Wave Speed and Critical Patch Size for Integro-Difference Equations with a Strong Allee Effect

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Abstract

Simplified conditions are given for the existence and positivity of wave speed for an integro-difference equation with a strong Allee effect and an unbounded habitat. The results are used to obtain the existence of a critical patch size for an equation with a bounded habitat. It is shown that if the wave speed is positive there exists a critical patch size such that for a habitat size above the critical patch size solutions can persist in space, and if the wave speed is negative solutions always approach zero. An analytical integral formula is developed to determine the critical patch size when the Laplace dispersal kernel is used, and this formula shows existence of multiple equilibrium solutions. Numerical simulations are provided to demonstrate connections among the wave speed, critical patch size, and Allee threshold.

1 Introduction

In this paper, we are concerned with the spatial dynamics of populations governed by integro-difference equations in the form

$$u_{n+1}(x) = \int_{\Omega} k(x-y)g(u_n(y))dy, \tag{1.1}$$

where the function $u_n(x)$ represents the density of the population at point x at time n, $k(x)$ is the dispersal kernel, $g(u_n(x))$ describes the population growth at point x at time n, and Ω is the habitat for the population to grow and disperse. Integro-difference equations describe a process in which individuals first undergo reproduction and then offspring redistribute before reproduction occurs once again. They have been used to predict changes in gene frequency [19, 20, 21, 27, 32], and have been applied to ecological problems [5, 6, 7, 9, 10, 11, 12].

Allee effects are a density-dependent phenomenon in which per capita population birth rates decline at low densities. A strong Allee effect is an Allee effect with a critical population density. Allee effects may occur via various mechanisms [1, 2, 3, 4, 25]. Lui [21] showed that for model (1.1) with $\Omega = (-\infty, \infty)$, when $g(u)$ exhibits a strong Allee effect, under certain conditions there is a spreading speed, which is the unique speed of traveling waves connecting zero and the carrying capacity. Wang et al. [31] gave conditions under which the wave speed is positive, negative or zero. When the spreading speed is positive, a population with an initial distribution above the Allee threshold on a sufficiently large interval expands its spatial range. The results from [21] and [31] have been widely used in the studies of biological invasions [4, 9, 13, 17, 22, 24, 28, 29]. The reader is refereed to the monograph by Lutscher [23] for a thorough review on the results for spreading dynamics of (1.1) with/without Allee effect.

The results obtained by Liu [21] and Wang et al. [31] are important in understanding spatial population dynamics with a strong Allee effect. However there are serious obstacles faced in applying them to specific models. In [21], it is assumed that $g'(a)$ with a the Allee threshold value is the maximum value of $g'(u)$. This may not be satisfied by a biologically meaningful growth function. In [31], it is required that for a traveling wave profile $w(x)$, all order derivatives $\frac{d^i g(w(x))}{dx^i}$, $i = 1, 2, ...$, are uniformly bounded. This in general is difficult to verify as the formula for $w(x)$ is unknown. In this paper, we remove these strong hypotheses, develop a set of simplified and easily verified hypotheses on $g(u)$ and $k(x)$ to establish spreading speeds and traveling waves, and show that the sign of wave speed can be determined without any restriction on $g(u)$ and $k(x)$ other than those needed to guarantee the existence of spreading speeds and traveling waves. We particularly demonstrate that the sign of wave speed depends on $g(u)$ only.

The investigations of species persistence in integro-difference models in the form of (1.1) with a bounded habitat $\Omega = [-l, l]$ have received much attention; see Chapter 3 in Lutscher [23] for a review. When there is no Allee affect, species persistence depends on the principal eigenvalue of the associated linearized integral operator, and if the principal eigenvalue value is greater than (less then) 1 then the species persists (dies out). The critical patch size is then determined by setting the equation for the principal eigenvalue value to 1. When there exists an Allee effect, an approach other than linearization is needed. Lutscher conducted a case study for (1.1) with a strong Allee effect, positive equilibrium, and Laplace kernel, and observed that even when there is almost no dispersal related loss from the habitat, the spatial model may not have a positive equilibrium (or critical patch size) (Section 4.5 in [23]), and that a positive equilibrium on a bounded domain can exist only if the spreading speed is positive (end of Section 6.4 in [23]).

In this paper, we rigorously establish the existence of a positive equilibrium for (1.1) with $\Omega = [-l, l]$. Particularly, we prove that if the traveling wave speed is positive there is a critical patch size l^* such that for $l > l^*$ there is a positive equilibrium, and if the wave speed is negative all the solutions approach zero and thus there is no positive equilibrium. The mathematical analysis makes use of properties of the traveling wave speed as well as certain limit processes. We give some general results about properties of equilibrium solutions and a lower bound for the critical patch size, and provide a theorem regarding bifurcations of critical patch size as the standard deviation of k varies. We also study the case of the Laplace kernel and develop an analytical integration formula for the critical patch size, and show that when the habitat size is above the critical patch size, there are multiple positive equilibrium solutions. Numerical simulations are provided to demonstrate connections among the wave speed, critical patch size, and Allee threshold when the Laplace kernel is used.

This paper is organized as follows. In the next section, hypotheses for (1.1) are provided and the comparison principle is given. The mathematical results regarding spreading speeds and traveling waves are presented in Section 3. Section 4 is about critical patch size. Section 5 presents the study for a Laplace kernel. Section 6 includes some concluding remarks and discussions.

2 The hypotheses

For convenience, we use Q as a shorthand, and define

$$Q[u](x) := \int_{\Omega} k(x-y)g(u(y))dy, \tag{2.2}$$

so that (1.1) can be written in the form

$$u_{n+1}(x) = Q[u_n](x).$$

We are interested in the case of $\Omega = \mathbb{R} = (-\infty, \infty)$ and the case of $\Omega = [-l, l]$ where l is a positive number. For the former case we study spreading speeds and traveling waves, and for the later case we investigate the critical patch size for persistence.

We make the following assumptions.

Hypotheses 2.1.

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). $B_1 = -\infty$ *or* $B_2 = \infty$ *is allowed so that* $k(x)$ *need not have compact support.*

ii. $k(x)$ *is continuous in* $\mathbb{R}$ *except possibly at* B_1, B_2 *where* $lim_{x \to B_1^+} k(x) = p_1$, $lim_{x \to B_2^-} k(x) = p_2$. *Also* $k(x)$ *may be written in the form*

$$k(x) = k_a(x) - p_1 \chi_{(-\infty, B_1]} - p_2 \chi_{[B_2, \infty)},$$

where $k_a(x)$ *is absolutely continuous and* χ_S *is the indicator function of the set* S.

iii. $\int_{\mathbb{R}} k(x)dx = 1$.

iv. $\int_{\mathbb{R}} e^{\mu x} k(x)dx$ *is finite for one positive* μ *and one negative* μ.

v. $g \in C^1[0, 1]$.

vi. $g(0) = 0,\ g(1) = 1$.

vii. *There exists a constant* $\alpha \in (0, 1)$ *such that* $g(u) < u$ *in* $(0, \alpha)$ *and* $g(u) > u$ *in* $(\alpha, 1)$.

viii. $g'(u) \geq 0$ *in* $[0, 1]$. *If*

$$\sigma_1 = \inf\{u : g(u) > 0\},\ \sigma_2 = \sup\{u : g(u) < 1\},$$

then $g'(u) > 0$ *in* (σ_1, σ_2).

ix. $g'(0) < 1,\ g'(\alpha) > 1,\ g'(1) < 1$.

Hypotheses 2.1 (i)-(iv) show that the dispersal kernel may or may not have compact support, and is absolutely continuous. They are satisfied by various dispersal kernels used in applications. Recall that a function $\psi(x)$ is absolutely continuous if $\psi'(x)$ exists almost everywhere and for all s and t and $\psi(s) - \psi(t) = \int_s^t \psi'(x)dx$. Hypotheses 2.1 (v)-(ix) indicate that the growth function is continuously differentiable and nondecreasing, and it has three equilibria $0, \alpha, 1$ with 0 and 1 asymptotically stable and α the Allee threshold value. Hypotheses 2.1 (viii) allows $g(u)$ to be zero on an interval $[0, \sigma_1]$ with $\sigma_1 > 0$ and $g(u)$ to be 1 on an interval $[1 - \sigma_2, 1]$ with $\sigma_2 > 0$.

Hypotheses 2.1 represent a subset of the hypotheses given in Liu [21]. We have dropped the hypothesis $g'(u) \leq g'(\alpha)$ for $u \in [0, 1]$, which is hypothesis (xi) in [21]. We have replaced the hypothesis that $\int_{\mathbb{R}} e^{\mu x} k(x)dx$ is finite for all real μ (hypothesis (iv) in [21]) by the weaker hypothesis (iv). Finally we have also dropped the hypotheses (v) and (xii) in [21], which were used to study asymptotic properties of traveling waves.

We finish this section with the following useful lemma.

Lemma 2.1. *Lemma 1 (Comparison principle) Assume that Hypotheses 2.1 hold. If* $u_n(x)$ *and* $v_n(x)$ *are two sequences of continuous and nonnegative functions with the properties* $v_{n+1}(x) \leq Q[v_n](x)$ *and* $u_{n+1}(x) \geq Q[u_n](x)$ *for all nonnegative* n *and* $0 \leq v_0(x) \leq u_0(x) \leq 1$, *then* $0 \leq v_n(x) \leq u_n(x) \leq 1$ *for all positive integer* n.

This lemma can be easily shown to be true by using the method of induction.

3 Spreading speeds and traveling waves

In this section we study spreading speeds and traveling waves for (1.1) with $\Omega = (-\infty, \infty)$. We first recall the framework developed in Lui [21]. Let $\phi(x)$ be a continuous nonincreasing function such that $\phi(-\infty) \in (\alpha, 1)$ and $\phi(x) = 0$ for $x \geq 0$. Define the sequence

$$a_{n+1}(c, x) = R_c[a_n](x) := \max\{\phi(x), Q[a_n](x + c)\}, \quad a_0(c, x) = \phi(x).$$

$a_n(c, x)$ is nondecreasing in n and x for each fixed c, and $a_n(c, x)$ increases to a limit function $a(c, x)$ as $n \to \infty$. Define

$$c_+^* = \sup\{c : a(c, \infty) = 1\}.$$

It was shown that c_+^* is independent of the choice of ϕ. c_+^* is the wave speed in the positive direction. c_+^* is a finite number or $c_+^* = \infty$. The wave speed in the negative direction c_-^* can be defined by starting with the function $\phi(x)$, $\phi(x)$ continuous and nondecreasing function, $\phi(\infty) \in (\alpha, 1)$ and $\phi(x) = 0$ for $x \leq 0$ and letting $\bar{a} = \phi$, $\bar{a}_{n+1} = R_c[\bar{a}_n]$. Then $\bar{a}_n(c, x)$ increases to a limit function $\bar{a}(c, x)$ and $c_-^* = \inf\{c : \bar{a}(c, -\infty) = 1\}$.

Let $m = \max_{u \in [0,1]} \frac{g(u)}{u}$. Clearly $m > 1$. Define $h(u) = mu$ in the internal $[0, 1/m]$ and $h(u) = 1$ in the interval $(1/m, 1]$. Let $H[u](x)$ be $Q[u](x)$ with $g(u)$ replaced by $h(u)$. It is easily seen $Q[u](x) \leq H[u](x)$ for $0 \leq u(x) \leq 1$. Consequently c_+^* is bounded above by $\inf_{\mu > 0} \frac{1}{\mu} \ln \{m\{\int_{\mathbb{R}} e^{\mu x} K(x) dx\}$, which is the rightward spreading speed of the operator H and which is a finite number under Hypotheses 2.1 (iv) (see Weinberger and Zhao [34]). Similarly c_-^* is also a finite number.

We have the following theorem.

Theorem 3.1. *Assume that Hypotheses 2.1 are satisfied. The following statements hold:*

i. Assume that $u_0(x)$ is piecewise continuous, $u_0(x) = 0$ for large x, $0 \leq u_0(x) \leq \theta < 1$ in $\mathbb{R}$ where θ is a constant. If u_n is defined by the recursion (1.1) then

$$\lim_{n \to \infty} \sup_{x \geq nc} u_n(x) = 0 \qquad \text{for every } c > c_+^*.$$

ii. Assume that $u_0(x)$ is piecewise continuous and $0 \leq u_0(x) \leq 1$. Let $c_-^* < c_1 < c_2 < c_+^*$. For any $\sigma > \alpha$, there exists a constant $r_\sigma > 0$ such that if $u_0(x) \geq \sigma$ on an interval of length equal to r_σ, then u_n defined by the recursion (1.1) satisfies

$$\lim_{n \to \infty} \min_{nc_1 \leq x \leq nc_2} u_n(x) = 1.$$

iii. There exists a nonincreasing traveling wave solution $u_n(x) = w(x - nc_+^*)$ of the operator Q such that $w(-\infty) = 1$ and $w(\infty) = 0$, and c_+^* is the only wave speed for which a nonincreasing traveling wave with values 1 at $-\infty$ and 0 at ∞ can exist.

Statements (i)-(iii) of Theorem 3.1 justify that c_+^* is the rightward spreading speed and c_+^* is the unique speed of nonincreasing traveling waves connecting 1 and 0. Statement (i) is Theorem 1 a$'$, statement (ii) is Theorem 1b, and statement (iii) is the combination of Theorem 5 and Corollary 1 in Lui [21] where additional hypotheses are needed. Results similar to Theorem 3 for c_-^* also hold. Particularly, $-c_-^*$ is the leftward spreading speed and $-c_-^*$ is the unique speed of nondecreasing traveling waves connecting 1 and 0.

Proof. As shown in the proof of Theorem 1b of Lui [21], the proof of Theorem 6.2 of Weinberger [33] works to prove statement (ii). In [21], statement (iii) was proven using Proposition 4 in the paper that involves the hypothesis $g'(u) \leq g'(\alpha)$ for $u \in [0,1]$. One can see that the proof of the proposition given in [21] is still valid if $g'(\alpha)$ is replaced by the maximum value of $g'(u)$ on $[0,1]$, so that $g'(u) \leq g'(\alpha)$ in $[0,1]$ is not needed. Finally for $u_0(x)$ given in statement (i) and for a nonincreasing traveling wave $w(x - nc_+^*)$ with $w(-\infty) = 1$ and $w(\infty) = 0$, there is a real number s such that $u_0(x) \leq w(x - s)$. Lemma 2.1, the comparison principle, shows $u_n(x) \leq w(x - s - nc_+^*)$ for all n and x. For any $c > c_+^*$ and $x \geq nc$,

$$\sup_{x \geq nc} u_n(x) \leq w(n(c - c_+^*) - s).$$

This and $\lim_{n\to\infty} w(n(c - c_+^*) - s) = 0$ lead to statement (i). The proof is complete. □

We now study the sign of c_+^* when $k(x)$ is even. In this case $c_+^* = -c_-^*$.

Theorem 3.2. *Assume that Hypotheses 2.1 are satisfied and $k(x)$ is even. The following statements hold:*

i. $c_+^* > 0$ *if and only if* $\int_0^1 [g(u) - u]du > 0$.

ii. $c_+^* = 0$ *if and only if* $\int_0^1 [g(u) - u]du = 0$.

iii. $c_+^* < 0$ *if and only if* $\int_0^1 [g(u) - u]du < 0$.

Proof. Let $w(x)$ be a nonincreasing traveling wave profile with speed c_+^* such that $w(-\infty) = 1$ and $w(\infty) = 0$. $w(x)$ satisfies

$$w(x - c_+^*) = \int_{\mathbb{R}} k(x - y)g(w(y))dy = \int_{\mathbb{R}} k(y)g(w(x - y))dy. \tag{3.1}$$

Lemma 5 in Lui [19] and its corollary imply that $w(x)$ is in $C^1(\mathbb{R})$ and

$$w'(x - c_+^*) = \int_{\mathbb{R}} k(y)g'(w(x - y))w'(x - y)dy.$$

Since $w(x)$ is nonincreasing, $w'(x) \leq 0$. As in the proof of Theorem 2.1 in Wang et al. [31], we write $g(w(x - y))$ as the sum of an odd and an even function in y

$$g(w(x - y)) = g_o(x, y) + g_e(x, z),$$

where

$$g_o(x, y) = \frac{1}{2}[g(w(x - y) - g(w(x + y))],$$

and

$$g_e(x, y) = \frac{1}{2}[g(w(x - y) + g(w(x + y))].$$

We therefore have

$$\int_{\mathbb{R}} k(y)g(w(x - y))dy = \int_{\mathbb{R}} k(y)g_o(x, y)dy + \int_{\mathbb{R}} k(y)g_e(x, y)dy. \tag{3.2}$$

Observe that the right-hand side of (3.2) is well defined as both g_0 and g_e are bounded functions. Since $k(y)g_o(x,y)$ is odd in y, $\int_{\mathbb{R}} k(y)g_o(x,y)dy = 0$. It follows that

$$\int_{\mathbb{R}} k(y)g(w(x-y))dy = \int_{\mathbb{R}} k(y)g_e(x,y)dy.$$

This and (3.1) show

$$w(x-c_+^*) - w(x) = \int_{\mathbb{R}} k(y)g_e(x,y)dy - w(x). \tag{3.3}$$

Since $g'(u) \geq 0$ for $0 \leq u \leq 1$, $\frac{dg(w(x))}{dx} = g'(w(x))w'(x) \leq 0$ for $x \in \mathbb{R}$, and furthermore

$$\int_{\mathbb{R}} \frac{dg(w(x))}{dx}dx = g(w(x))\Big|_{x=-\infty}^{x=\infty} = g(w(\infty)) - g(w(-\infty)) = g(0) - g(1) = -1.$$

Since $0 \leq w(x) \leq 1$, $\int_{\mathbb{R}} w(x)\frac{dg(w(x))}{dx}dx$ and $\int_{\mathbb{R}} w(x-c_+^*)\frac{dg(w(x))}{dx}dx$ are convergent. From (3.3) we have

$$\int_{\mathbb{R}} [w(x-c_+^*) - w(x)]\frac{dg(w(x))}{dx}dx = \int_{\mathbb{R}}\int_{\mathbb{R}} k(y)g_e(x,y)\frac{dg(w(x))}{dx}dydx - \int_{\mathbb{R}} w(x)\frac{dg(w(x))}{dx}dx. \tag{3.4}$$

Since $\frac{dg(w(x))}{dx}$ is non-positive and thus $k(y)g_e(x,y)\frac{dg(w(x))}{dx}$ does not change sign, by Tonelli's theorem (Wheeden and Zygmund [35]), we can switch the order of the double integral in (3.4) to obtain

$$\begin{aligned} &\int_{\mathbb{R}}\int_{\mathbb{R}} k(y)g_e(x,y)\frac{dg(w(x))}{dx}dydx \\ &= \int_{\mathbb{R}}\int_{\mathbb{R}} k(y)g_e(x,y)\frac{dg(w(x))}{dx}dxdy \\ &= \tfrac{1}{2}\int_{\mathbb{R}} k(y)\int_{\mathbb{R}}[g(w(x-y) + g(w(x+y))]\frac{dg(w(x))}{dx}dxdy. \end{aligned} \tag{3.5}$$

Using integration by parts, we find

$$\int_{\mathbb{R}} g(w(x+y))\frac{dg(w(x))}{dx}dx = g(w(x+y))g(w(x))\Big|_{x=-\infty}^{x=\infty} - \int_{\mathbb{R}} g(w(x))\frac{dg(w(x+y))}{dx}dx. \tag{3.6}$$

Note

$$g(w(x+y))g(w(x))\Big|_{x=-\infty}^{x=\infty} = g(w(\infty))g(w(\infty)) - g(w(-\infty))g(w(-\infty)) = g(0)g(0) - g(1)g(1) = -1. \tag{3.7}$$

Using a variable change $x \mapsto x+y$, we find

$$\int_{\mathbb{R}} g(w(x))\frac{dg(w(x+y))}{dx}dx = \int_{\mathbb{R}} g(w(x-y))\frac{dg(w(x))}{dx}dx. \tag{3.8}$$

Combining (3.5) - (3.8), we have

$$\int_{\mathbb{R}}\int_{\mathbb{R}} k(y)g_e(x,y)\frac{dg(w(x))}{dx}dydx = -\frac{1}{2}\int_{\mathbb{R}} k(y)dy = -\frac{1}{2}.$$

On the other hand,

$$\int_{\mathbb{R}} g(w(x))\frac{dg(w(x))}{dx}dx = \frac{g^2(w(x))}{2}\Big|_{x=-\infty}^{x=\infty} = -\frac{1}{2}.$$

We therefore have

$$\int_{\mathbb{R}}\int_{\mathbb{R}} k(y)g_e(x,y)\frac{dg(w(x))}{dx}dydx = \int_{\mathbb{R}} g(w(x))\frac{dg(w(x))}{dx}dx.$$

This and (3.4) yield

$$\int_{\mathbb{R}}[w(x-c_+^*)-w(x)]\frac{dg(w(x))}{dx}dx=\int_{\mathbb{R}}[g(w(x))-w(x)]\frac{dg(w(x))}{dx}dx. \tag{3.9}$$

It is shown in the proof of Theorem 4 in [21] that $w'(x)<0$ if $w(x)\in(0,1)$. Since $w(-\infty)=1$ and $w(\infty)=0$ and $w'(x)$ is continuous, there are two numbers $d_1>d_2$, where d_1 is allowed to be ∞ and d_2 is allowed to be $-\infty$, such that (i) $w(d_1)=0,\ w(d_2)=1$, (ii) $w'(x)<0$ for $x\in(d_2,d_1)$, (iii) $w(x)\equiv 1$ for $x\le d_2$ if d_2 is finite, and (iv) $w(x)\equiv 0$ for $x\ge d_1$ if d_1 is finite. Consider Hypotheses 2.1 (viii) where σ_1 is either 0 or a positive number and σ_2 is either 1 or a positive number less than 1. Let δ_1 be the number such that (i) if $\sigma_1=0, d_1=\infty$, $\delta_1=\infty$, (ii) if $\sigma_1=0, d_1<\infty$, δ_1 is the smallest solution $w(\delta_1)=0$, and (iii) if $\sigma_1>0$, δ_1 is the smallest solution $w(\delta_1)=\sigma_1$. Let δ_2 be the number such that (i) if $\sigma_2=1, d_2=-\infty$, $\delta_2=-\infty$, (ii) if $\sigma_2=1, d_2>-\infty$, δ_2 is the largest solution $w(\delta_2)=1$, and (iii) if $\sigma_2<1$, δ_2 is the largest solution $w(\delta_2)=\sigma_2$. We see that $\frac{g(w(x))}{dx}=g'(w(x))w'(x)<0$ in (δ_2,δ_1) and $\frac{g(w(x))}{dx}=g'(w(x))w'(x)=0$ outside this interval if one of δ_1 and δ_2 is finite. Form (3.9), we find

$$\int_{\mathbb{R}}[w(x-c_+^*)-w(x)]\frac{dg(w(x))}{dx}dx=\int_{\delta_2}^{\delta_1}[g(w(x))-w(x)]\frac{dg(w(x))}{dx}dx=\int_1^0[u-g^{-1}(u)]du, \tag{3.10}$$

where $u=g(w(x))$. In the $u-y$ plane, the graph of $y=g^{-1}(u)$ for $0\le u\le 1$ and the graph of $y=g(u)$ for $\sigma_1\le u\le\sigma_2$ are symmetric about the line $y=u$. This shows that the sum of $\int_0^1 g(y)dy$ and $\int_0^1 g^{-1}(y)dy$ is the area of the unit square with vertices $(0,0)$ and $(1,1)$. Thus

$$\int_0^1 g(y)dy+\int_0^1 g^{-1}(y)dy=1.$$

This, (3.10), and the simple fact $1-\int_0^1 udu=\int_0^1 udu$ show

$$\int_{\mathbb{R}}[w(x)-w(x-c_+^*)]\frac{dg(w(x))}{dx}dx=\int_1^0[g(u)-u]du,$$

which is equivalent to

$$\int_{\delta_2}^{\delta_1}[w(x)-w(x-c_+^*)]\frac{dg(w(x))}{dx}dx=\int_0^1[g(u)-u]du.$$

Recall that $0<w(x)<1$, $w'(x)<0$, and $\frac{dg(w(x))}{dx}<0$ in (δ_2,δ_1), and that $w(x)\equiv 0$ if $x\le\delta_2$ for $\delta_2\ne-\infty$ and $w(x)\equiv 1$ if $x\ge\delta_1$ for $\delta_1\ne\infty$. If $\int_0^1[g(u)-u]du>0$, then there exist a number $x_0\in(\delta_2,\delta_1)$ such that $w(x_0)-w(x_0-c_+^*)<0$ which implies $c_+^*>0$. This proves statement (i). Statement (iii) can be shown in a similarly way. Statement (ii) follows from statements (i) and (iii). The proof is complete. □

Wang et al. [31] proved statements (i)-(iii) under the conditions that a nonincreasing traveling wave $w(x-nc^*)$ connecting 0 and 1 satisfies $w(x)\in C^\infty(\mathbb{R})$, $w'(x)<0$ for all x,

$$\lim_{x\to\infty}\frac{d^iw}{dx^i}=\lim_{x\to-\infty}\frac{d^iw}{dx^i}=0,\quad i=1,2,...,$$

and there exists a positive number M such that

$$|\frac{d^ig(w(x))}{dx^i}|\le M\quad\text{for all } x\ \text{ and } i=1,2,....$$

These conditions are dropped in Theorem 3.2.

4 Critical patch size

In this section we study the critical patch size for (1.1) when $\Omega = [-l, l]$. To avoid possible confusion, we use $Q_{\mathbb{R}}$ and Q_l to denote Q defined by (2.2) for $\Omega = \mathbb{R}$ and $\Omega = [-l, l]$, respectively. A function $u(x)$ is said to be a positive equilibrium for Q_l if $u(x) = Q_l[u](x)$, $u(x) \geq 0$, and $u(x) \not\equiv 0$ for $x \in [-l, l]$.

Consider the sequence $a_n(l, x)$ defined by

$$a_{n+1}(l, x) = \int_{-l}^{l} k(x-y) g(a_n(l, y)) dy, \quad a_0(l, x) \equiv 1. \tag{4.1}$$

We have the following lemma.

Lemma 4.1. *Assume that Hypotheses 2.1 hold and $k(x)$ is even. $a_n(l, x)$ defined by (4.1) are even functions, $0 \leq a_{n+1}(l, x) \leq a_n(l, x)$ for all $n \geq 0$ and for $x \in [-l, l]$, and $a_n(l, x)$ converges to a nonnegative even function $a(l, x)$, i.e.,*

$$a(l, x) = \lim_{n \to \infty} a_n(l, x), \tag{4.2}$$

satisfying $0 \leq a(l, x) \leq 1$, $a(l, x) < 1$ if $\sigma_2 = 1$, and

$$a(l, x) = \int_{-l}^{l} k(x-y) g(a(l, y)) dy. \tag{4.3}$$

Furthermore $a(l, x)$ is differentiable in x.

Proof. It is easily seen that $0 \leq a_1(l, x) = \int_{-l}^{l} k(x-y) g(1) dy = \int_{-l}^{l} k(x-y) dy \leq 1$, so that $0 \leq a_1(l, x) \leq a_0(l, x)$ for $x \in [-l, l]$. On the other hand, since $k(x)$ is even, $a_1(l, x) = \int_{-l}^{l} k(x-y) dy = \int_{x-l}^{x+l} k(y) dy$ is even. Furthermore

$$a_2(l, x) = \int_{-l}^{l} k(x-y) g(a_1(l, y)) dy = \int_{-l}^{l} k(x+y) g(a_1(l, -y)) dy = \int_{x-l}^{x+l} k(-x-y) g(a_1(l, y)) dy = a_2(l, -x)$$

so that $a_2(l, x)$ is even. Induction shows that for all $n \geq 0$, $a_n(l, x)$ is even, and $0 \leq a_{n+1}(l, x) \leq a_n(l, x)$ for $x \in [-l, l]$. Consequently, $a_n(l, x)$ converges to a limit function $a(l, x)$, which is even, nonnegative, and no bigger than 1. By taking limits on both sides of (4.1) and using the dominate convergence theorem, we find that $a(l, x)$ satisfies (4.3) and $0 \leq a(l, x) \leq 1$. On the other hand, for $\sigma_2 = 1$ and $n_0 = [[\frac{2l}{\text{length of support of } k}]] + 1$, where $[[\cdot]]$ is the largest integer function, $a_{n_0}(l, x) < 1$ for $x \in [-l, l]$. This leads to $a(l, x) < 1$ for $x \in [-l, l]$. Finally differentiability of $a(l, x)$ follows from absolute continuity of $k(x)$ given in Hypotheses 2.1 (ii). The proof is complete.

□

Lemma 4.2. *Assume that Hypotheses 2.1 hold and $k(x)$ is even. Let $l_2 > l_1 > 0$. Then for $a(l, x)$ given by (4.2), $a(l_2, x) \geq a(l_1, x)$ for $x \in [-l_1, l_1]$.*

Proof. Consider the sequences a_n defined by (4.1) for l_1 and l_2. For $x \in [-l_1, l_1]$,

$$a_1(l_1, x) = \int_{l_1}^{l_1} k(x-y) dy \leq \int_{-l_2}^{l_2} k(x-y) dy = a_1(l_2, x),$$

and

$$\begin{aligned} a_2(l_1,x) &= \int_{-l_1}^{l_1} k(x-y)g(a_1(l_1,y))dy \le \int_{-l_1}^{l_1} k(x-y)g(a_1(l_2,y))dy \le \int_{-l_2}^{l_2} k(x-y)g(a_1(l_2,y))dy \\ &= a(l_2,x). \end{aligned}$$

Induction shows that for $x \in [-l_1, l_1]$, $a_n(l_1,x) \le a_n(l_2,x)$ for all n. This leads to the conclusion of this lemma. The proof is complete. □

Lemma 4.3. *Assume that Hypotheses 2.1 hold and $k(x)$ is even, and $\int_0^1 [g(u)-u]du > 0$. Then for $a(l,x)$ given by (4.2), $a(l,x) \not\equiv 0$ for sufficiently large l, and $a(l,x) \equiv 0$ for sufficiently small l.*

Proof. Let $\zeta(s)$ be a differentiable decreasing function with the properties

$$\zeta(s) = \begin{cases} 1, & \text{for } s \le 1/2, \\ 0, & \text{for } s \ge 1. \end{cases}$$

For $m > 0$, let $k_m(x) = k(x)\zeta(\frac{|x|}{m})$. Clearly $k_m(x) \to k(x)$ and $\ell_m := \int_{-\infty}^{\infty} k_m(x)dx \to 1$ as $m \to \infty$. Consider

$$Q_{\mathbb{R},m}[u](x) := \int_{\mathbb{R}} \ell_m g(u(y)) \frac{k_m(x-y)}{\ell_m} dy = \int_{\mathbb{R}} g(u(y)) k_m(x-y)dy.$$

$\frac{k_m(x)}{\ell_m}$ is a probability density with $\int_{\mathbb{R}} \frac{k_m(x)}{\ell_m}dx = 1$. For a sufficiently large m, Hypotheses 2.1 for $g(u)$ show that $\ell_m g(u(y))$ has three equilibria 0, α_m, β_m with $\alpha_m \ge \alpha$ and $\beta_m \le 1$. Furthermore as $m \to \infty$, $\alpha_m \to \alpha$ and $\beta_m \to 1$. Since $\int_0^1 [g(u)-u]du > 0$, we may assume that m_0 is so large that $\int_0^1 [\frac{\ell_{m_0} g(\beta_{m_0} u)}{\beta_{m_0}} - u]du > 0$. It is easily seen that $k_{m_0}(x)$ and $\frac{\ell_{m_0} g(\beta_{m_0} u)}{\beta_{m_0}}$ satisfy Hypotheses 2.1 with $k(x)$ replaced by $\frac{k_{m_0}(x)}{\ell_{m_0}}$ and $g(u)$ replaced by $\frac{\ell_{m_0} g(\beta_{m_0} u)}{\beta_{m_0}}$. By Theorem 3.1 and Theorem 3.2, the rightward spreading speed $c^*_{m_0,+}$ for $Q_{\mathbb{R},m_0}[u](x)$ has the property $c^*_{m_0,+} > 0$. $c^*_{m_0,+}$ is also the rightward spreading speed for $Q_{\mathbb{R},m_0}$.

Choose a positive number c such that $c^*_{m_0,+} > c$. Let $l > 0$ and choose σ such that $\beta_{m_0} > \sigma > \alpha_{m_0}$. By Theorem 3.1 (ii), there exists a positive number r_σ such that for $v_0(x) \equiv \sigma$ in $[-r_\sigma/2, r_\sigma/2]$ and 0 elsewhere, v_n defined by the recursion $v_{n+1}(x) = Q_{\mathbb{R},m_0}[v_n](x)$ satisfies

$$\lim_{n\to\infty} \min_{-nc \le x \le nc} v_n(x) = \beta_{m_0}.$$

This, $c > 0$, and $\beta_{m_0} > \sigma$ show that there exists a positive integer n_0 such that

$$v_{n_0}(x) > v_0(x) \equiv \sigma \text{ on } [-r_\sigma/2, r_\sigma/2]. \tag{4.4}$$

Let

$$Q_{l,m}[u](x) := \int_{-l}^{l} k_m(x-y)g(u(y))dy.$$

Consider the interval $[-n_0(c+D) - r_\sigma/2, n_0(c+D) + r_\sigma/2]$ where D is the length of the support of $k_{m_0}(x)$, and let l_0 be half of the length of this interval. We therefore have that

$$Q^{(n)}_{\mathbb{R},m_0}[v_0](x) \equiv Q^{(n)}_{l_0,m_0}[v_0(x)], n = 1, 2, ..., n_0,$$

where $Q^{(n)}_{\mathbb{R},m_0}$ is the nth iteration of the operator $Q_{\mathbb{R},m_0}$, and $Q^{(n)}_{l_0,m_0}$ is the nth iteration of the operator $Q^{(n)}_{l_0,m_0}$. It follows from this and (4.4) that

$$Q^{(n_0)}_{l_0,m_0}[v_0(x)] > v_0(x).$$

This and monotonicity of $Q^{(n_0)}_{l_0,m_0}$ imply

$$Q^{(\ell n_0)}_{l_0,m_0}[v_0(x)] > v_0(x), \quad \ell = 1, 2, ... \tag{4.5}$$

Since $Q_{l_0}[u](x) \geq Q_{l_0,m_0}[u](x)$ for $\beta_{m_0} \geq u(x) \geq 0$, (4.5) shows

$$Q^{(\ell n_0)}_{l_0}[v_0(x)] > v_0(x), \quad \ell = 1, 2, ... \tag{4.6}$$

where $Q^{(\ell n_0)}_{l_0}$ is the ℓn_0th iteration of Q_{l_0}.

We now consider the sequence $a_n(l_0, x)$ defined by (4.1) with $l = l_0$. Since $a_0(l_0, x) \equiv 1 > v_0(x)$, Lemma 2.1 and (4.6) show that for any positive integer ℓ, $a_{\ell n_0}(l_0, x) \geq v_{\ell n_0}(x) > v_0(x)$, which leads to $a(l_0, x) \geq \sigma$ for $x \in [-\frac{r_\sigma}{2}, -\frac{r_\sigma}{2}]$. It follows from Lemma 4.2 that for any $l > l_0$ and $x \in [l_0, l_0]$, $a(l, x) \geq a(l_0, x) > \sigma$ for $x \in [-\frac{r_\sigma}{2}, -\frac{r_\sigma}{2}]$. We have shown that for $l > l_0$, $a(l, x) \not\equiv 0$.

Equation (4.1) shows that for $x \in [-l, l]$, $a_1(l, x) \leq 2lM$ where M is the maximum value of $k(x)$. Hypotheses 2.1 (v)-(iv) indicate that for $\frac{g(u)}{u}$ with $\frac{g(0)}{0}$ defined to be $g'(0)$ is bounded above by a number $A > 1$ for $u \in [0, 1]$. We see that $a_2(l, x) \leq 2AlM$ for $x \in [-l, l]$. Induction shows $a_n(l, x) \leq A^{n-1}(2lM)^n < (2AlM)^n$ $x \in [-l, l]$. If l is sufficiently small such that $2AlM < 1$, then $a_n(l, x)$ converges to zero so that $a(l, x) \equiv 0$ for $x \in [-l, l]$. The proof is complete. □

We are now ready to define the critical patch size under the condition that $\int_0^1 [g(u) - u]du > 0$. Lemma 4.1- Lemma 4.3 show that the maximum value of $a(l, x)$ for $x \in [-l, l]$ is nondecreasing in l, and the maximum value is positive for sufficiently large l, and zero for sufficiently small l. Define

$$l^* := \inf\{l : \text{ maximum value of } a(l, x) > 0\}.$$

l^* is well defined and $l^* > 0$. This definition is equivalent to

$$l^* := \inf\{l : a(l, x) \not\equiv 0\}.$$

We have the following theorem regarding the existence of critical patch size.

Theorem 4.1. *Assume that Hypotheses 2.1 hold and $k(x)$ is even. Then the following statements hold:*

- *i. If $\int_0^1 [g(u) - u]du > 0$, then*
  - *a. for $l > l^*$, there is a positive equilibrium $a(l, x)$ for Q_l defined by (4.2) with $a(l, x)$ even, $0 \leq a(l, x) \leq 1$, and $a(l, x) < 1$ if $\sigma_2 = 1$, such that for $a(l, x) \leq u_0(x) \leq 1$, $\lim_{n\to\infty} u_n(x) = a(l, x)$ for $x \in [-l, l]$, and*
  - *b. for $l < l^*$, there is no positive equilibrium for Q_l, and every solution $u_n(x)$ of $u_{n+1} = Q_l[u_n](x)$ with $0 \leq u_0(x) \leq 1$ converges to zero as $n \to \infty$.*

ii. *If* $\int_0^1 [g(u) - u]du < 0$*, for any* $l > 0$*, there is no positive equilibrium for* Q_l*, and in this case every solution* $u_n(x)$ *of* $u_{n+1} = Q_l[u_n](x)$ *with* $0 \le u_0(x) \le \rho$ *where* $\rho < 1$ *converges to zero as* $n \to \infty$*.*

Proof. Lemma 4.1-Lemma 4.3 and the definition l^* show that for $l > l^*$ the sequence $a_n(l, x)$ defined by (4.2) with $a_0(l, x) \equiv 1$ converges to an even function $a(l, x) \not\equiv 0$ with $0 \le a(l, x) \le 1$ and $a(l, x) < 1$ if $\sigma_2 = 1$. For $a(l, x) \le u_0(x) \le a_0(l, x) \equiv 1$, Lemma 4.1 and induction show $a(l, x) \le u_0(x) \le a_n(l, x)$ for all n. Since $\lim_{n\to\infty} a_n(l, x) = a(l, x)$, $\lim_{n\to\infty} u_n(x) = a(l, x)$ for $x \in [-l, l]$. A similar proof shows that for $l < l^*$, $\lim_{n\to\infty} u_n(x) = a(l, x) \equiv 0$. This proves (i).

We now prove statement (ii). Let $w(x-nc_+^*)$ be a nonincreasing traveling wave solution of (1.1) with $w(-\infty) = 1$ and $w(\infty) = 0$. Since $\int_0^1 [g(u)-u]du < 0$, by Theorem 3.2, $c_+^* < 0$. Since $0 \le u_0(x) \le \rho < 1$, there exists a number h such that $u_0(x) < w(x - h)$. We have that for $x \in [0, l]$,

$$u_1(x) = Q_l[u_0](x) \le Q_{\mathbb{R}}[u_0](x) \le Q_{\mathbb{R}}[w](x - h) = w(x - c_+^* - h).$$

Induction shows $u_m(x) \le w(x - mc_+^* - h)$. As $m\to\infty$, $w(x - mc_+^* - h)\to 0$ for $x \in [-l, l]$ and thus $u_{n_0+m}(x)\to 0$ for $x \in [0, l]$ and there is no nonnegative nontrivial equilibrium. The proof is complete.

□

Let $\bar{a}$ denote the maximum of $a(l, x)$.

Proposition 4.1. *Assume that Hypotheses 2.1 are satisfied,* $k(x)$ *is even, and* $\int_0^1 [g(u) - u]du > 0$*. Then the following statements hold:*

i. *For* $l > l^*$*,* $\alpha < \bar{a} \le 1$*, and* $\bar{a} < 1$ *if* $\sigma_2 = 1$*.*

ii. *If* $k(x)$ *is nonincreasing for* $x > 0$*, then* $\frac{d}{dx} a(l, x) \le 0$ *for* $x > 0$*.*

iii. $\int_{-l^*}^{l^*} k(x)dx \ge \inf_{\alpha < u \le 1} \frac{u}{g(u)}$*.*

Proof. Let $l > l^*$. In view of Lemma 4.1, $0 \le a(l, x) \le 1$, and $a(l, x) < 1$ if $\sigma_2 = 1$ for all x so that $0 \le \bar{a} \le 1$, and $\bar{a} < 1$ if $\sigma_2 = 1$. If $\bar{a} \le \alpha$, we derive a contradiction as follows. In this case, for $n_0 = [[\frac{2l}{\text{length of support of } k}]] + 1$ where $[[\cdot]]$ is the largest integer function, $a(l, x) = Q_l^{(n_0)}[a](l, x) < \alpha$ for $x \in [-l, l]$, so that there exists $\tilde{\alpha}$ with $0 \le \tilde{\alpha} < \alpha$ such that $a(l, x) \le \tilde{\alpha}$ for $x \in [-l, l]$. Note $a(l, x) = Q_l[a](l, x) \le g(\tilde{\alpha})$. Induction shows that $a(l, x) = Q_l^{(m)}[a](l, x) \le g^{(n)}(\tilde{\alpha})$ which approaches zero as $m\to\infty$, so that $a(l, x) \equiv 0$, a contraction. We have proven statement (i).

Consider $a_n(l, x)$ defined by (4.2) with $a_0(l, x) \equiv 1$.

$$a_1(l, x) = \int_{-l}^{l} k(x - y)dy = \int_{x-l}^{x+l} k(y)dy,$$

For $x > 0$,

$$a_1'(l, x) = k(x + l) - k(x - l) \le 0,$$

because $k(x)$ is even and nonincreasing for $x > 0$ and $|x - l| < |x + l|$.

$$\begin{aligned} a_2'(l, x) &= \tfrac{d}{dx} \textstyle\int_{x-l}^{x+l} k(y)a_1(l, x - y)dy \\ &= k(x + l)a_1(l, -l) - k(x - l)a_1(l, l) + \textstyle\int_{x-l}^{x+l} k(y)a_1'(l, x - y)dy \\ &= [k(x + l) - k(x - l)]a_1(l, l) + \textstyle\int_{x-l}^{x+l} k(y)a_1'(l, x - y)dy. \end{aligned}$$

For $x > 0$, $k(x+l) - k(x-l) \leq 0$. Furthermore for $x > 0$,

$$\int_{x-l}^{x+l} k(y)a_1'(l, x-y)dy = \int_{-l}^{l} k(x-y)a_1'(l,y)dy = \int_0^l [k(x-y) - k(x+y)]a_1'(l,y)dy \leq 0$$

since $a_1'(l,x) \leq 0$ and $|x-y| < |x+y|$ for $y \geq 0$. We therefore have $a_2'(l,x) \leq 0$ for $x > 0$. Induction shows that $a_n'(l,x) \leq 0$ for all n. Consequently the limit function $a(l,x)$ is even and nonincreasing in x for $x > 0$. The equation (4.3) shows $\frac{d}{dx}a(l,x)$ is continuous and thus $\frac{d}{dx}a(l,x) \leq 0$. We have proven statement (ii).

For $l > l^*$, since $a(l,x) = \int_{-l}^{l} k(x-y)g(a(l,y))dy \leq g(\bar{a})\int_{-l}^{l} k(x-y)dy$, we have

$$\bar{a} \leq g(\bar{a}) \int_{-l}^{l} k(x-y)dy,$$

or

$$\int_{-l}^{l} k(x-y)dy \geq \frac{\bar{a}}{g(\bar{a})}.$$

This and the fact that $\alpha < \bar{a} \leq 1$ show

$$\int_{-l}^{l} k(x)dx \geq \inf_{\alpha < u \leq 1} \frac{u}{g(u)}.$$

Since this is true for any $l > l^*$, statement (iii) is true. The proof is complete. □

Statements (i)-(ii) of this proposition discuss some properties of the nontrivial equilibrium $a(l,x)$. Statement (iii) provides a lower bound for the critical patch size.

We finally investigate how the critical patch size depends on the standard deviation of k. Let λ be the standard deviation of k. We use $k(\lambda, x)$ to denote k and write

$$k(\lambda, x) = \frac{1}{\lambda}p(\frac{x}{\lambda}).$$

Theorem 4.2. *Assume that Hypotheses 2.1 hold, $k(\lambda,x)$ is even in x, and $\int_0^1 [g(u)-u]du > 0$. Then for any fixed $l > 0$, there is a $\lambda^* > 0$ such that*

a. *for $\lambda < \lambda^*$, there is an even positive equilibrium $b(\lambda,x)$ with $0 \leq b(\lambda,x) \leq 1$, and $b(\lambda,x) < 1$ if $\sigma_2 = 1$, such that for $b(\lambda,x) \leq u_0(x) \leq 1$, $\lim_{n\to\infty} u_n(x) = b(\lambda,x)$ for $x \in [-l,l]$, and*
b. *for $\lambda > \lambda^*$, there is no positive equilibrium for Q_l, and every solution $u_n(x)$ of $u_{n+1} = Q[u_n](x)$ with $0 \leq u_0(x) \leq 1$ converges to zero as $n \to \infty$.*

Proof. Let l be any fixed positive number. Consider

$$b_{n+1}(\lambda,x) = \int_{-l}^{l} \frac{1}{\lambda}p(\frac{x-y}{\lambda})g(b_n(\lambda,y))dy, \quad b_0(\lambda,x) \equiv 1.$$

Using $y \mapsto \frac{y}{\lambda}$, we obtain

$$b_{n+1}(\lambda,\lambda x) = \int_{-\frac{l}{\lambda}}^{\frac{l}{\lambda}} p(x-y)g(b_n(\lambda,\lambda y))dy, \quad b_0(\lambda,\lambda x) \equiv 1.$$

Consider the sequence

$$a_{n+1}(\frac{l}{\lambda},x)=\int_{-\frac{l}{\lambda}}^{\frac{l}{\lambda}}p(x-y)g(a_n(\frac{l}{\lambda},y))dy,\quad a_0(\frac{l}{\lambda},x)\equiv 1.$$

We see that $b_n(\lambda,\lambda x)\equiv a_{n+1}(\frac{l}{\lambda},x)$ for all n and $x\in[-\frac{l}{\lambda},\frac{l}{\lambda}]$. The sequence $a_{n+1}(\frac{l}{\lambda},x)$ is the same as the sequence given by (4.3) with l replaced by $\frac{l}{\lambda}$. Clearly $\frac{l}{\lambda}\to 0$ as $\lambda\to\infty$, and $\frac{l}{\lambda}\to\infty$ as $\lambda\to 0$. The conclusion of the this theorem follows from Lemma 4.1-Lemma 4.3 and Theorem 4.1. The proof is complete. □

5 Laplace kernel

In this section, we study the critical patch size and positive equilibria for (1.1) when $k(x)$ is a Laplace kernel, i.e.,

$$k(x)=\frac{1}{2}be^{-b|x|},\quad b>0, \tag{5.7}$$

with the standard deviation $\sqrt{2}b$. This is a commonly used kernel in integro-difference equations for studying population dynamics [11, 14, 15, 17]. It satisfies Hypotheses 2.1 (i)-(iv). With this kernel and a growth function $g(u)$ satisfying Hypotheses 2.1 (v)-(ix), all the results obtained in Section 3 and Section 4 are valid.

According to Proposition 4.1, $a(l,x)$ defined by (4.3) is differentiable in x. This can be also verified by directly taking derivatives on the equation (4.3) with $k(x)$ given by (5.7). One can further take the second order derivative to find that $u(x):=a(l,x)$ satisfies the differential equation

$$u''=b^2[u-g(u)].$$

Direct calculations lead to the boundary conditions

$$u'(-l)=bu(-l),\ u'(l)=-bu(l).$$

We integrate orbits in the phase plane to obtain an expression for l^*. This method was used in other contexts (see Li et al. [17], Ludwig et al. [18], and Pouchol et al. [26]). We follow the work in [17] to find l^* under the condition $\int_0^1[g(u)-u]du>0$. Letting $v=u'$, we have

$$\begin{aligned}&u'=v,\\&v'=b^2[u-g(u)],\\&u'(-l)=bu(-l),\ u'(l)=-bu(l).\end{aligned} \tag{5.8}$$

There are three equilibria: $(0,0)$ (saddle), $(\alpha,0)$ (source), and $(1,0)$ (saddle). It follows from (5.8) that

$$\frac{dv}{du}=\frac{b^2[u-g(u)]}{v}. \tag{5.9}$$

The following two trajectories in the $u-v$ plane play important roles in studying equilibrium solutions:

$$T_0:\quad v^2=2b^2\textstyle\int_0^u(\tau-g(\tau))d\tau,\quad u=0\Longrightarrow v=0,$$

$$T_1:\quad v^2=2b^2\textstyle\int_u^1(g(\tau)-\tau)d\tau,\quad u=1\Longrightarrow v=0.$$

T_0 and T_1 are obtained by integrating (5.9). T_0 is the heteroclinic loop describing the stable and unstable manifold of $(0,0)$ with $u > 0$. B_0 is the positive number such that $\int_0^{B_0}[g(u) - u]du = 0$. $\alpha < B_0 < 1$. T_1 represents the stable manifold and unstable manifold of $(1,0)$ with $0 \le u < 1$. T_0 and T_1 are symmetric about the u-axis and T_0 and T_1 do not intersect (see Li et al. [17]). The equation for T_0 shows $v^2 \le 2b^2 \int_0^u \tau d\tau = b^2u^2$ so that T_0 lies between $v = bu$ and $v = -bu$. From Hypotheses 2.1 (viii), we see that T_0 is given by $v = \pm bu$ for $0 \le u \le \sigma_1$. T_1 intersects with the v-axis at the number $2b^2 \int_0^1 (g(u) - u)du > 0$. We use $\bar{s}$ to denote the u-coordinate of the point where T_1 and $v = au$ intersect. $\bar{s}$ is the positive solution of the equation

$$u^2 = 2\int_u^1 (g(\tau) - \tau)d\tau.$$

An equilibrium of the boundary value problem (5.8) corresponds to an orbit T that starts at the line $v = bu$, lies between T_0 and T_1, and ends on the line $v = -bu$. Let (s, bs) with $\sigma_1 < s < \bar{s}$ be a point on $v = bu$ at which T starts. T is given by

$$v^2 = 2b^2 \int_s^u (u - g(u))du + b^2 s^2.$$

This is obtained by integrating (5.9). We use $B(s)$ to denote the number at which T intersects with the u-axis. $B(s)$ is the solution of the equation

$$2\int_s^u (\tau - g(\tau))d\tau + s^2 = 0.$$

See Figure 2 for a graphical demonstration.

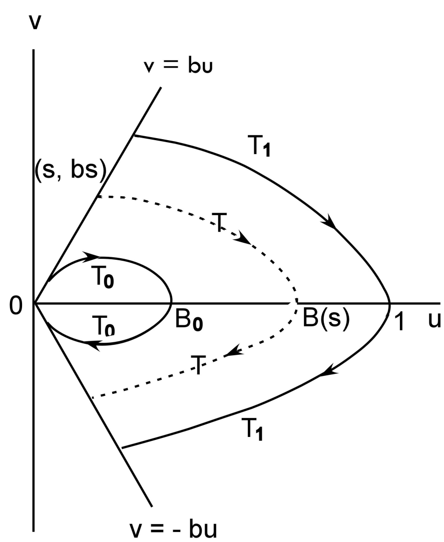

Figure 1: Graphical demonstration of an equilibrium solution T (dash curve).

In view of the first equation of (5.8) and symmetry of T, for $s < u < B(s)$ and $-l \le x \le 0$ in the first quadrant T is governed by

$$\frac{du}{dx} = b\sqrt{2\int_s^u (\tau - g(\tau))d\tau + s^2}.$$

Integration leads to

$$l = \int_s^{B(s)} \frac{1}{b\sqrt{2\int_s^u (\tau - g(\tau))d\tau + s^2}} du. \tag{5.10}$$

Here l is defined as a function of s for $\sigma_1 < s < \bar{s}$.

As $s \to \bar{s}$, $B(s) \to 1$. On the other hand the definition of T_1 shows

$$2\int_{\bar{s}}^1 (\tau - g(\tau))d\tau + \bar{s}^2 = 0.$$

Furthermore,

$$\frac{d}{du}(2\int_{\bar{s}}^u (\tau - g(\tau))d\tau + \bar{s}^2) = u - g(u),$$

which is 0 when $u = 1$. It follows that the order of zero of $2\int_s^u (\tau - g(\tau))d\tau + s^2$ for $s = \bar{s}$ and $u = B(\bar{s}) = 1$ is at least 2, and thus as $s \to \bar{s}$, $l(s) \to \infty$.

If $\sigma_1 = 0$, a similar argument shows that as $s \to 0$, $l(s) \to \infty$. However for $\sigma_1 > 0$, the function $2\int_{\sigma_1}^u (\tau - g(\tau))d\tau + {\sigma_1}^2 \neq 0$ for $u = \sigma_1$, and thus $l(\sigma_1)$ is a finite number. We conclude that

$$l^* = \inf_{\sigma_1 < s < \bar{s}} \int_s^{B(s)} \frac{1}{b\sqrt{2\int_s^u (\tau - g(\tau))d\tau + s^2}} du, \tag{5.11}$$

is always well-defined, and that if $\sigma_1 = 0$ for $l > l^*$ the equation (5.10) has at least two different corresponding values for s. This implies that if $\sigma_1 = 0$ for $l > l^*$ there are at least two different equilibrium solutions. Since the trajectories do not intersect, the phase diagram shows multiple equilibria are ordered and there are a largest equilibrium and a smallest equilibrium. The largest equilibrium is always the positive equilibrium given by (4.3).

We conduct numerical simulations for $k(x)$ given by (5.7) with $b = \frac{1}{\sqrt{2}}$ and the growth function

$$g(u) = \frac{(1+a)u^2}{a + u^2}$$

with the Allee threshold a and carrying capacity 1. This kind of growth function is used in [30]. It should be noted that with this choice of growth function, $c^* := c_+^* = c_-^* = 0$ when $a = 0.436$.

We first numerically integrate (5.11) to determine the graph of $l(s)$ (see Figure 2), which indicates that $l^* = 2.676$ and when $l > l^*$ there are two equilibria. In this case $\sigma_1 = 0$ and $\bar{s} = 0.268$. Figure 3 and Figure 4 depict c^* vs a and l^* vs a, respectively. We see that the wave speed c^* is a decreasing function of a, and the critical patch size is an increasing function of a. Figure 5 shows the direct connection between c^* and l^*, and as c^* increases l^* decreases. Figure 6 indicates that the log-log plot of l^* in terms of c^* is not linear, so that the dependence of l^* on c^* is not a simple power relation. This is in contrast to a reaction diffusion equation without Allee effect where the two quantities are inversely proportional for a fixed diffusion coefficient. It is well known that for a reaction diffusion equation with diffusion coefficient d and intrinsic growth rate r, the spreading speed is $c^* = 2\sqrt{rd}$ and the critical patch size for zero value boundary condition is $l^* = \pi\sqrt{\frac{d}{r}}$, so that $c^* l^* = 2d\pi$. To numerically determine c^* vs. a and l^* vs. a we used a first order uniform mesh spatial discretization with FFT accelerated convolution using Mathematica. For c^* iterations were left shifted by c_n so $u_{n+1}(0 - c_n) = 0.5$ and iterated until a

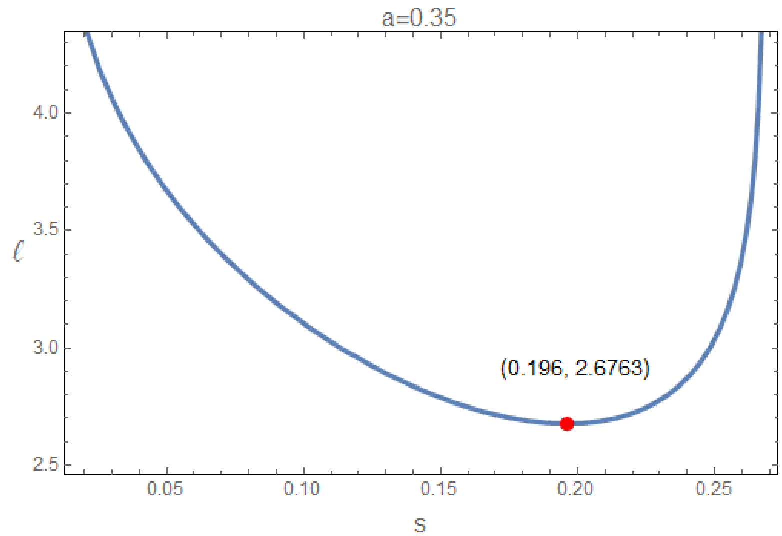

Figure 2: l vs. s as determined by (5.11).

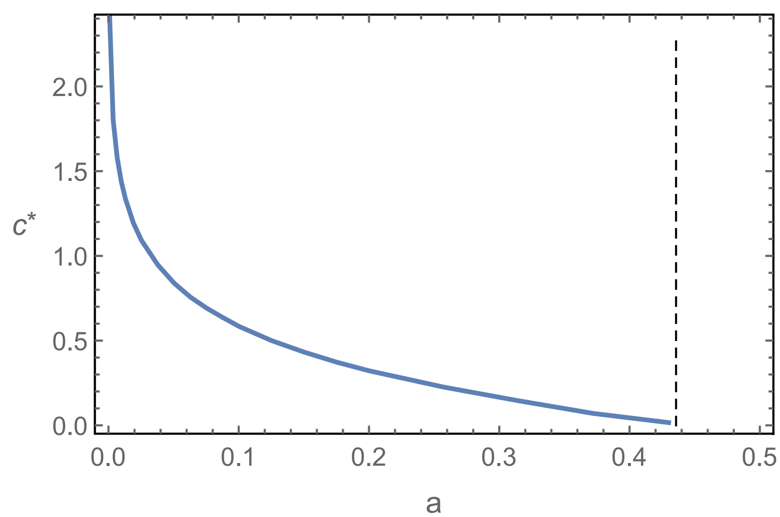

Figure 3: c^* vs. a.

fixed point condition for both $u_{n+1}(x)$ and c_n were met. To determine l^*, an upper and lower bound for l^* were identified and solutions were iterated until a fixed point condition for $u_n(x)$ was met, or until the maximum value of $u_n(x)$ became less than a. Bisection was then used to narrow the upper and lower bounds until an accuracy tolerance was reached. The results of this method were in excellent agreement with those from (5.11).

It is worth noting that figures similar to 3-6 were created for the case when $k(x)$ is the Gaussian kernel, with qualitatively similar results.

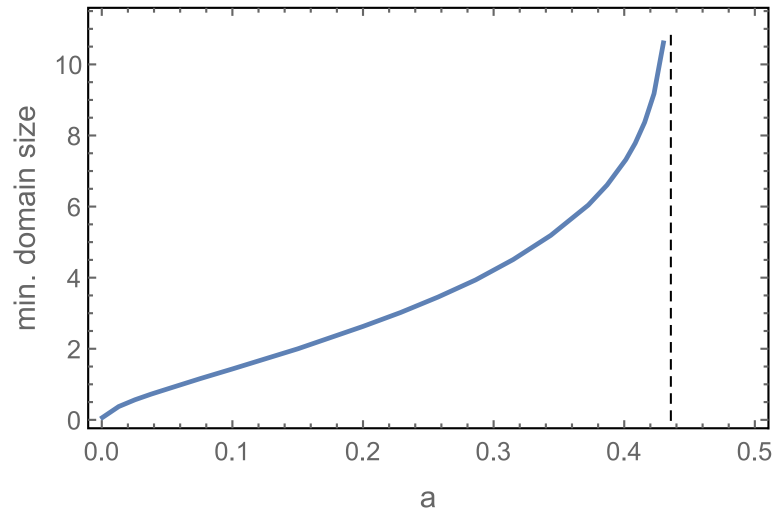

Figure 4: minimum domain size ($2l^*$) vs. a.

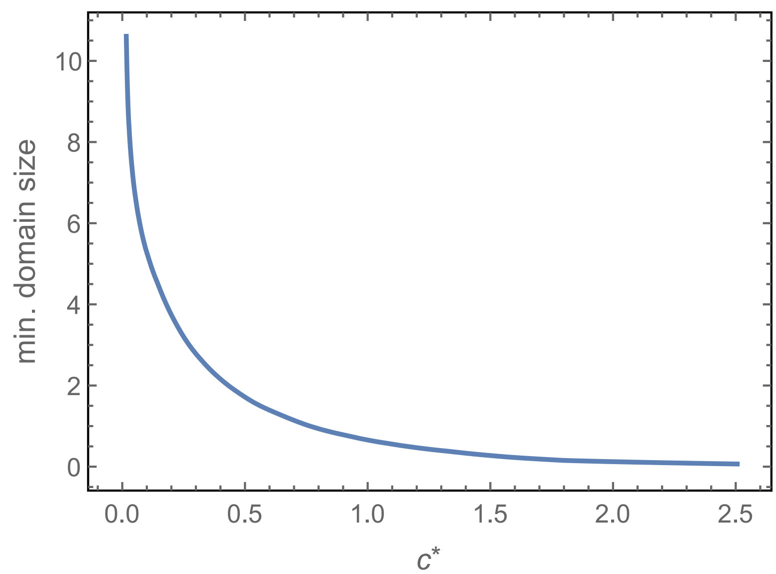

Figure 5: minimum domain size ($2l^*$) vs. c^*.

6 Discussion

In this paper, we studied the wave speed and critical patch size for (1.1) with a strong Allee effect. For $\Omega = (-\infty, \infty)$, we provided a set of simplified hypotheses on $k(x)$ and $g(u)$ for the existence of spreading speed and traveling waves, and positivity of wave speed. These hypotheses are satisfied by a variety of dispersal kernels and growth functions. Particularly, we showed that the sign of the wave speed is the same as that of $\int_0^1 [g(u) - u]du$ without any additional hypotheses other than those for the existence of spreading speeds and traveling waves. We have dropped one strong hypothesis made in

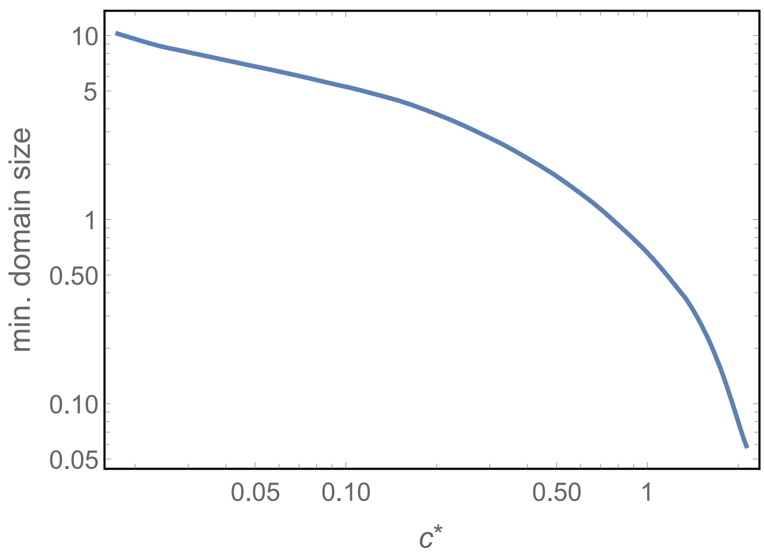

Figure 6: log-log plot of minimum domain size ($2l^*$) vs. a.

Lui [21] and substantially improved the main theoretical result in Wang et al. [31]. Our results can be easily applied to spatial population models described by (1.1).

For (1.1) with $\Omega = [-l, l]$ and $k(x)$ even, we proved that if $\int_0^1 [g(u) - u]du > 0$ there is a critical patch size l^* such that for $l > l^*$ there exists a positive equilibrium and for $l < l^*$ all the solution approaches zero, and if $\int_0^1 [g(u) - u]du < 0$ for any $l > 0$ all the solutions approach zero. In the latter case the population cannot persist in space although the corresponding non-spatial model may predict positive equilibrium dynamics. It is interesting to see the direct connection between the positivity of traveling wave speed and existence of critical patch size and positive equilibrium in a bounded habitat. Our analysis showed that the equilibrium obtained by (4.3) for $l > l^*$ attracts solutions from above. Consequently there exists a large class of initial distributions for which the solutions persist in space. We provided Theorem 4.2 about bifurcations of critical patch size (or positive equilibrium) as the standard deviation of k varies under the condition $\int_0^1 [g(u) - u]du > 0$. It should be pointed out that if $\int_0^1 [g(u) - u]du < 0$, no matter how small the deviation is, there is no positive equilibrium. Our study for the Laplace kernel in Section 5 indicates the existence of ordered multiple positive equilibria when $\int_0^1 [g(u) - u]du > 0$ and $l > l^*$. We conjecture that this is true for other biologically meaningful kernels. We further conjecture that in general the smallest equilibrium is a repeller and the largest one is an attractor. Some new techniques may be needed to address these conjectures.

The methods developed for establishing the critical patch size for populations with a strong Allee effect are also useful in studying populations with a weak Allee effect or no Allee effect. In these two cases if growth occurs (i.e., $g'(0) > 1$) and $k(x)$ is even, the spreading speed is positive (see Weinberger [33]), and the analysis presented in Section 3 shows the existence of a critical patch size so that the population can persist. This particularly provides an alternative approach to investigate the critical patch size for integro-difference equations without Allee effect. In the case that there is a weak Allee effect and a Laplace kernel is used, one can follow the work in Section 4.5 and derive a similar integration formula for determining the critical patch size.

This paper assumes the growth function to be monotone. It is possible that a growth function is non-monotone, i.e., there exists overcompensation in population growth [8, 14]. It would be of interest to analytically study the spread and persistence for models with a strong Allee effect and a non-monotone growth function. Integro-difference equations with moving bounded or unbounded habitats in response to climate change have been studied for growth functions with no Allee affect [13, 15, 16, 36]. It is worth investigating the dynamics of populations with Allee effects in moving habitats. We leave these problems for future investigations.

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