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

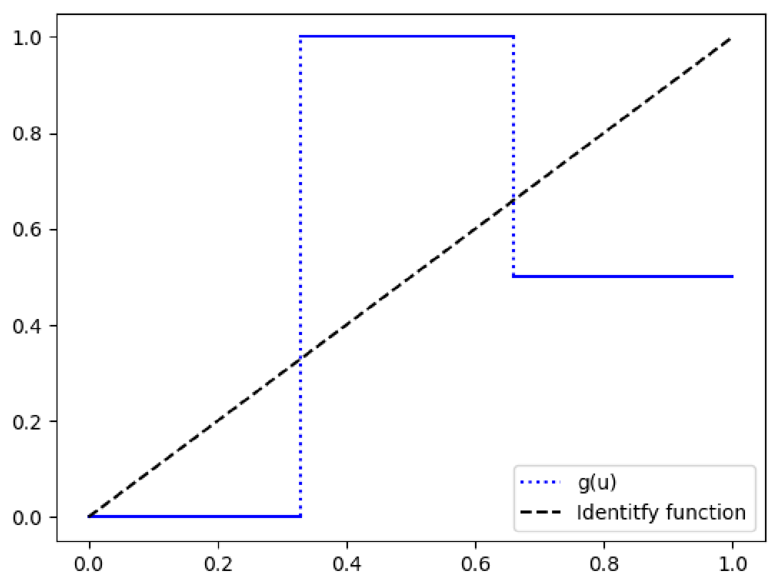
$$u_{n+1}(x) = Q[u_n](x) := (k * (g \circ u_n))(x) = \int_{-\infty}^{\infty} k(x-y)\, g\big(u_n(y)\big)\, \mathrm{d}y, \tag{1.1}$$

where

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

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

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

Theorem 2.1. *If $||w_2||_\infty \le b$, then equation (1.1) has a periodic traveling wave solution given by*

$$u_n(x) = \begin{cases} w_1(x - nc^*) & n \text{ even} \\ w_2(x - nc^* + c^*) & n \text{ odd} \end{cases} \tag{2.4}$$

for all $n \ge 0$.

Lemma 2.2. *If* $||w_2||_\infty \leq b$*, then* w_1 *and* w_2 *satisfy*

$$Q[w_1](x) = w_2(x) \tag{2.5}$$

and

$$Q[w_2](x) = w_1(x - 2c^*) \tag{2.6}$$

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

$$c^* = \frac{1}{2} \sup\{x \in \mathbb{R} \mid w_2(x) \geq a\} \tag{2.7}$$

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

$$g(w_1(x)) = \begin{cases} n_1 & x < x_b \\ n_2 & x_b \leq x \leq x_a \\ 0 & x > x_a \end{cases} \tag{2.8}$$

Applying the integro-difference operator yields

$$Q[w_1](x) = n_1 \int_{-\infty}^{x_b} k(x-y)\, dy + n_2 \int_{x_b}^{x_a} k(x-y)\, dy \tag{2.9}$$

Using a substitution on both integrals yields equation (2.2), proving the first part of the lemma.

To prove the second half, we differentiate w_2 with respect to x:

$$\frac{dw_2}{dx} = n_2 k(x - x_a) - (n_2 - n_1) k(x - x_b) \tag{2.10}$$

A transformation of coordinates shows that equation (2.10) is proportional to $k(x) - \frac{n_2 - n_1}{n_2} k(x + x_a - x_b)$; by hypothesis (H4), $\frac{dw_2}{dx}$ has at most one real zero.

It can be shown by cases that w_2 is either monotonically decreasing or has a unique turning point $x_0 \in \mathbb{R}$. In both cases, the curve $u = w_2(x)$ crosses the horizontal line $u = a$ exactly once at the point $x = 2c^*$, where c^* is defined by (2.7). In the latter case, we make the additional assumption that $||w_2||_\infty \leq b$. In all the cases,

$$g(w_2(x)) = \begin{cases} 1 & x \leq 2c^* \\ 0 & x > 2c^* \end{cases} \tag{2.11}$$

Thus,

$$
\begin{aligned}
Q[w_2](x) &= \int_{-\infty}^{\infty} k(x-y)g(w_2(y))\,dy \\
&= \int_{-\infty}^{2c^*} k(x-y)\,dy \\
&= \int_{x-2c^*}^{\infty} k(y)\,dy \\
&= w_1(x-2c^*).
\end{aligned}
\tag{2.12}
$$

□

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 which spreads in space with a mean speed of c^* and alternates in shape every two time steps.

Proof of Theorem 2.1. It suffices to show that equation (2.4) 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

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

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

$$
\begin{aligned}
Q[u_n](x) &= Q[w_2](x-nc^*+c^*) \\
&= w_1(x-nc^*-c^*) \\
&= u_{n+1}(x)
\end{aligned}
\tag{2.14}
$$

by Lemma 2.2. □

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 $c_n = \xi_n - \xi_{n-1}$.

We now introduce an additional hypothesis for the spread of solutions with compactly supported initial condition.

Hypothesis 2. For sufficiently large r_b, with $r_a > r_b > 0$ and $\lambda \in (0,1)$, the equation

$$k(x+r_a) - k(x-r_a) - \lambda k(x+r_b) + \lambda k(x-r_b)$$

has at most 3 solutions.

Theorem 2.3. *If* $\sup_{x\in\mathbb{R}} w_2(x) \le b$*, then for all* $\epsilon > 0$*, the sequence 2.4 satisfies*

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

and

$$\lim_{n\to\infty} \inf_{x<2n(c^*-\epsilon)} u_{2n+1}(x) = n_1 \tag{2.16}$$

and

$$\lim_{n\to\infty} \sup_{x>n(c^*+\epsilon)} u_n(x) = 0. \tag{2.17}$$

Proof.

$$\begin{aligned} \lim_{n\to\infty} \inf_{x<2n(c^*-\epsilon)} u_{2n}(x) &= \lim_{n\to\infty} \inf_{x<2n(c^*-\epsilon)} w_1(x-2nc^*) \\ &= \lim_{n\to\infty} \inf_{x<-2n\epsilon} w_1(x) \\ &= \liminf_{x\to-\infty} w_1(x) \\ &= 1. \end{aligned} \tag{2.18}$$

$$\begin{aligned} \lim_{n\to\infty} \inf_{x<2n(c^*-\epsilon)} u_{2n+1}(x) &= \lim_{n\to\infty} \inf_{x<2n(c^*-\epsilon)} w_2(x-2nc^*) \\ &= \lim_{n\to\infty} \inf_{x<-2n\epsilon} w_2(x) \\ &= \liminf_{x\to-\infty} w_2(x) \\ &= n_1. \end{aligned} \tag{2.19}$$

$$\begin{aligned} \lim_{n\to\infty} \sup_{x>n(c^*+\epsilon)} u_n(x) &\le \lim_{n\to\infty} \sup_{x>n(c^*+\epsilon)} \sup\{w_1(x-nc^*), w_2(x-nc^*)\} \\ &= \lim_{n\to\infty} \sup_{x>n\epsilon} \sup\{w_1(x), w_2(x)\} \\ &= \limsup_{x\to\infty} \sup\{w_1(x), w_2(x)\} \\ &= \sup\{\limsup_{x\to\infty} w_1(x), \limsup_{x\to\infty} w_2(x)\} \\ &= 0. \end{aligned} \tag{2.20}$$

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

2.1 Spreading solutions

Let $u_n(x)$ be a sequence of continuous functions. For every $c \in \mathbb{R}$, define the sequence $a_n(x,c)$ by

$$a_n(x,c) = u_n(x+nc)$$

Now, define

$$a(x,c) = \limsup_{n\to\infty} a_n(x,c).$$

Note that since a_n is bounded, this quantity must be finite.

We say the rightware spreading speed of u_0 is defined by

$$c_+^* = \inf\{c \in \mathbb{R} \mid \lim_{x\to\infty} a(x,c) = 0\}$$

Theorem 2.4. *Let $w(x) = \int_x^\infty k(y)\,dy$. Define*

$$c^* = \frac{1}{2}\sup\{x \in \mathbb{R} | Q[w](x) \geq a\}$$

Let $w_1(x) = w(x)$ and $w_2(x) = Q[w](x+c^*)$. Define the sequence

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

Then $u_n(x)$ satisfies $u_{n+1}(x) = Q[u_n](x)$ for $n \geq 0$ and has a rightward spreading speed of c^*.

Proof. We have

$$a_n(x,c) = \begin{cases} w_1(x + n(c - c^*)) & n \text{ even} \\ w_2(x + n(c - c^*)) & n \text{ odd} \end{cases}$$

Thus,

$$\begin{aligned} a(x,c) &= \limsup_{n\to\infty} a_n(x,c) \\ &= \limsup_{n\to\infty} \max\{w_1(x + n(c-c^*)), w_2(x + n(c-c^*))\} \\ &= \begin{cases} 1 & c < c^* \\ \max\{w_1(x), w_2(x)\} & c = c^* \\ 0 & c > c^* \end{cases} \end{aligned}$$

Taking the limit as $x \to \infty$,

$$a(\infty, c) = \begin{cases} 1 & c < c^* \\ 0 & c \geq c^* \end{cases}$$

□

For a given $r \geq 0$, let $\phi(x,r) = \chi_{[-r,r]}(x)$, where χ is the indicator function, or simply ϕ_r for brevity. Define the operator $R[u] = g\left(Q[k * u](x)\right)$.

$$R[u](x) = g\left(\int k(x-y) g\left(\int k(y-z)u(z)\,dz\right)\,dy\right) \tag{2.21}$$

Lemma 2.5. *Let $u_n(x)$ be a sequence of functions satisfying $u_{n+1}(x) = Q[u_n](x)$ for all $n \geq 0$ with initial condition $u_0 \in C(\mathbb{R}; [0,1])$. Then $u_{2n}(x) = (k * R^{n-1}[g \circ u])(x)$ for all $n \geq 1$.*

Lemma 2.6. *For sufficiently large $r \geq 0$, we have $R[\phi_r] = \phi_{r+\delta(r)}$, where $\delta(r)$ is a scalar function of r. It can be expressed as*

$$\delta(r) = \int R[\phi_r](x)\,dx$$

Lemma 2.7. $\lim_{r\to\infty} \delta(r) = 2c^*$

Consider the sequence $A_n(x,r) = R^n[\phi_r](x)$.

Lemma 2.8. *If r is sufficiently large, then $A_1(x,r) = R[\phi_r](x) = \phi_{r+\delta(r)}(x)$. Similarly, $A_2(x,r) = \phi_{r+\delta(r)+\delta(r+\delta(r))}$.*

Consider the sequence ξ_n defined by $\xi_0 = r_0$ and $\xi_{n+1} = \xi_n + \delta(\xi_n)$. Then $\xi_n = 2c^* n + O(1)$.

Consider the operator $R[u] = g \circ (k * u)$. Observer that $k * R[g \circ u] = Q^2[u]$; equivalently $g \circ Q[k * u] = R^2[u]$.

Or just define dimensionless parameters $a = A/N_2$, $b = B/N_2$, and $m = N_1/N_2$.

For each $r \geq 0$, let $\phi_r = \chi_{[-r,r]}$, where χ is the indicator function.

Lemma 2.9. *If r is sufficiently large, then $R^2[\phi_r] = \phi_s$, where $s = s(r)$ is a function of r, and $\lim_{r\to\infty}(s - r) = 2c^*$.*

Proof. We have

$$(k * \phi_r)(x) = K(x+r) - K(x-r)$$

Note that $(k*\phi_r)(0) = 2K(r) - 1$, assuming a symmetryic dispersal kernel. Thus, assuming $\frac{d}{dx}(k * \phi_r)$ has at most one zero, a lower bound of $r \geq K^{-1}\left(\frac{b+1}{2}\right)$ guarantees

$$R[\phi_r] = \begin{cases} n_1 & |x| < r_1 \\ n_2 & r_1 \leq |x| \leq r_2 \\ 0 & |x| > r_2 \end{cases}$$

$\square$

for some $r_2 > r_1 \geq 0$.

Applying the convolution operator to this expression yields

$$k * R[\phi_r](x) = n_2 \int_{-r_2}^{r_2} k(x-y)\,dy - (n_2 - n_1) \int_{-r_1}^{r_1} k(x-y)\,dy$$

$$= n_2 \left[K(x + r_2) - K(x - r_2)\right] - (n_2 - n_1) \left[K(x + r_1) - K(x - r_1)\right]$$

Taking the derivative, we find

$$\frac{d}{dx}\left[k * R[\phi_r]\right] = n_2 \left[k(x + r_2) - k(x - r_2)\right] - (n_2 - n_1) \left[k(x + r_1) - k(x - r_1)\right]$$

We now require the following hypothesis on the disperal kernel:

(H5) For all $r_2 > r_1 > 0$ and $\lambda \in (0, 1)$, the equation

$$k(x + r_2) - k(x - r_2) - \lambda k(x + r_1) + \lambda k(x - r_1) = 0$$

has at most 3 solutions.

If hypothesis (H5) holds, we can then deduce that $k * R[\phi_r]$ has at most 3 turning points. This leaves only two cases: either $k * R[\phi_r]$ has a single turning point at $x = 0$, or has 3 turning points, one at $x = 0$, and two diametrically opposed turning points $+t$ and $-t$. In both cases, there is a unique $r_3 > 0$ satisfying $(k * R[\phi_r])(x) \geq a$ for $|x| \leq r_3$ and $(k * R[\phi_r])(x) < a$ otherwise. If $r_3 < r$, then the conclusion does not follow. But if $r_2 \geq r$, then the

$$\delta(r) = ||Q[\chi_{[-r,r]}]||_1 = \int_{-\infty}^{\infty} Q[\chi_{[-r,r]}](x)\,dx$$

Lemma 2.10. $\lim_{r\to\infty}(\delta(r) - r) = 4c^*$

$$\lim_{r\to\infty} \left(\left(\int_{-\infty}^{\infty} Q^2[\chi_{[-r,r]}(x)\,dx \right) - r \right) = 4c^* \tag{2.22}$$

In this section, we consider how the periodic traveling wave solutions in the preceding results correspond to solutions with a compactly supported initial population density. For simplicity, we restrict our attention to initial conditions where the maximum population value does not exceed the overcompensation threshold.

Let $\chi_{[-r,r]}$ denote the indicator function on $[-r, r]$. Suppose u_0 is a continuous function with compact support, and suppose u_0 satisfies $a \leq u_0(x) \leq b$ for $|x| \leq r$ and $u_0(x) < a$ otherwise. It follows that

$$g(u_0(x)) = \mathbf{1}_{[-r_0,r_0]}(x)$$

We have

$$Q[u_0](x) = (k * (g \circ u_0))(x) = K(x + r_0) - K(x - r_0)$$

Assuming r_0 is large enough so that $Q[u_0](x) = 2K(r_0) - 1 \geq b$, it follows that

$$g(Q[u_0](x)) = \begin{cases} n_1 & |x| < r_1 \\ n_2 & r_1 \leq |x| \leq r_2 \\ 0 & |x| > r_2 \end{cases}$$

It follows that

$$Q^2[u_0](x) = n_2 \int_{-r_2}^{r_2} k(x-y)\,dy - (n_2 - n_1) \int_{-r_1}^{r_1} k(x-y)\,dy$$

$$= n_2 K(x + r_2) - n_2 K(x - r_2) - (n_2 - n_1)K(x + r_1) + (n_2 - n_1)K(x - r_1)$$

Taking the derivative, we find

$$\frac{d}{dx} Q^2[u_0](x) = n_2 k(x + r_2) - n_2 k(x - r_2) - (n_2 - n_1)k(x + r_1) + (n_2 - n_1)k(x - r_1)$$

We now require the following hypothesis on the disperal kernel:
(H5) For all $r_2 > r_1 > 0$ and $\lambda \in (0, 1)$, the equation

$$k(x + r_2) - k(x - r_2) - \lambda k(x + r_1) + \lambda k(x - r_1) = 0$$

has at most 3 solutions.

If hypothesis (H5) holds, we can then deduce that $\frac{d}{dx} Q^2[u_0]$ has at most 3 zero-crossings, hence, $Q^2[u_0]$ has at most 3 turning points. This leaves only two cases: either $Q^2[u_0]$ has a single turning point at $x = 0$, or $Q^2[u_0]$ has 3 turning points, one at $x = 0$, and two diametrically opposed turning points $+t$ and $-t$. In both cases, there is a unique $r_2 > 0$ satisfying $Q^2[u_0](x) \geq a$ for $|x| \leq r_2$ and $Q^2[u_0](x) < a$ otherwise. If $r_2 < r$, then the conclusion does not follow. But if $r_2 \geq r$, then the

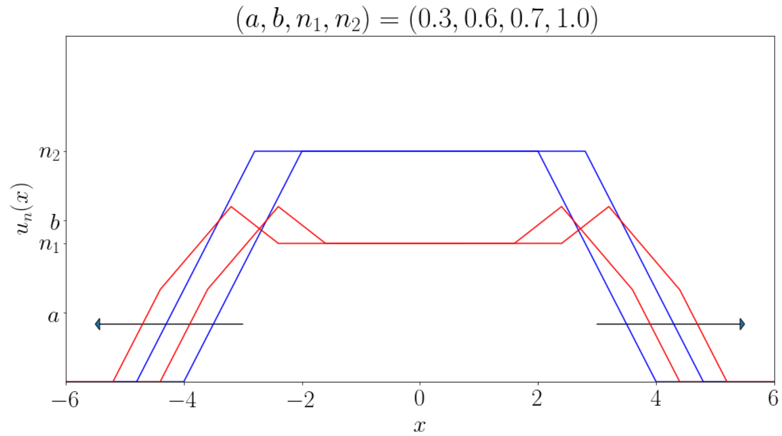
The next theorem concerns the spreading behavior of solutions to the IDE (1.1) with compactly supported initial data.

Remark 2.11. 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 Blossoming solution

In addition to the behavior mentioned earlier, we noticed the phenomena of blossoming solution. Whenever

Figure 2: 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.



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 is given by

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

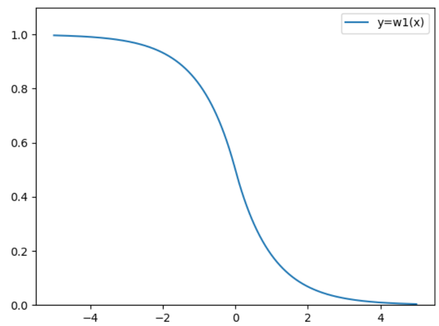
The reader can easily verify that the Laplace kernel satisfies hypotheses (H1) - (H3); the proof of (H4) is left in the appendix A.1.

The periodic traveling wave profiles are given by

$$w_1(x) = \begin{cases} n_2 - \frac{1}{2} n_2 e^{x} & x \leq 0 \\ \frac{1}{2} n_2 e^{-x} & x > 0 \end{cases} \tag{3.2}$$

and

$$w_2(x) = \begin{cases} n_1 + \left(\frac{1}{2}(n_2 - n_1)e^{-x_b} - \frac{1}{2} n_2 e^{-x_a}\right) e^{x} & x < x_b \\ n_2 - \frac{1}{2} n_2 e^{-x_a} e^{x} - \frac{1}{2}(n_2 - n_1) e^{x_b} e^{-x} & x_b \leq x \leq x_a \\ \left(\frac{1}{2} n_2 e^{x_a} - \frac{1}{2} n_2 (n_2 - n_1) e^{x_b}\right) e^{-x} & x_a < x \end{cases} \tag{3.3}$$



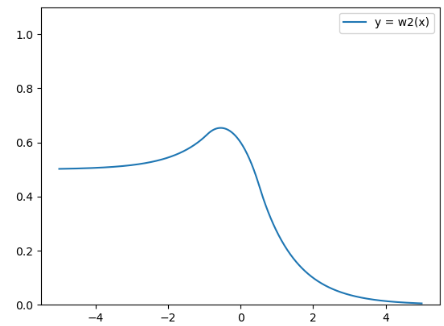


Figure 3: The shape of the two periodic traveling wave profiles with Laplace dispersal kernel and growth parameters $a = 0.3$, $n_1 = 0.5$, and $b = 0.8$.

with $x_a = F(a)$, $x_b = F(b)$, and

$$F(p) = \begin{cases} -\ln(2p) & p \le \frac{1}{2} \\ \ln(2-2p) & p > \frac{1}{2} \end{cases} \tag{3.4}$$

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

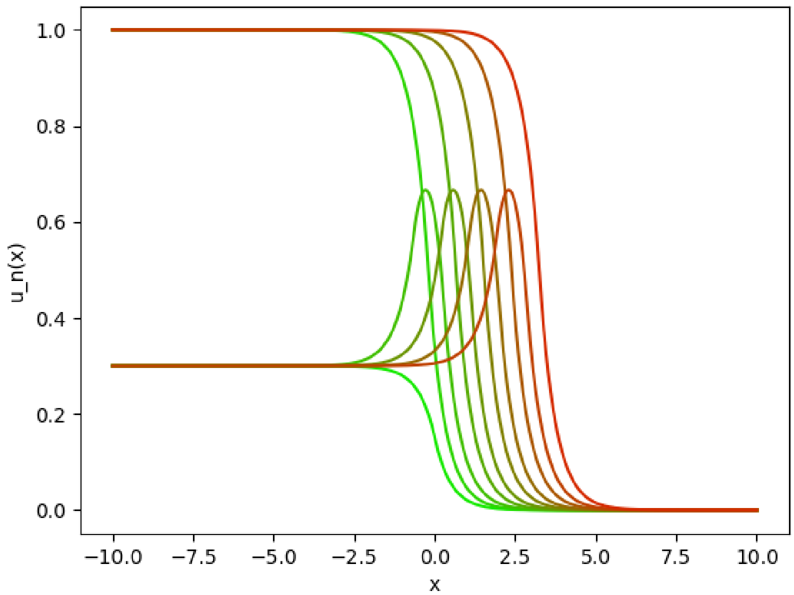
$$c^* = \begin{cases} \frac{1}{2}\log\left(\frac{1}{2a}n_2 e^{x_a} - \frac{1}{2a}(n_2-n_1)e^{x_b}\right) & a \le w_2(x_a) \\ \frac{1}{2}\log\left(\frac{1}{n_2}e^{-x_a}\left(n_1 - a + \sqrt{(n_1-a)^2 - n_2(n_2-n_1)e^{x_b-x_a}}\right)\right) & w_2(x_a) < a < w_2(x_b) \\ \frac{1}{2}\log\left(\frac{2(a-n_1)}{(n_2-n_1)\exp(-x_b) - n_2\exp(-x_a)}\right) & a \ge w_2(x_b) \end{cases} \tag{3.5}$$

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

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

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

Figure 4: 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.



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,

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

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

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

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 2.1, 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

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

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 (2.4) if $m - a < m(b - a)$.

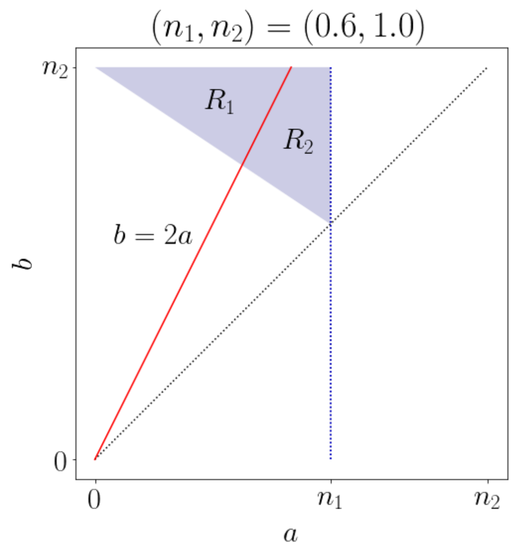
We can also explicitly calculate the speed of the wave given by

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

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 $(a, b) \in R_2$.

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.



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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 $C_1 \leq 0$, 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 $a \in \mathbb{R}$ 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. □

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

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

$\square$