin{cases} \mu + \frac{1-\mu-4\alpha(1-\beta)}{4(1-\beta)}e^x & x < \ln(2-2\beta) \\ 1 - \alpha e^x - (1-\mu)(1-\beta)e^{-x} & \ln(2-2\beta) < x < -\ln(2\alpha) \\ \frac{1-4\alpha(1-\mu)(1-\beta)}{4\alpha}e^{-x} & x > -\ln(2\alpha) \end{cases} \tag{3.12}$$

We have $w_2(x_\alpha) = \frac{1-4\alpha(1-\mu)(1-\beta)}{2}$ and $w_2(x_\beta) = \frac{1+\mu-4\alpha(1-\beta)}{2}$. Thus,

$$c^* = \begin{cases} \frac{1}{2}\ln\left(\frac{1-4\alpha(1-\mu)(1-\beta)}{4\alpha^2}\right) & a < \frac{1-4\alpha(1-\mu)(1-\beta)}{2} \\ \frac{1}{2}\ln\left(\frac{1-\alpha+\sqrt{(1-\alpha)^2-4\alpha(1-\mu)(1-\beta)}}{2\alpha}\right) & \frac{1-4\alpha(1-\mu)(1-\beta)}{2} \leq \alpha \leq \frac{1+\mu-4\alpha(1-\beta)}{2} \\ \frac{1}{2}\ln\left(\frac{4(\alpha-\mu)(1-\beta)}{1-\mu-4\alpha(1-\beta)}\right) & \alpha > \frac{1+\mu-4\alpha(1-\beta)}{2} \end{cases} \tag{3.13}$$

Case 3. $\alpha > \frac{1}{2}$, $\beta > \frac{1}{2}$.

$$w_2(x) = \begin{cases} \mu - \frac{1-\beta+\mu(1-\alpha)}{4(1-\alpha)(1-\beta)} e^x & x < \ln(2-2\beta) \\ 1 - \frac{1}{4(1-\alpha)} e^x - (1-\mu)(1-\beta)e^{-x} & \ln(2-2\beta) < x < \ln(2-2\alpha) \\ (1-\alpha-(1-\mu)(1-\beta))e^{-x} & x > \ln(2-2\alpha) \end{cases} \tag{3.14}$$

Thus, $w_2(x_\alpha) = \frac{1-\alpha-(1-\mu)(1-\beta)}{2(1-\alpha)}$ and $w_2(x_\beta) = \mu - \frac{1-\beta+\mu(1-\alpha)}{2(1-\alpha)}$

$$c^* = \begin{cases} \frac{1}{2}\ln\left(\frac{1-\alpha-(1-\mu)(1-\beta)}{\alpha}\right) & \alpha < \frac{1-\alpha-(1-\mu)(1-\beta)}{2(1-\alpha)} \\ \frac{1}{2}\ln\left(2(1-\alpha)\left[1-\alpha+\sqrt{\frac{(1-\alpha)^3-(1-\mu)(1-\beta)}{1-\alpha}}\right]\right) & \frac{1-\alpha-(1-\mu)(1-\beta)}{2(1-\alpha)} \le \alpha \le \frac{\beta-1+\mu(1-\alpha)}{2(1-\alpha)} \\ \frac{1}{2}\ln\left(\frac{4(\mu-\alpha)(1-\alpha)(1-\beta)}{1-\beta+\mu(1-\alpha)}\right) & \alpha > \frac{\beta-1+\mu(1-\alpha)}{2(1-\alpha)} \end{cases} \tag{3.15}$$

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

$$w_1(x) = \Phi(-x) \tag{3.16}$$

and

$$w_2(x) = \mu - \Phi(x - \Phi^{-1}(\alpha)) + (1-\mu)\Phi(x - \Phi^{-1}(\beta)) \tag{3.17}$$

w_2 has a unique global maximum at $x^* = \frac{x_\alpha + x_\beta}{2} + \frac{1}{x_\alpha - x_\beta}\ln(1-\mu)$. Thus, by Theorem 2.4, w_1 and w_2 are a periodic traveling wave solution if $w_2(x^*) \le \beta$.

Example 3.3. Consider the uniform dispersal kernel given by

$$k(x) = \begin{cases} \frac{1}{2} & |x| \le 1 \\ 0 & |x| > 1 \end{cases} \tag{3.18}$$

Then w_1 is given by

$$w_1(x) = \begin{cases} 1, & x \in (-\infty, -1), \\ \frac{1}{2} - \frac{1}{2}x, & x \in [-1, 1], \\ 0, & x \in (1, \infty), \end{cases} \tag{3.19}$$

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

$$w_2(x) = \begin{cases} m, & x \in (-\infty, \beta - 1), \\ \frac{1-m}{2}x + m + b - mb, & x \in [\beta - 1, \alpha - 1), \\ -\frac{m}{2}x + m + b - mb - a, & x \in [\alpha - 1, \beta + 1), \\ -\frac{1}{2}x - a + 1, & x \in [\beta + 1, \alpha + 1], \\ 0, & x \in (\alpha + 1, \infty). \end{cases} \tag{3.20}$$

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 2.5, the pair w_1 and w_2 are a solution to equation (2.9) if $m - a < m(b - a)$.

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

$$c^* = \begin{cases} 1 - 2a & \text{if } a \le b/2, \\ 1 - b + \frac{b-2a}{m} & \text{if } a > b/2. \end{cases} \tag{3.21}$$

Remark 3.4. $w_1(x)$ is positive for $x < 1$ and zero for $x \ge 1$, and $w_2(x)$ is positive for $x < 2 - 2a$ and zero for $x \ge 2 - 2a$. 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 $a \le b/2$, 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 **??**.

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 $R_1 = \{(a, b) \in R : a \le b/2\}$ 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

Proof of Proposition 2.1. Let $u(x)$ be non-negative, continuous, and bounded.

(i.) For $t \in \mathbb{R}$, let T^t denote the translation operator defined $T^t[u](x) = u(x+t)$. Then,

$$\begin{aligned} Q[T^t[u]](x) &= \int_{-\infty}^{\infty} k(x-y) g(T^t[u](y))\, dy \\ &= \int_{-\infty}^{\infty} k(x-y) g(u(y+t))\, dy \end{aligned} \tag{A.1}$$

Let $z = y + t$.

$$\begin{aligned} Q[T^t[u]](x) &= \int_{-\infty}^{\infty} k(x-z+t) g(u(z))\, dz \\ &= Q[u](x+t) \\ &= T^t[Q[u]](x) \end{aligned} \tag{A.2}$$

(ii.) Suppose $\lim_{x\to\infty} u(x) = \ell$.

□

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

Proof. let $f = f_{m,y}$ be the scalar function of x with two parameters $y \in \mathbb{R}$ and $\mu \in (0,1)$ defined by

$$f(x) = f_{m,y}(x) = \frac{1}{2} e^{-|x|} - \frac{\mu}{2} e^{-|x-y|}$$

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

Under this assumption, f is strictly increasing on $(-\infty, 0)$, and strictly decreasing on $(0, y)$. The behavior on (y, ∞) is determined by the sign of $e^{-y} - m$. There are three cases:

1. if $y < \ln \frac{1}{m}$, then f is decreasing on $(0, \infty)$, hence has no zero-crossings;
2. if $y > \ln \frac{1}{m}$, then f has a unique zero-crossing at $x = \frac{1}{2}(y - \ln(m))$;
3. if $y = \ln \frac{1}{m}$, then f vanishes on (y, ∞), 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 $C_1 \leq 0$, or if $C_1 > 0$ and $w_2 \left(\ln \sqrt{\frac{C_3}{C_2}} \right) \leq b$.*

Proof. We can proceed in cases. If $C_1 \leq 0$, 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:

$$\left.\frac{dw_2}{dx}\right|_{\beta<x<\alpha} = C_3 e^{-x} - C_2 e^{x}$$

Setting this expression equal to zero and multiplying by e^x, we obtain $C_3 - C_2 e^{2x} = 0$, 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 $y \in \mathbb{R}$ and $\mu \in (0,1)$. Then

$$\begin{aligned} k(x) - \mu k(x-y) &= \frac{1}{\sqrt{2\pi}}\left(e^{-\frac{x^2}{2}} - \mu e^{-\frac{-(x-y)^2}{2}}\right) \\ &= \frac{1}{\sqrt{2\pi}} e^{-\frac{x^2}{2}}\left(1 - \mu e^{\frac{2xy-y^2}{2}}\right) \end{aligned} \tag{A.3}$$

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

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

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

□