# NORTHWESTERN UNIVERSITY 

# Traveling Waves in Models of Population Dynamics with Nonlocal Interactions 

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ABSTRACT<br>Traveling Waves in Models of Population Dynamics with Nonlocal Interactions

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This thesis focuses on ecological models of population dynamics and the traveling, migratory waves that can result when a stable state either displaces an unstable state, or displaces another stable state. We consider the effect of nonlocal interactions, where members of the species interact over a distance. This gives rise to integro-partial differential equations of reaction-diffusion type. Our work has encompassed two projects. The first considers a single species competing nonlocally with itself, while the second considers a food chain system of three species. In both, we consider traveling waves and determine how nonlocality can affect the speed of propagation, the stability of the equilibria, and the shape of the fronts.

In our first project, we developed a piecewise linear, reaction-diffusion model describing the growth and movement of a single species, $u$, so that when we considered a particular form of nonlocality, we were able to reduce the integro-PDE to a system of algebraic
equations. This allowed a full description of the traveling wave solutions. We also considered the effects of asymmetric nonlocality, where the distance over which the nonlocal interactions occurred was different to the left and to the right of a given location. We were able to show how the extent of the nonlocality and the strength of the asymmetry affected the speed of propagation of the traveling fronts, and how they could cause a loss of monotonicity in the solutions. Finally, we considered cases where the waves could propagate in either direction.

In our second project, we considered a three species food chain model, where species $u$ was preyed upon by species $v$, which in turn was preyed upon by species $w$. Our primary focus was on biological control, where the bottom species $u$ is an important crop, while $v$ is a pest that has infested the crop. The superpredator $w$ is introduced into this pestinfested environment in an attempt to restore the system to a pest-free state. For this model, we considered two types of nonlocality: one where the crop species $u$ competes nonlocally with itself, and the other where the superpredator $w$ is assumed to be highly mobile and therefore preys upon the pest $v$ in a nonlocal fashion. In this context, we examined how biological control could prove to be highly susceptible to noise, and could fail outright if the pest species was highly diffusive. We showed, however, that control could be restored if the superpredator was sufficiently diffusive, and that the control could be made robust if the superpredator behaved nonlocally. Since our focus was on biological control, where the superpredator is generally introduced artificially, our results point to properties of the superpredator which can lead to successful control.

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## Dedication

To my dad, who taught me to love learning.

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## CHAPTER 1

## Introduction

The focus of this thesis is on the behavior of traveling waves in models of population dynamics with nonlocal interactions. In this context, traveling wave solutions correspond to migratory behaviors of the species being modeled, while nonlocality refers to interactions that occur over a distance. The results of this thesis come from two distinct projects. The first project centers on the migratory behavior of a single species whose members compete nonlocally with each other for resources. We consider a piecewise linear simplification of the governing equation to create an analytically tractable model, and we fully describe the behavior of this resulting model. The second project in this thesis focuses on a three species foodchain model, along with several different types of nonlocality. We consider nonlocal intraspecies competition as in the first project, but also consider the effects of nonlocal predation on solutions of this foodchain model.

### 1.1. Traveling Waves in Population Models

The main focus of the projects presented in this thesis is on traveling wave solutions in models of population dynamics, which represent migrations. These solutions can be found through a transformation to a traveling coordinate, and they correspond to fronts that propagate rigidly at uniform speeds in the original, untransformed models. Our main goals when considering traveling wave solutions are to determine the speed of propagation and to describe the shape of the traveling fronts. We note that not all of the behaviors
discussed in this thesis are traveling wave solutions, as some do not travel at a uniform speed, and so do not correspond to solutions in a traveling frame. The techniques used for describing the propagation speed and front shapes, however, can still prove useful in these contexts.

The traveling waves discussed in this thesis tend to involve a front connecting two equilibrium states of the governing system, where one state displaces the other at a fixed rate, causing the connecting front to propagate. For most of the fronts presented, the propagation speed can be determined through considering the existence or stability of the state ahead of the front that is being displaced. Meanwhile, the shape of the front, and the existence of any patterns formed behind the front, can be determined by considering the stability of the state behind the front. We will see these techniques used throughout.

### 1.2. Nonlocality in Population Models

Nonlocality in models of population dynamics refers to interactions between individual organisms that occur over a distance, specifically, on a larger spatial scale than the organism's 'home range' where it resides. These long range interactions are often attributed to the relative mobility of the species involved. For example, members of a species may travel a distance to attain a scarce resource, competing with others for the resource, to both individuals' detriment, despite residing a distance from them. High mobility can also be used as a justification for nonlocal predation, where a mobile predator may seek out prey over a large distance, or where a mobile prey may wander into a predator's 'home range'. While mobility is a commonly used example of nonlocal interactions in biology, there are other mechanisms that give rise to long distance interactions. Plants that share
a water-table, whether through the use of extensive root systems or due to geographic effects such as a sloped hill, can compete nonlocally despite lacking basic mobility. There are even examples of species of plants, ants, and bacteria that release toxins into their environment to drive other individuals away, a behavior that would also create nonlocal interactions.

Mathematically, nonlocal interactions are represented through the use of a weighted average of the population about a given location, given by the integral of the population against a kernel function controlling the weighting. These convolution integrals then replace the population itself in the competition or predation terms in the governing equations. For example, intraspecies competition of a single species $u$ is represented through a mass action between two members of species $u$, that gives the quadratic term $-u^{2}$. When nonlocal competition is considered, the mass action is taken to be between a member of species $u$ and the weighted average of the species represented by the convolution $\varphi * u$ (where $\varphi$ is the kernel function), which gives instead the term $-u(\varphi * u)$.

### 1.3. An Analytically Tractable Switching Model

The first project detailed in this thesis centers on the migratory behavior of a single species whose members compete nonlocally with each other for resources, with a key simplification: the source term is taken to be piecewise linear, with a population threshold that acts as a switch between behaviors for small and large populations, and as a switch between local and nonlocal behavior. This piecewise linear simplification, along with the particular choice of kernel function and a transformation to a traveling frame, allows us to reduce the governing integro-partial differential equation to a system of algebraic
equations, which in turn allows for a full description of the solutions. The piecewise linear simplification not only allows for a description of the solutions, but also allows us to consider two important versions of the problem: the monostable version where extinction is unstable and even small populations grow; and the bistable version where extinction is stable and sufficiently small populations will die off.

The main results of this project center on how parameters representing the local net birth rate, the extent of the nonlocality, and the strength of the asymmetry of the kernel function affected the speed and shape of the traveling wave solutions. For the monostable problem, we determined a minimum speed above which traveling waves solutions exist. We were able to determine conditions under which the traveling front would lose its monotonicity and would have either decaying oscillations or a 'hump', a single local maximum, behind the front. For the bistable problem, we determined the unique propagation speed, along with conditions for the existence of decaying oscillations or a 'hump' in the wave front.

This project resulted in a paper published in Nonlinearity, [1], and this paper is included in its entirety in Chapter 2.

### 1.4. A Three Species Foodchain

The second project detailed in this thesis centers on a three species foodchain model, where the species $u$ is preyed upon by species $v$, which in turn is preyed upon by species $w$. The focus of this project is the problem of biological control. The prey species $u$ is considered a valuable crop while the species $v$ is a pest that has infested the crop. Biological control is the introduction of the superpredator species $w$ in an attempt to kill
off the pest $v$ and restore the crop $u$ to its pest-free state. With this system, we consider two types of nonlocality: nonlocal intraspecies competition of the crop species $u$; and nonlocal predation of the pest $v$ by the superpredator $w$. We note that the governing system of equations for this foodchain include ratio-dependent predation terms, which are discussed in detail in Chapter 3.

As with the first project, we were again interested in traveling waves, their propagation speed, and their shape. To that end, we analytically determined conditions for the stability of the various equilibrium states and described procedures for determining the critical extent of the nonlocality that would give rise to cellular patterns. Since our main focus was on biological control, we also considered when biological control was attainable, how it could fail, and what factors could ensure its success. Specifically, our results point to properties of the superpredator that can lead to successful control. While we did observe fronts of complete biological control, where a traveling pulse of the superpredator eliminated the pest and restored the pest-free state behind the front, we also observed a number of mechanisms that would trigger a resurgence of the pest: sufficient noise in the system, a high diffusivity of the pest species, or a moderate level of nonlocal predation by the superpredator. We also found, however, mechanisms that could suppress these triggers. If the diffusivity of the superpredator was high enough, or if the extent of the superpredator's nonlocal predation was large enough, successful biological control was obtainable.

This project led to a paper titled 'Biological Control with Nonlocal Interactions' accepted for publication in Mathematical Biosciences, which is included in its entirety in Chapter 4.

## CHAPTER 2

## A Nonlocal, Piecewise Linear Reaction-Diffusion Model

We consider an analytically tractable switching model that is a simplification of a nonlocal, nonlinear reaction-diffusion model of population growth where we take the source term to be piecewise linear. The form of this source term allows us to consider both the monostable and bistable versions of the problem. By transforming to a traveling frame and choosing specific kernel functions, we are able to reduce the problem to a system of algebraic equations. We construct solutions and examine the propagation speed and monotonicity of the resulting waves.

### 2.1. Introduction

In this chapter we develop an analytically tractable model to describe population migration waves for species with nonlocal intraspecies competition. The model permits an analytic description of wave propagation speeds, wave structure, and parameter dependencies. The model is applicable both to the monostable case, where the natural net birth rate is positive (extinction state unstable), and the bistable case, where the natural net birth rate is negative (extinction state stable). Furthermore, the model permits a description both of cases where the nonlocality is symmetric and where the nonlocality is asymmetric.

Our primary focus in the monostable case involves propagation of a species into an uninhabited region, facilitated by the instability of the extinction state and characterized
by a propagating traveling wave connecting a populated state to the extinction state. In the bistable case propagation can go in the opposite direction for some parameter ranges.

In animal species, propagating waves have been observed in a variety of species e.g., budmoths, grouses and voles [2]. These waves are often attributed to gradients in habitat productivity, and so are due to varying levels of resource scarcity. The biological mechanism underlying the traveling waves considered here is nonlocal competition for a scarce resource in a population where diffusion allows a degree of mobility, and where asymmetries in the nonlocal competition can represent resource gradients. There are of course a number of other mechanisms that may describe some of these observed waves: random, synchronized external forcing (e.g., weather events) $[\mathbf{2}, \mathbf{3}]$, direct trophic relationships with a synchronized or mobile population (e.g., mating events in a food source or a mobile predator species) [4], and landscape obstacles [2]. We do not consider such mechanisms in this chapter. Propagating waves of vegetation also occur in nature and are often attributed to competitive interactions for a scarce resource (often the scarce resource is water as these waves are commonly found in arid or semi-arid environments) [5].

In Section 2.2, we provide a background of reaction-diffusion population models and nonlocality, along with a review of relevant literature and a description of our piecewise linear switching model. A summary of our results can be found in Section 2.3. In Sections 2.4 and 2.5 we analytically describe solutions to our model in the monostable and bistable cases, respectively. Section 2.6 discusses numerical validation of our results. We present a summary of these results along with concluding remarks in Section 2.7.

### 2.2. Model

### 2.2.1. Traveling Waves in Reaction-Diffusion Models and Nonlocality

We begin with a well-known reaction-diffusion model, the local KPP equation [6]

$$
\begin{equation*}
\frac{\partial U}{\partial t}=\frac{\partial^{2} U}{\partial z^{2}}+F(U) \tag{2.1}
\end{equation*}
$$

where $F(U)$ is a nonlinear source term such that
(2.2a) $\quad F(0)=F(1)=0$,
(2.2b) $\quad F(U)>0, \quad 0<U<1$,
(2.2c) $\quad F^{\prime}(U)<F^{\prime}(0), \quad 0<U \leq 1$.

Traveling wave solutions of (2.1), i.e., solutions of the form $U(z, t)=u(x), x=z-c t$ satisfy

$$
\begin{equation*}
u^{\prime \prime}+c u^{\prime}+F(u)=0 \tag{2.3}
\end{equation*}
$$

along with the boundary conditions

$$
\begin{equation*}
u(-\infty)=1, \quad u(+\infty)=0 \tag{2.4}
\end{equation*}
$$

Throughout this chapter, we will use just $u$ to refer to the population level for both the traveling coordinate and time dependent problems (i.e. saying that the $u=1$ state is stable). A classical example of (2.1) is the Fisher equation [7], in which the nonlinearity
has a logistic form

$$
\begin{equation*}
F(U)=\mu U(1-U) \tag{2.5}
\end{equation*}
$$

with $\mu$ being a given positive constant.
From condition (2.2a), the only spatially homogeneous equilibria in the interval $[0,1]$ are $u=0$ and $u=1$, while condition (2.2b) guarantees that $u=0$ is unstable and $u=1$ is stable. This gives us the monostable problem, where extinction is unstable and even very small populations will tend towards the $u=1$ state. While this holds true for a wide variety of species, there are many populations that must exceed a threshold in order to survive - a phenomenon known as the Allee effect [8]. To model this, we remove conditions (2.2b), (2.2c), and instead assume that both the $u=0$ and $u=1$ states are stable. This gives us the bistable problem, which can be modeled with a simple cubic nonlinearity

$$
\begin{equation*}
F(U)=\mu U(U-\theta)(1-U) \tag{2.6}
\end{equation*}
$$

which now has $u=\theta$ as the unstable equilibrium state between stable states $u=0$ and $u=1$.

We next introduce nonlocality into the model. Nonlocal models were first considered in $[\mathbf{9}, \mathbf{1 0}]$, where biological motivations for nonlocality were presented. The papers were concerned with (2.1), taking the form of the nonlinear source term to be

$$
\begin{equation*}
F(U)=U\left[1+a U-b U^{2}-(1+a-b) \phi_{\delta} * U\right] . \tag{2.7}
\end{equation*}
$$

Here $\varphi_{\delta} * U$ is the convolution of the solution $U$ with the kernel $\varphi_{\delta}$,

$$
\varphi_{\delta} * U=\int_{-\infty}^{\infty} \varphi_{\delta}(x-y) U(y) d y
$$

(the dependence of the solution on time $t$ is omitted), where $\varphi_{\delta}$ is a scaled kernel function $\varphi$,

$$
\varphi_{\delta}(\omega)=\frac{1}{\delta} \varphi\left(\frac{\omega}{\delta}\right), \quad \delta>0, \quad \varphi(\omega) \geq 0, \quad \int_{-\infty}^{\infty} \varphi(\omega) d \omega=1
$$

so that $\varphi_{\delta}(\omega)$ approaches a delta function as $\delta \rightarrow 0$. Notice that the convolution $\varphi_{\delta} * U$ in the nonlinear source term (2.7) represents a nonlocal, weighted averaging of the population $U$ with the weighting independent of location. The kernel function $\varphi_{\delta}$ provides the weights while parameter $\delta$ controls the extent of the nonlocal averaging.

A nonlocal generalization of (2.5) that is often considered is

$$
\begin{equation*}
F(U)=\mu U\left(1-\phi_{\delta} * U\right) \tag{2.8}
\end{equation*}
$$

while a nonlocal generalization of (2.6) often takes the form

$$
\begin{equation*}
F(U)=\mu U(U-\theta)\left(1-\phi_{\delta} * U\right) \tag{2.9}
\end{equation*}
$$

We next provide a review of known results for these nonlocal models.

### 2.2.2. Literature Review

It is convenient to recall results for traveling waves in a local KPP equation $[\mathbf{6}, \mathbf{7}]$ that can be used for comparison with nonlocal equations. The main existence result for the local
problem (2.3) with conditions (2.2a), (2.2b), (2.2c) is that there exists a unique (up to translations in $x$ ) monotone solution with $u>0$ for any $c \geq c_{\mathrm{KPP}}$, where

$$
\begin{equation*}
c_{\mathrm{KPP}}=2 \sqrt{F^{\prime}(0)} \tag{2.10}
\end{equation*}
$$

A similar result is true for the problem (2.3) with only conditions (2.2a) and (2.2b), i.e. the monostable problem without the derivative condition (2.2c). The only difference being that the minimum speed $c_{\text {min }}$ is not necessarily given by (2.10); it may be greater than $c_{\mathrm{KPP}}$ and satisfies

$$
c_{\mathrm{KPP}} \leq c_{\min } \leq \sup _{0<u<1} 2 \sqrt{\frac{F(u)}{u}}
$$

which reduces to (2.10) if (2.2c) is also satisfied [11].
We now turn to a nonlocal generalization of the Fisher equation with logistic nonlinearity, i.e., (2.1) with nonlinear term (2.8). We remark that this equation can be rescaled as

$$
U(z, t)=\tilde{U}(\tilde{z}, \tilde{t}), \quad \tilde{z}=\mu^{1 / 2} z, \quad \tilde{t}=\mu t, \quad \tilde{\delta}=\mu^{1 / 2} \delta
$$

resulting in the problem with $\mu=1$, or

$$
U(z, t)=\tilde{U}(\tilde{z}, \tilde{t}), \quad \tilde{z}=\frac{z}{\delta}, \quad \tilde{t}=\frac{t}{\delta^{2}}, \quad \tilde{\mu}=\mu \delta^{2}
$$

resulting in the problem with $\delta=1$. It is convenient, however, to keep both $\mu$ and $\delta$ in the equation as these parameters signify different physical processes - the natural net birth rate $(\mu)$ and the extent of nonlocality ( $\delta$ ). We note that in the limit $\delta \rightarrow 0$, (2.8)
becomes the local logistic nonlinearity (2.5) and one might expect that the results for the nonlocal problem with $\delta \ll 1$ will be similar to those for the local problem.

An important difference between the nonlocal problem (2.1), (2.8) and its local version is that the stationary state $U=1$ is necessarily stable for the local equation, but may be unstable in the nonlocal case, depending on the kernel function. Indeed, linearizing (2.1), (2.8) about $U=1$, i.e. $U \sim 1+\epsilon \exp (\lambda t+i k x)$, gives the eigenvalues $\lambda(k)=-k^{2}-\mu \tilde{\varphi}_{\delta}(k)$, where $k$ is the wavenumber of the perturbation and $\tilde{\varphi}_{\delta}(k)$ is the Fourier transform of $\varphi_{\delta}$. Thus, if $\tilde{\varphi}_{\delta}(k)>0$ for all $k$, then $\lambda(k)<0$ for all $k$, and the stationary solution $U=1$ is stable. If, however, there are intervals of $k$ where $\tilde{\varphi}_{\delta}(k)<0$, it is possible that there will be positive $\lambda(k)$ for some $k$ so that the solution will be unstable to perturbations with these wavenumbers.

Two sets of boundary conditions for the traveling wave solutions are considered: the conditions (2.4) and the generalized conditions
(2.11) $\liminf _{x \rightarrow-\infty} u(x)>0, \quad u(+\infty)=0$.

The condition in (2.11) states that as $x$ goes to $-\infty$, the solution remains positive, and is appropriate when there is non-decaying oscillatory behavior behind the wavefront. We will also impose the physical restriction that $u(x) \geq 0$. However, neither monotonicity of $u(x)$ nor the condition $u(x)<1$ is in general required.

Solutions to (2.3), (2.8) satisfying either conditions (2.4) or (2.11) will describe stationary waves (with respect to the traveling coordinate $x$ ) that connect a populated state near $-\infty$ to an uninhabited region near $\infty$.

Important questions addressed in the literature are the existence of traveling waves and their behavior as $x \rightarrow-\infty$, i.e., whether they satisfy (2.4) or (2.11), as well as whether the wave is monotone, has one or more 'humps' in the populated region, or is oscillatory as $x \rightarrow-\infty$.

## Review: Monostable Case.

Studies of nonlocal models described in $[\mathbf{9}, \mathbf{1 0}]$, were concerned with (2.1) along with the monostable nonlinearity (2.7) (in [10], the nonlocal term also includes temporal averaging). In $[\mathbf{1 2}],(2.7)$ is studied for the Laplacian kernel, which allows one to reduce the nonlocal equation to a system of local equations. In particular, numerical simulations of traveling waves exhibiting hump solutions and formation of stationary periodic structure behind the front are presented. In [13] the limiting case of $\delta \gg 1$ (large extent nonlocality) is considered for (2.7) with the Laplacian kernel.

A number of works $[\mathbf{1 4 - 1 6}]$ are devoted to analysis of the nonlocal Fisher equation (2.3), (2.8). In $[\mathbf{1 4}]$ the problem is considered with $\delta=1$ under the additional conditions that the kernel $\varphi$ is sufficiently smooth and has a finite second moment. It is proved that for any $c \geq c_{\text {min }}=2 \sqrt{\mu}$, there exists at least one traveling wave solution $u(x) \geq 0$ that satisfies (2.3), (2.8), with conditions (2.11), and there are no traveling wave solutions $u(x) \geq 0$ with $c<c_{\text {min }}$. If $\mu$ is sufficiently small then for any $c \geq c_{\text {min }}$ there is a traveling wave solution that satisfies $(2.3),(2.8)$, with conditions (2.4). If $\tilde{\varphi}_{\delta}(k)>0$ for all real $k$, then the traveling waves satisfy (2.3), (2.8), with conditions (2.4) for all $\mu>0$ and all $c \geq c_{\text {min }}$. Finally, it is shown that for $\mu$ sufficiently large, the wave is not monotonic even if $u(-\infty)=1$.

In [16], it is shown that for $\mu=1$ and $\delta$ sufficiently small ('near-local' case) traveling waves that satisfy (2.4) exist. Also, an asymptotic analysis demonstrating existence of the wave for large propagation speed $c$ (with $\delta=1$ ) for the problem $(2.3),(2.8),(2.4)$ is performed (following the approach of $[\mathbf{1 7}]$ in the local case). Non-monotonic structure of the wave (a wave with a hump) is proved.

Some detailed results on existence of monotone traveling waves that connect $u=1$ and $u=0$, i.e., satisfy (2.4), are presented in $[\mathbf{1 5}]$ for kernels that satisfy some conditions of exponential decay (e.g. Laplacian or Gaussian kernels). Here (2.3), (2.8) with $\mu=1$ is considered and it is proved that for any $c \geq c_{\text {min }}$ there exists $\delta(c) \in(0,+\infty]$ such that (2.3), (2.8), (2.4) has a monotone traveling wave solution if and only if $\delta \leq \delta(c)$. Moreover, it is shown that for any $c \geq c_{\min }$ and $\delta<\delta(c)$ there are no other traveling waves such that $0<u(x)<1$.

## Review: Bistable Case.

There are a number of works devoted to nonlocal equations with bistable nonlinearities. In particular, in [18], (2.1) with a nonlinearity of the form (2.9) is considered. Existence of a traveling wave solution with the boundary conditions (2.11) is proved (for the near-local case, it is proved that the solution satisfies (2.4)). In [19-21], (2.1) with the nonlinear term taking the form

$$
F(U)=-a U+(a+1) U^{2}-U \cdot\left(\phi_{\delta} * U^{2}\right)
$$

is considered. The choice of nonlocality here is such that the problem becomes variational, which simplifies its analysis. The authors focus on both traveling waves and interacting
fronts that give rise to stationary pulse-like solutions. In [22] the nonlinearity of the form

$$
F(U)=U \cdot(1-U) \cdot\left(\phi_{\delta} * U\right)-a U
$$

is considered, and existence of a monotone traveling wave that connects two stable equilibria is proved.

### 2.2.3. Description of the Piecewise Linear Model

In this chapter, we consider a simplification of the full nonlinear problem where we take instead a piecewise linear source term. For specifically chosen kernel functions, we are able to reduce the problem to a system of algebraic equations, which allows us to examine the model's behavior analytically. Our piecewise linear model also allows us to consider both the monostable and bistable versions of the problem by changing the sign of a single parameter $(A)$. Furthermore, we find that this simplified model can still allow for a full range of monotonic, 'hump', and oscillatory solutions.

The model is

$$
\begin{equation*}
u^{\prime \prime}+c u^{\prime}+f(u)=0, \quad u(-\infty)=1, \quad u(\infty)=0 \tag{2.12}
\end{equation*}
$$

where

$$
f(u)= \begin{cases}A u, & u<\theta  \tag{2.13}\\ 1-\varphi * u, & u>\theta\end{cases}
$$

with some constants $A$ and $\theta$, where $0<\theta<1$.

- Assumption 1: In order to pin the traveling wave solution, it is assumed throughout the chapter that $u(0)=\theta$.
- Assumption 2: We assume that $u(x)>\theta$ for negative $x$ and $u(x)<\theta$ for positive $x$, which allows us to solve each case in its own region.

In this chapter we consider two kernel functions: the symmetric Laplacian kernel

$$
\begin{equation*}
\varphi_{\alpha}(x)=\frac{\alpha}{2} e^{-\alpha|x|}, \quad \alpha>0 \tag{2.14}
\end{equation*}
$$

and the asymmetric Laplacian kernel

$$
\Phi(x)=\frac{\alpha_{\ell} \alpha_{r}}{\alpha_{\ell}+\alpha_{r}}\left\{\begin{array}{ll}
e^{\alpha_{\ell} x}, & x<0,  \tag{2.15}\\
e^{-\alpha_{r} x}, & x>0
\end{array} \quad \alpha_{\ell}, \alpha_{r}>0\right.
$$

( $[\mathbf{1 6}]$ discusses how these kernels relate to resource-consumer dynamics). Since the Fourier transforms of these kernel functions are always positive, the $u=1$ state will be stable for all values of $\alpha$.

We note that when $\alpha_{\ell}=\alpha_{r}=\alpha$, the asymmetric kernel (2.15) reduces to the symmetric kernel (2.14). Thus the relative magnitudes of $\alpha_{\ell}$ and $\alpha_{r}$ control the degree of asymmetry. Now consider the limit where $\alpha, \alpha_{\ell}, \alpha_{r} \rightarrow \infty$. The kernel functions approach a delta function, and (2.12), (2.13) reduce to a completely local problem. The parameter $\alpha$ controls the extent of the nonlocality, where the extent of the nonlocality decreases as the magnitude of $\alpha$ grows. So for this new parameter $\alpha \sim 1 / \delta$.

The formulation (2.12), (2.13) allows us to consider two different cases based on the sign of $A$. When $A>0$, we have the monostable case where the stationary point $u=0$ is unstable, making $u=1$ the only stable equilibrium state (recall that we are using $u$ to
designate the population level in both the traveling wave and time dependent problem). When $A<0$, we have the bistable case as extinction is also stable.

In this chapter we will consider both the monostable and bistable cases of (2.12), (2.13), and examine how the strength of the local net birth rate $(|A|)$, the nonlocal threshold $(\theta)$, the extent of the nonlocality $(\alpha)$, and the degree of asymmetry ( $\alpha_{\ell}$ and $\alpha_{r}$ ) affect the propagation speed and monotonicity of traveling wave solutions. To this end, we use Assumption 2 to solve (2.12), (2.13). For the $u>\theta, x<0$ region, we can do this by using the specific kernel functions (2.14) or (2.15) to reduce the equation to a fourth order system [12] (see Appendix B), or we can more generally solve via a Laplace transform (see Appendix C). Either method yields a quartic equation for the eigenvalues. Appendix A contains an analysis of this equation, and this provides the form of the solution we take as an ansatz throughout this chapter.

To understand this model, we can consider the biological significance of the parameters $A$ and $\theta$, and the kernel function $\varphi$. Parameter $A$ is the local natural net birth rate which determines how rapidly a population below the $u=\theta$ threshold grows (monostable) or decays (bistable). If we now consider the parameter $\theta$, we first notice that $\theta$ appears as a population threshold below which a population will behave locally, and above which a population will exhibit nonlocal behavior. In the monostable case, $\theta$ defines the population level where the competition has begun to overtake the local natural net birth rate. So we take $u=\theta$ to be the population threshold between local $(u<\theta)$ and nonlocal $(u>\theta)$ behaviors. In the bistable case, $u=\theta$ represents the unstable state between stable extinction and the stable $u=1$ state. In this case, we see the Allee Effect - that sufficiently small populations tend to die off. Thus $\theta$ is the critical population threshold
for the Allee Effect in the bistable case. We assume then that if a population is too small to persist, it is also too small to behave nonlocally, and so we again have $\theta$ as the switch between local and nonlocal behaviors.

Our model is similar to the analytically tractable switching problem considered in [23], which takes the piecewise linear source term

$$
F(u)= \begin{cases}A u(x), & u<\theta  \tag{2.16}\\ 1-u(x-a), & u>\theta\end{cases}
$$

In [23], traveling waves are analytically constructed, including monotonic waves, nonmonotonic waves, and waves that exhibit an oscillatory state behind the wavefront. The main difference between our model and that in [23] is the way in which the nonlocality is incorporated. In our model, the nonlocality enters as a full convolution term, while in (2.16) the nonlocality is represented as a spatial translation (or equivalently as a delta function kernel centered at $x=a$ ), so that the nonlocality is always asymmetric. The difference in the nonlocality gives rise to some qualitatively different results. In [23], the existence of traveling waves connecting $u=0$ to a purely oscillatory 'wavetrain' state is shown. For our nonlocal problem (2.13), we find that such 'wavetrains' do not exist, and instead only 'decaying wavetrains' are present (this is the case because the $u=1$ state is stable for the kernel functions we consider). Finally, we also consider the bistable problem where $A<0$.

### 2.3. Summary of Results

Our main results for the monostable case $(A>0)$ are:

- There is a unique traveling wave solution that satisfies the boundary conditions (2.4), i.e. the wave in which the stable state $u=1$ displaces the unstable state $u=0$, for all parameter values and all $c \geq c_{\text {min }}$.
- The minimum speed, $c_{\text {min }}$, has been determined. It is $c_{\text {min }}=c_{\mathrm{KPP}}=2 \sqrt{A}$ for $A \geq A_{c r}$ and is greater than the KPP speed for $A<A_{c r}$.
- In the near-local case $(\alpha \gg 1)$ an asymptotic analysis gives asymptotically correct results at $O(1)$ and $O\left(\alpha^{-2}\right)$.
- It has been shown that the eigenvalues of the problem can be complex, which leads to solutions with an exponentially decaying oscillatory tail, and the boundary in parameter space separating real and complex eigenvalues has been determined for both symmetric and asymmetric kernels.
- In the case of real eigenvalues, conditions for the existence of a single hump are derived.

Our main results for the bistable case $(A<0)$ are:

- The bistable case has a unique propagation speed for any choice of parameter values. This speed has been determined for both the local and nonlocal problems, and for both the symmetric and asymmetric kernels.
- There exists a critical value $A_{c r}$, which has been determined for both the local and nonlocal problems, for which the wave speed $c=0$. For $A>A_{c r}$ the wave propagates to the left (i.e., the $u=0$ state displaces the $u=1$ state and $c<0$ ), while for $A<A_{c r}$, the $u=1$ state displaces the $u=0$ state.
- Conditions for the existence of a single hump are derived.


### 2.4. Monostable Case $(A>0)$

We start by considering the monostable version of the problem, given by (2.12), (2.13) with $A>0$. We reiterate that as $\alpha \rightarrow \infty, \varphi_{\alpha}(x) \rightarrow \delta(x)$, so in this regime one can expect to recover the solution of the local problem. For comparison purposes, we first consider the local problem.

### 2.4.1. Local Monostable Problem

The local version of (2.13) is given by

$$
f(u)= \begin{cases}A u, & u<\theta \\ 1-u, & u>\theta\end{cases}
$$

so that we solve

$$
\begin{align*}
& u^{\prime \prime}+c u^{\prime}+A u=0, \quad x>0, \quad 0<u<\theta,  \tag{2.17}\\
& u^{\prime \prime}+c u^{\prime}+1-u=0, \quad x<0, \quad u>\theta .
\end{align*}
$$

We want to determine both the solution and the values of $c>0$ for which this solution exists. Note that we are interested in the solution $u$ such that $u>0$. The form of the solution is

$$
u(x)= \begin{cases}u_{+}(x) \equiv p_{1}^{0} e^{\mu_{1} x}+p_{2}^{0} e^{\mu_{2} x}, & x>0  \tag{2.18}\\ u_{-}(x) \equiv 1+q_{0} e^{\lambda_{0} x}, & x<0\end{cases}
$$

with the matching conditions

$$
\begin{equation*}
u_{-}(0)=u_{+}(0)=\theta, \quad u_{-}^{\prime}(0)=u_{+}^{\prime}(0) . \tag{2.19}
\end{equation*}
$$

Here

$$
\begin{equation*}
\mu_{1}=-\frac{c}{2}+\sqrt{\frac{c^{2}}{4}-A}<0, \quad \mu_{2}=-\frac{c}{2}-\sqrt{\frac{c^{2}}{4}-A}<0, \quad \lambda_{0}=-\frac{c}{2}+\sqrt{\frac{c^{2}}{4}+1}>0 \tag{2.20}
\end{equation*}
$$

We note now that the case of repeated roots, when $c=c_{\mathrm{KPP}}=2 \sqrt{A}$, will follow from this general case in the limit as $c \rightarrow c_{\mathrm{KPP}}$. Indeed all of the results we obtain throughout remain unchanged under this limit. Using the matching conditions (2.19) we obtain

$$
\begin{equation*}
p_{1}^{0}=-\frac{(1-\theta) \lambda_{0}+\theta \mu_{2}}{\mu_{1}-\mu_{2}}, \quad p_{2}^{0}=\theta-p_{1}^{0}=\frac{(1-\theta) \lambda_{0}+\theta \mu_{1}}{\mu_{1}-\mu_{2}}, \quad q_{0}=-(1-\theta) \tag{2.21}
\end{equation*}
$$

We now discuss for what values of $c$ the solution exists. An expected condition would be that it exists for any $c \geq c_{\text {min }}=c_{\mathrm{KPP}}$, which is dictated by the behavior of the solution at $+\infty$. It turns out however that the condition that $u>0$ can impose more restrictions on the minimum speed. It can be easily shown that the condition $u>0$ is equivalent to $p_{1}^{0}>0$, from which

$$
(1-\theta) \sqrt{\frac{c^{2}}{4}+1}<\frac{c}{2}+\theta \sqrt{\frac{c^{2}}{4}-A} .
$$

Taking the square of both sides of this inequality yields the condition

$$
g(c) \equiv c \theta \sqrt{\frac{c^{2}}{4}-A}+\frac{1}{2} \theta c^{2}>(1-\theta)^{2}+A \theta^{2}
$$

Since $g(c)$ is a monotonically increasing function of $c$ with the domain of definition $c \geq$ $2 \sqrt{A}$, if $g(2 \sqrt{A})>(1-\theta)^{2}+A \theta^{2}$ then the inequality is satisfied for all $c \geq 2 \sqrt{A}$, i.e., the
minimum value of $c$ is $c_{\text {min }}=c_{\mathrm{KPP}}$. If, however, $g(2 \sqrt{A})<(1-\theta)^{2}+A \theta^{2}$, i.e.,

$$
\begin{equation*}
A<\frac{(1-\theta)^{2}}{2 \theta-\theta^{2}} \equiv A_{c r} \tag{2.22}
\end{equation*}
$$

then the minimum speed is determined by the equation

$$
g\left(c_{\min }\right)=(1-\theta)^{2}+A \theta^{2}
$$

resulting in

$$
\begin{equation*}
c_{\text {min }}^{2}=\frac{\left[(1-\theta)^{2}+A \theta^{2}\right]^{2}}{\theta(1-\theta)[1-\theta(A+1)]} \tag{2.23}
\end{equation*}
$$

We observe that $c_{\text {min }} \geq c_{\text {KPP }}$ for all $A$ and $\theta$. The graphs of the two dependencies as function of $A$ touch at $A=A_{c r}$, and $c_{m i n}$ will be realized as the minimum speed for $A<A_{c r}$.

### 2.4.2. Nonlocal Equation with Symmetric Kernel $\varphi_{\alpha}$

We now consider the full nonlocal problem. Here we are solving

$$
\begin{array}{ll}
u^{\prime \prime}+c u^{\prime}+A u=0, & x>0, \quad 0<u<\theta  \tag{2.24}\\
u^{\prime \prime}+c u^{\prime}+1-\phi_{\alpha} * u=0, & x<0, \quad u>\theta
\end{array}
$$

The solution can be written as

$$
u(x)= \begin{cases}u_{+}(x) \equiv p_{1} e^{\mu_{1} x}+p_{2} e^{\mu_{2} x}, & x>0  \tag{2.25}\\ u_{-}(x) \equiv 1+q_{1} e^{\lambda_{1} x}+q_{2} e^{\lambda_{2} x}, & x<0\end{cases}
$$

with the matching conditions

$$
\begin{equation*}
u_{-}(0)=u_{+}(0)=\theta, \quad u_{-}^{\prime}(0)=u_{+}^{\prime}(0) \tag{2.26}
\end{equation*}
$$

Here $q_{1}, q_{2}, p_{1}, p_{2}$ are as yet undetermined coefficients, and $\mu_{1}, \mu_{2}$ are the same as in (2.20) so that $u_{+}$is a solution of (2.24) for $x>0$. We now consider the region $x<0$ and substitute the solution (2.25) into (2.24). Performing the calculation we obtain
(2.27a) $u^{\prime \prime}+c u^{\prime}+1-\phi * u=$

$$
\begin{align*}
& \text { (2.27b) } q_{1} e^{\lambda_{1} x}\left[\lambda_{1}^{2}+c \lambda_{1}-\frac{\alpha^{2}}{\alpha^{2}-\lambda_{1}^{2}}\right]+q_{2} e^{\lambda_{2} x}\left[\lambda_{2}^{2}+c \lambda_{2}-\frac{\alpha^{2}}{\alpha^{2}-\lambda_{2}^{2}}\right]+  \tag{2.27b}\\
& (2.27 \mathrm{c})
\end{align*} \frac{\alpha}{2} e^{\alpha x}\left[\frac{1}{\alpha}-\frac{q_{1}}{\lambda_{1}-\alpha}-\frac{q_{2}}{\lambda_{2}-\alpha}+\frac{p_{1}}{\mu_{1}-\alpha}+\frac{p_{2}}{\mu_{2}-\alpha}\right] .
$$

To ensure (2.27b) is equal to zero, $\lambda_{1}$ and $\lambda_{2}$ must satisfy

$$
\begin{equation*}
R(\lambda) \equiv\left(\lambda^{2}+c \lambda\right)\left(1-\frac{\lambda^{2}}{\alpha^{2}}\right)=1 \tag{2.28}
\end{equation*}
$$

It is easy to verify that depending on the parameters $c$ and $\alpha$,(2.28) can have either two positive solutions or no positive solutions. Here $0<\lambda<\alpha$ are the only positive values of $\lambda$ where $R(\lambda)$ is positive, and thus all of the positive roots to (2.28) must be in that interval.

In order for the solution (2.25) to satisfy (2.24) we need to impose the condition that (2.27c) is also equal to zero, which together with the matching conditions (2.26) represents a system of four linear equations for the four constants $q_{1}, q_{2}, p_{1}$ and $p_{2}$. Solving this system of equations we obtain

$$
\begin{equation*}
p_{1}=\frac{\left(\mu_{1}-\alpha\right)\left[\theta\left(\mu_{2}-\lambda_{2}\right)\left(\mu_{2}-\lambda_{1}\right)+\frac{1}{\alpha} \lambda_{1} \lambda_{2}\left(\mu_{2}-\alpha\right)\right]}{\left(\mu_{1}-\mu_{2}\right)\left[\lambda_{1} \lambda_{2}-\mu_{1} \mu_{2}-\alpha\left(\lambda_{1}+\lambda_{2}-\mu_{1}-\mu_{2}\right)\right]}, \tag{2.29a}
\end{equation*}
$$

$$
\begin{equation*}
p_{2}=\theta-p_{1} \tag{2.29b}
\end{equation*}
$$

(2.29c) $q_{1}=p_{1} \frac{\mu_{1}-\mu_{2}}{\lambda_{1}-\lambda_{2}}+\frac{(1-\theta) \lambda_{2}+\theta \mu_{2}}{\lambda_{1}-\lambda_{2}}$,
$(2.29 \mathrm{~d}) q_{2}=\theta-1-q_{1}$.
2.4.2.1. Complex $\lambda$. We now want to examine when (2.28) has complex solutions. Note that when $\lambda$ are real, the solution (2.25) can be monotonic (though it does not necessarily have to be, as we will see later when we discuss hump conditions). When $\lambda$ are complex, we instead have an exponentially decaying oscillatory tail behind the wavefront for $x<0$.

We begin by deriving a parametric dependence of the solution of (2.28), specifically, $\lambda_{1}, \lambda_{2}$ and $c$, with $s$ being the parameter, $\alpha$ and $\theta$ fixed. We introduce

$$
\sigma_{1}=\lambda_{1}+\lambda_{2}, \quad \sigma_{2}=\lambda_{1} \lambda_{2}
$$

Then following the calculations in Appendix A, (2.28) gives the symmetric parameterization

$$
\begin{equation*}
\frac{\sigma_{1}}{\sigma_{2}}=\alpha \sqrt{\frac{\left(s^{2}+s+\frac{1}{\alpha^{2}}\right)\left(s+\frac{1}{\alpha^{2}}\right)}{1+s}} \equiv h_{0}(s), \quad \sigma_{2}=\frac{1}{s}, \quad c=h_{0}(s) \frac{s^{2}-\frac{1}{\alpha^{2}}}{s\left(s+\frac{1}{\alpha^{2}}\right)} . \tag{2.30}
\end{equation*}
$$

The dependence of $\sigma_{1}$ and $\sigma_{2}$ on $s$ can be easily translated into a dependence of $\lambda_{1}$ and $\lambda_{2}$ on $s$ since the $\lambda$ 's satisfy

$$
\begin{equation*}
\lambda^{2}-\sigma_{1} \lambda+\sigma_{2}=0 \quad \longrightarrow \quad \lambda_{1,2}=\frac{1}{2 s}\left[h_{0} \pm \sqrt{h_{0}^{2}-4 s}\right] \tag{2.31}
\end{equation*}
$$

Now (2.31) can be used to distinguish between the cases of real and complex $\lambda$. Indeed, the critical condition is $h^{2}=4 s$, from which

$$
\begin{equation*}
\frac{1}{\alpha^{2}}=\frac{3}{2} s^{2}+s \pm \frac{1}{2} s \sqrt{9 s^{2}+8 s}, \quad c=\frac{2}{\sqrt{s}} \frac{s^{2}-\frac{1}{\alpha^{2}}}{s+\frac{1}{\alpha^{2}}} \tag{2.32}
\end{equation*}
$$



Figure 2.1. The boundary of existence of real positive solutions $\lambda$ in the $(\alpha, c)$ plane. There are two real positive solutions $\lambda$ above the boundary (which corresponds to the minus sign in (2.32)), and complex conjugate solutions with positive real part below.

Figure 2.1 shows this boundary of the existence of real eigenvalues $\lambda$. Here we see that as $\alpha$ decreases, i.e. the extent of the nonlocality increases, $\lambda$ becomes complex for a larger range of wave speeds, so that waves with exponentially decaying oscillatory tails
dominate. This observation is in agreement with known results for the nonlocal Fisher equation (2.3), (2.8) [14].

Figures 2.2 a and 2.2 b show the solution $u$ from (2.25) for $\alpha=4$ and $\alpha=0.01$, respectively, with $c=2, \theta=0.5$, and $A=1$ for both cases. Figure 2.2 a shows the typical behavior of a monotonic wave, while Figure 2.2b shows a solution with complex eigenvalues, which gives the exponentially decaying oscillatory tails. In Figure 2.2c, we consider the same wave as in Figure 2.2b, but now show $\log |u-1|$ on the vertical axis. This allows us to more readily see the decaying oscillations in the wave as $x \rightarrow-\infty$.


(c) $\alpha=0.01, c=2, \theta=0.5, A=1$

Figure 2.2. A plot of the solution $u$ for two sets of parameters $\alpha, c, \theta$, and A. 2.2a: the typical behavior of monotonic wavefronts that exist for larger values of $\alpha ; 2.2 \mathrm{~b}$ : the typical behavior of wavefronts with exponentially decaying oscillatory tails that exist for smaller values of $\alpha$; 2.2c: the value of $\log |u-1|$ for the same wave as 2.2 b , which allows us to see the decaying oscillations in the wave.
2.4.2.2. Near-local problem: $\alpha \gg 1$. We now consider the problem with large $\alpha$. We expect that in the limit as $\alpha \rightarrow \infty$ we will recover the solution of the local problem. The expansion of the eigenvalues $\lambda_{1}$ and $\lambda_{2}$ for $\alpha \gg 1$ are

$$
\begin{align*}
& \lambda_{1}=\alpha-\frac{1}{2 \alpha}+\frac{c}{2 \alpha^{2}}+O\left(\frac{1}{\alpha^{3}}\right)  \tag{2.33}\\
& \lambda_{2}=\lambda_{0}+\frac{1}{\alpha^{2}} \frac{\lambda_{0}^{2}}{2 \lambda_{0}+c}+O\left(\frac{1}{\alpha^{4}}\right) \tag{2.34}
\end{align*}
$$

where $\lambda_{0}$ is the exponent that appears in the local problem, (cf. (2.20)). Substituting these expansions into the expressions for the coefficients we indeed obtain the solution of the local problem at the leading order (cf. (2.21)) and small corrections that account for large $\alpha$ :

$$
\left.\begin{array}{l}
p_{1} \sim-\frac{(1-\theta) \lambda_{0}+\theta \mu_{2}}{\mu_{1}-\mu_{2}}-\frac{1}{\alpha^{2}} \frac{\lambda_{0}^{2}}{\left(2 \lambda_{0}+c\right)\left(\mu_{1}-\mu_{2}\right)}=p_{1}^{0}-\frac{1}{\alpha^{2}} \frac{\lambda_{0}^{2}}{\left(2 \lambda_{0}+c\right)\left(\mu_{1}-\mu_{2}\right)}, \\
p_{2} \sim \frac{(1-\theta) \lambda_{0}+\theta \mu_{1}}{\mu_{1}-\mu_{2}}+\frac{1}{\alpha^{2}} \frac{\lambda_{0}^{2}}{\left(2 \lambda_{0}+c\right)\left(\mu_{1}-\mu_{2}\right)}=p_{2}^{0}+\frac{1}{\alpha^{2}} \frac{\lambda_{0}^{2}}{\left(2 \lambda_{0}+c\right)\left(\mu_{1}-\mu_{2}\right)}, \\
q_{1} \sim-\frac{1}{\alpha^{3}} \frac{\lambda_{0}^{2} \theta}{\left(2 \lambda_{0}+c\right)}=O\left(\frac{1}{\alpha^{3}}\right), \\
q_{2}
\end{array}\right) \sim-(1-\theta)+\frac{1}{\alpha^{3}} \frac{\lambda_{0}^{2} \theta}{\left(2 \lambda_{0}+c\right)}=q_{0}+\frac{1}{\alpha^{3}} \frac{\lambda_{0}^{2} \theta}{\left(2 \lambda_{0}+c\right)} .
$$

These results allow us to see, in particular, how the nonlocality affects the minimum speed of the wave, at least for large $\alpha$. Since the condition that determines the allowed speed is $p_{1}>0$, and since the $O\left(\alpha^{-2}\right)$ correction to the local value of $p_{1}$ is negative, we see that the nonlocality reduces the parameter range where the minimum speed is the KPP speed $2 \sqrt{A}$. The minimum speed for $\alpha$ not necessarily large will be addressed later.

### 2.4.3. Nonlocal Equation with Asymmetric Kernel $\Phi$

We now consider the asymmetric problem using the kernel (2.15). Substituting the solution (2.25), where $\lambda_{1}$ and $\lambda_{2}$ are yet to be determined, into (2.24) for $x<0$ with this kernel, we obtain
(2.35a) $u^{\prime \prime}+c u^{\prime}+1-\phi * u=$

$$
\begin{align*}
& q_{1} e^{\lambda_{1} x}\left[\lambda_{1}^{2}+c \lambda_{1}-\frac{\alpha_{\ell} \alpha_{r}}{\left(\alpha_{\ell}-\lambda_{1}\right)\left(\alpha_{r}+\lambda_{1}\right)}\right]+  \tag{2.35b}\\
& q_{2} e^{\lambda_{2} x}\left[\lambda_{2}^{2}+c \lambda_{2}-\frac{\alpha_{\ell} \alpha_{r}}{\left(\alpha_{\ell}-\lambda_{2}\right)\left(\alpha_{r}+\lambda_{2}\right)}\right]+ \\
& \frac{\alpha_{\ell} \alpha_{r}}{\alpha_{\ell}+\alpha_{r}} e^{\alpha_{\ell} x}\left[\frac{1}{\alpha_{\ell}}-\frac{q_{1}}{\lambda_{1}-\alpha_{\ell}}-\frac{q_{2}}{\lambda_{2}-\alpha_{\ell}}+\frac{p_{1}}{\mu_{1}-\alpha_{\ell}}+\frac{p_{2}}{\mu_{2}-\alpha_{\ell}}\right]
\end{align*}
$$

Thus, $\lambda_{1}$ and $\lambda_{2}$ must satisfy

$$
\begin{equation*}
R(\lambda) \equiv\left(\lambda^{2}+c \lambda\right)\left(1-\frac{\lambda}{\alpha_{\ell}}\right)\left(1+\frac{\lambda}{\alpha_{r}}\right)=1 \tag{2.36}
\end{equation*}
$$

Notice again that $0<\lambda<\alpha_{\ell}$ are the only positive values of $\lambda$ where $R(\lambda)$ is positive, and thus all of the positive roots to (2.36) must be in that interval.

Since $\lambda_{1}$ and $\lambda_{2}$ satisfy (2.36), (2.35b) and (2.35c) are equal to zero. In order for the solution (2.25) to satisfy (2.24) we need to impose the condition that (2.35d) is equal to zero, which together with the matching conditions (2.26) represents a system of four linear equations for the four constants $q_{1}, q_{2}, p_{1}$, and $p_{2}$. Solving this system of equations we obtain

$$
\begin{equation*}
p_{1}=\frac{\left(\mu_{1}-\alpha_{\ell}\right)\left[\theta\left(\mu_{2}-\lambda_{2}\right)\left(\mu_{2}-\lambda_{1}\right)+\frac{1}{\alpha_{\ell}} \lambda_{1} \lambda_{2}\left(\mu_{2}-\alpha_{\ell}\right)\right]}{\left(\mu_{1}-\mu_{2}\right)\left[\lambda_{1} \lambda_{2}-\mu_{1} \mu_{2}-\alpha_{\ell}\left(\lambda_{1}+\lambda_{2}-\mu_{1}-\mu_{2}\right)\right]}, \tag{2.37a}
\end{equation*}
$$

(2.37b) $p_{2}=\theta-p_{1}$,

$$
\begin{align*}
& \text { (2.37c) } q_{1}=p_{1} \frac{\mu_{1}-\mu_{2}}{\lambda_{1}-\lambda_{2}}+\frac{(1-\theta) \lambda_{2}+\theta \mu_{2}}{\lambda_{1}-\lambda_{2}},  \tag{2.37c}\\
& (2.37 \mathrm{~d}) q_{2}=\theta-1-q_{1} .
\end{align*}
$$

Notice that these are the same coefficients as in (2.29a)-(2.29d) for the symmetric case, except with $\alpha_{\ell}$ now replacing $\alpha$, and the $\lambda$ now satisfying (2.36) instead of (2.28).
2.4.3.1. Complex $\lambda$. As in the symmetric case, we introduce

$$
\sigma_{1}=\lambda_{1}+\lambda_{2}, \quad \sigma_{2}=\lambda_{1} \lambda_{2},
$$

and obtain the asymmetric parametric dependence derived in Appendix A
(2.38a) $\frac{\sigma_{1}}{\sigma_{2}}=h(s) \equiv \frac{\left(\alpha_{\ell}-\alpha_{r}\right)\left(s^{2}+s-\frac{1}{\alpha_{\ell} \alpha_{r}}\right)}{2(s+1)}+$

$$
\sqrt{\frac{\left(\alpha_{\ell}-\alpha_{r}\right)^{2}\left(s^{2}+s-\frac{1}{\alpha_{\ell} \alpha_{r}}\right)^{2}}{4(s+1)^{2}}+\frac{\left(\alpha_{\ell}-\alpha_{r}\right)^{2} \frac{s}{\alpha_{\ell}^{2} \alpha_{r}^{2}}+\left(s+\frac{1}{\alpha_{\ell} \alpha_{r}}\right)\left(s^{2}+s+\frac{1}{\alpha_{\ell} \alpha_{r}}\right)}{\frac{1}{\alpha_{\ell} \alpha_{r}}(s+1)}},
$$

(2.38b) $\sigma_{2}=\frac{1}{s}$,
(2.38c) $c(s)=h(s) \frac{s^{2}-\frac{1}{\alpha_{\ell} \alpha_{r}}}{s\left(s+\frac{1}{\alpha_{\ell} \alpha_{r}}\right)}+\frac{\alpha_{\ell}-\alpha_{r}}{1+\alpha_{\ell} \alpha_{r} s}$.

We again notice that the $\lambda$ 's satisfy

$$
\lambda^{2}-\sigma_{1} \lambda+\sigma_{2}=0 \quad \Longrightarrow \quad \lambda_{1,2}=\frac{1}{2 s}\left[h \pm \sqrt{h^{2}-4 s}\right]
$$

Thus the critical case for complex $\lambda$ is $h^{2}=4 s$. Using this condition we can solve for $\alpha_{\ell}$ as a function of $\alpha_{r}$ and $s$. This gives us

$$
\begin{align*}
& g\left(\alpha_{r}, s\right) \equiv \frac{2 s \sqrt{s}(s+1) \alpha_{r}^{2}+s(3 s+4) \alpha_{r}+2 \sqrt{s}}{2\left(s^{2}(s+1) \alpha_{r}^{2}+2 s \sqrt{s}(s+1) \alpha_{r}+s\right)}  \tag{2.39a}\\
& \alpha_{\ell}=g \pm \sqrt{g^{2}-\frac{s \alpha_{r}^{2}+2 \sqrt{s} \alpha_{r}+1}{s^{2}(s+1) \alpha_{r}^{2}+2 s \sqrt{s}(s+1) \alpha_{r}+s}}
\end{align*}
$$

Fixing $\alpha_{r}$ in (2.39a)-(2.39b) gives us, along with (2.38a)-(2.38c), a parametric curve in the $\left(\alpha_{\ell}, c\right)$ plane describing this boundary. We notice that the smaller root (with the minus sign) corresponds only to negative values of $c$, leaving the larger root (with the plus sign) as the only relevant root in this case.

Figure 2.3 shows this boundary for a range of $\alpha_{r}$ values. We again see that for sufficiently large nonlocality - behind the wavefront, in the $x<0$ region - there are only solutions with complex $\lambda$. When we consider the asymmetry, we see that as $\alpha_{r}$ increases, that is as the positive $x$ direction becomes more local, there is an increased range of parameters that give solutions with an exponentially decaying oscillatory tail.
2.4.3.2. Minimum speed. As in the local case, we want to determine the minimum speed $c_{\text {min }}$. We recall that for the local problem, if $A$ is sufficiently large the minimum speed is the KPP speed, $c_{\text {min }}=c_{\mathrm{KPP}} \equiv 2 \sqrt{A}$. However, for smaller $A, c_{\text {min }}>c_{\mathrm{KPP}}$. This result comes from the requirement that $u>0$, which translates into the condition $p_{1}^{0}>0$.


Figure 2.3. The boundary of existence of real positive solutions $\lambda$ in the ( $\alpha_{\ell}, c$ ) plane described by (2.39a)-(2.39b) for a range of $\alpha_{r}$ values (from bottom to top: $2^{-3}$ to $2^{3}$ ). The dashed line corresponds to $\alpha_{r}=1$. For a fixed value of $\alpha_{r},(2.36)$ will have two real, positive solutions $\lambda$ above the corresponding boundary, and a pair of complex conjugate solutions below.

The corresponding condition $p_{1}>0$ should be used in the nonlocal problem to guarantee $u>0$. The condition $p_{1}=0$ can be written as

$$
\begin{equation*}
\theta\left(\mu_{2}-\lambda_{1}\right)\left(\mu_{2}-\lambda_{2}\right)+\frac{1}{\alpha_{\ell}} \lambda_{1} \lambda_{2}\left(\mu_{2}-\alpha_{\ell}\right)=0 \tag{2.40}
\end{equation*}
$$

where $\mu_{2}$ is given in (2.20) and $\lambda_{1}, \lambda_{2}$ satisfy (2.36). We will again use the asymmetric parametric dependence (2.38a)-(2.38c) from Appendix A, and rewrite (2.40) in terms of the parameter $s$ and solve for $\mu_{2}$ to get

$$
\begin{equation*}
\mu_{2}(s)=\frac{1}{2 s}\left[h(s)-\frac{1}{\alpha_{\ell} \theta}-\sqrt{\left(h(s)-\frac{1}{\alpha_{\ell} \theta}\right)^{2}+4 s \frac{1-\theta}{\theta}}\right] \tag{2.41}
\end{equation*}
$$

and

$$
\begin{equation*}
A(s)=-\mu_{2}^{2}(s)-c(s) \mu_{2}(s) \tag{2.42}
\end{equation*}
$$

Thus, the minimum speed is given parametrically by (2.38a)-(2.38c) and (2.42).


Figure 2.4. The minimum speeds with $\alpha_{\ell}=1, \theta=0.5$. The solid curves are the minimum speeds for a range of $\alpha_{r}$ values (from bottom to top: $2^{-2}$ to $2^{2}$ ) as a function of $A$ for the nonlocal problem. The dashed line is the symmetric case where $\alpha_{r}=\alpha_{\ell}=1$, and the dotted line is the minimum speed for the local problem. The mixed dotted-dashed line at the bottom is the KPP speed. For each curve the KPP speed is the minimum speed beyond the point where the two curves meet.

Figure 2.4 shows this speed for fixed $\alpha_{\ell}=1$ and $\theta=0.5$, and a range of $\alpha_{r}$ values. For each value of $\alpha_{r}$, the KPP speed (the mixed dotted-dashed line) is realized for $A$ sufficiently large (to the right of the point where the curves touch), while the parametric dependence (2.38a)-(2.38c), (2.42) represents the minimum speed for smaller $A$ (to the left of the point where the curves touch).

We observe for the symmetric case, corresponding to the dashed line in Figure 2.4, that when $A$ becomes sufficiently large, the KPP speed is realized as the minimum speed, but for smaller values of $A$, the minimum speed is larger than the KPP speed. When asymmetry is added to the problem, as the extent of the nonlocality in the positive $x$ direction is diminished (as $\alpha_{r}$ becomes larger), the critical value of $A$ is increased and the minimum speed for small $A$ increases.

We also considered a range of $\theta$ values (not pictured) and found that in all cases, increasing $\theta$ decreases the minimum speed. All the other observations from Figure 2.4 remained qualitatively unchanged.
2.4.3.3. Hump conditions. We want to determine whether the solution $u_{-}(x)$ given in (2.25), (2.37a)-(2.37d) is monotonic or has a single 'hump' - a local maximum located at some point $x=x_{m}<0$ in the case when $\lambda_{1}, \lambda_{2}$ are real and positive, and, for concreteness, when $\lambda_{1}>\lambda_{2}$.

Conditions for the maximum are $u_{-}^{\prime}\left(x_{m}\right)=0, u_{-}^{\prime \prime}\left(x_{m}\right)<0$, which can be written as

$$
\begin{align*}
& u_{-}^{\prime}\left(x_{m}\right)=q_{1} \lambda_{1} e^{\lambda_{1} x_{m}}+q_{2} \lambda_{2} e^{\lambda_{2} x_{m}}=0 \quad \Longrightarrow \quad e^{\left(\lambda_{1}-\lambda_{2}\right) x_{m}}=-\frac{q_{2} \lambda_{2}}{q_{1} \lambda_{1}}  \tag{2.43}\\
& u_{-}^{\prime \prime}\left(x_{m}\right)=q_{1} \lambda_{1}^{2} e^{\lambda_{1} x_{m}}+q_{2} \lambda_{2}^{2} e^{\lambda_{2} x_{m}}<0 \quad \Longrightarrow \quad q_{1} \lambda_{1}^{2} e^{\left(\lambda_{1}-\lambda_{2}\right) x_{m}}+q_{2} \lambda_{2}^{2}<0 \tag{2.44}
\end{align*}
$$

Using the last equation in (2.43) to eliminate the exponential in (2.44), we get

$$
q_{1} \lambda_{1}^{2}\left(-\frac{q_{2} \lambda_{2}}{q_{1} \lambda_{1}}\right)+q_{2} \lambda_{2}^{2}<0 \quad \Longrightarrow \quad-q_{2} \lambda_{2}\left(\lambda_{1}-\lambda_{2}\right)<0
$$

Thus, a necessary condition for the maximum to exist is $q_{2}>0$. Next, consider the last equation in (2.43). Since the exponent is negative, we must have

$$
0<-\frac{q_{2} \lambda_{2}}{q_{1} \lambda_{1}}<1 \quad \Longrightarrow \quad q_{1}<0, \quad q_{1} \lambda_{1}+q_{2} \lambda_{2}<0
$$

It is sufficient to require that $q_{2}>0$. Indeed, if $q_{2}>0$ then using (2.29a)-(2.29d) and recalling that $\theta<1$, we have

$$
q_{1}=-(1-\theta)-q_{2}<0
$$

and

$$
q_{1} \lambda_{1}+q_{2} \lambda_{2}=-(1-\theta) \lambda_{1}-q_{2}\left(\lambda_{1}-\lambda_{2}\right)<0 .
$$

The condition $q_{2}>0$ can be written as

$$
\begin{aligned}
& q_{2}=-(1-\theta)-q_{1}=-p_{1} \frac{\mu_{1}-\mu_{2}}{\lambda_{1}-\lambda_{2}}-\frac{(1-\theta) \lambda_{2}+\theta \mu_{2}}{\lambda_{1}-\lambda_{2}}-(1-\theta)= \\
& -\frac{1}{\lambda_{1}-\lambda_{2}}\left[p_{1}\left(\mu_{1}-\mu_{2}\right)+(1-\theta) \lambda_{1}+\theta \mu_{2}\right]= \\
& \frac{\left(\alpha_{\ell}-\lambda_{2}\right)\left[(1-\theta)\left(\lambda_{1}-\mu_{1}\right)\left(\lambda_{1}-\mu_{2}\right)+\frac{1}{\alpha_{\ell}} \mu_{1} \mu_{2}\left(\lambda_{1}-\alpha_{\ell}\right)\right]}{\left(\lambda_{1}-\lambda_{2}\right)\left[\lambda_{1} \lambda_{2}-\mu_{1} \mu_{2}-\alpha_{\ell}\left(\lambda_{1}+\lambda_{2}-\mu_{1}-\mu_{2}\right)\right]}>0 .
\end{aligned}
$$

It can be shown that the denominator in the above expression is negative. Taking into account that $\lambda_{2}<\lambda_{1}<\alpha_{\ell}$, see (2.36), we see that the condition $q_{2}>0$ reduces to

$$
\begin{equation*}
(1-\theta)\left(\lambda_{1}-\mu_{1}\right)\left(\lambda_{1}-\mu_{2}\right)+\frac{1}{\alpha_{\ell}} \mu_{1} \mu_{2}\left(\lambda_{1}-\alpha_{\ell}\right)<0 . \tag{2.45}
\end{equation*}
$$

Using expressions (2.20) for $\mu_{1}$ and $\mu_{2}$ we obtain the condition

$$
\begin{equation*}
A\left(\theta-\frac{\lambda_{1}}{\alpha_{\ell}}\right)>(1-\theta)\left(\lambda_{1}^{2}+c \lambda_{1}\right) \tag{2.46}
\end{equation*}
$$

Expressing $c$ and $\lambda_{1}$ in terms of $s$ (see Appendix A) for fixed $\alpha_{\ell}, \alpha_{r}$, and $\theta$, we get the parametric dependence (2.38a)-(2.38c) along with

$$
\begin{equation*}
\lambda_{1}=\frac{1}{2 s}\left[h+\sqrt{h^{2}-4 s}\right], \quad A=\frac{(1-\theta)\left(\lambda_{1}^{2}+c \lambda_{1}\right)}{\theta-\frac{\lambda_{1}}{\alpha_{\ell}}}, \quad\left(\lambda_{1}<\alpha_{\ell} \theta\right) \tag{2.47}
\end{equation*}
$$

which determines the boundary of existence of the hump solution. An additional condition is that $c \geq c_{\text {min }}$.

Figure 2.5 shows this region of existence of hump solutions. We again see that increasing $\alpha_{r}$ leads to an increased range of parameters that give these hump solutions, while decreasing $\alpha_{r}$ inhibits such behavior. We note that in this monostable case, hump solutions only appear for values of $\theta$ very close to 1 .

Figure 2.6 shows the typical behavior of the hump solution. Pictured is the set of parameters $\alpha_{\ell}=1, \alpha_{r}=4, \theta=0.99$, and $A=10$. The corresponding speed is $c=$ $6.32 \ldots$

### 2.5. Bistable Case $(A<0)$

We now consider the bistable version of the problem, given by (2.12), (2.13) with $A<0$. To emphasize this, we write (2.13) as

$$
f(u)= \begin{cases}-|A| u, & u<\theta  \tag{2.48}\\ 1-\phi_{\alpha} * u, & u>\theta\end{cases}
$$



Figure 2.5. Regions of existence of the hump solution in the $(A, c)$ plane for $\alpha_{\ell}=2$ and two values of $\theta$. The solid curves are the parametric dependence (2.47) for a range of $\alpha_{r}$ values (bottom to top: $0.5,0.67,1$, and $2^{2}$ through $2^{7}$ ). The dotted curve is the symmetric case $\alpha_{r}=\alpha_{\ell}=2$. The dashed curve is the minimum KPP speed. Region of existence is bounded by the dashed curve from below and solid/dotted curve from above, i.e., there appears to be no hump solution for $\theta=0.95$, but $\theta=0.99$ can allow for a hump solution for large enough $\alpha_{r}$.

As before, we will assume that $u(0)=\theta$ and $u(x)>\theta$ for $x<0, u(x)<\theta$ for $x>0$. We again start by considering the local version of the problem.

### 2.5.1. Local Bistable Problem

For the local, bistable problem, we have to solve

$$
\begin{align*}
& u^{\prime \prime}+c u^{\prime}-|A| u=0, \quad x>0, \quad 0<u<\theta,  \tag{2.49}\\
& u^{\prime \prime}+c u^{\prime}+1-u=0, \quad x<0, \quad u>\theta
\end{align*}
$$



Figure 2.6. A plot of the solution $u$ for $\alpha_{\ell}=1, \alpha_{r}=4, \theta=0.99$, and $A=10$. This graph shows the typical behavior of hump wavefronts in the monostable case.

We want to determine both the solution $u$ and the values of $c$ for which this solution exists. Unlike the monostable case, there is no continuous interval of speeds, and the speed does not have to be positive - the wave can propagate in either direction or even be stationary. The solution can be written as

$$
u(x)= \begin{cases}u_{+}(x) \equiv \theta e^{\mu_{0} x}, & x>0  \tag{2.50}\\ u_{-}(x) \equiv 1-(1-\theta) e^{\lambda_{0} x}, & x<0\end{cases}
$$

with the matching conditions

$$
\begin{equation*}
u_{-}(0)=u_{+}(0)=\theta, \quad u_{-}^{\prime}(0)=u_{+}^{\prime}(0) \tag{2.51}
\end{equation*}
$$

Here $\lambda_{0}$ is given in (2.20) and

$$
\begin{equation*}
\mu_{0}^{2}+c \mu_{0}-|A|=0 \quad \longrightarrow \quad \mu_{0}=-\frac{c}{2}-\sqrt{\frac{c^{2}}{4}+|A|}<0 \tag{2.52}
\end{equation*}
$$

The last matching condition serves to determine the propagation speed

$$
\begin{equation*}
c=\frac{(1-\theta)^{2}-|A| \theta^{2}}{\sqrt{\theta(1-\theta)[1-\theta+|A| \theta]}} \tag{2.53}
\end{equation*}
$$

Note that the numerator in (2.53) is equal to $2 \int_{0}^{1} f(u) d u$, so that the sign of $c$, i.e., the direction of propagation, depends on the sign of the integral of the source function, which is a well-known result for a local bistable equation with a general $f(u)$ that can be obtained by multiplying the equation by $u^{\prime}$ and integrating the result over the entire $x$-axis [24]. In particular, the condition for the wave to not propagate, i.e. to have $c=0$, is

$$
|A|=|A|_{c r}(\infty) \equiv \frac{(1-\theta)^{2}}{\theta^{2}}
$$

For $|A|<|A|_{c r}(\infty)$ the propagation speed is positive, i.e., the wave goes to the right and the $u=1$ state displaces the $u=0$ state. For $|A|>|A|_{c r}(\infty)$ the wave goes to the left $(c<0)$, and extinction replaces the populated state.

### 2.5.2. Nonlocal Equation with Symmetric Kernel $\varphi_{\alpha}$

We next consider the nonlocal problem

$$
\begin{array}{ll}
u^{\prime \prime}+c u^{\prime}-|A| u=0, & x>0, \quad 0<u<\theta  \tag{2.54}\\
u^{\prime \prime}+c u^{\prime}+1-\varphi_{\alpha} * u=0, & x<0, \quad u>\theta
\end{array}
$$

and seek the solution in the form

$$
u(x)= \begin{cases}u_{+}(x) \equiv p_{1} e^{\mu_{0} x}, & x>0  \tag{2.55}\\ u_{-}(x) \equiv 1+q_{1} e^{\lambda_{1} x}+q_{2} e^{\lambda_{2} x}, & x<0\end{cases}
$$

subject to the matching conditions (2.26). Substituting (2.55) into (2.54) yields
(2.56a) $u^{\prime \prime}+c u^{\prime}+1-\phi_{\alpha} * u=$
$q_{1} e^{\lambda_{1} x}\left[\lambda_{1}^{2}+c \lambda_{1}-\frac{\alpha^{2}}{\alpha^{2}-\lambda_{1}^{2}}\right]+q_{2} e^{\lambda_{2} x}\left[\lambda_{2}^{2}+c \lambda_{2}-\frac{\alpha^{2}}{\alpha^{2}-\lambda_{2}^{2}}\right]+$
(2.56c) $\frac{\alpha}{2} e^{\alpha x}\left[\frac{1}{\alpha}-\frac{q_{1}}{\lambda_{1}-\alpha}-\frac{q_{2}}{\lambda_{2}-\alpha}+\frac{p_{1}}{\mu_{0}-\alpha}\right]$.

As in the case of the monostable equation, $\lambda_{1}$ and $\lambda_{2}$ satisfy (2.28). Thus, in order for the solution (2.55) to satisfy (2.54) we need to impose the condition that the expression in (2.56c) is equal to zero, which, together with the matching conditions (2.26), represents a system of four linear equations for the four unknowns, $q_{1}, q_{2}, p_{1}$ and $c$. Solving these equations we obtain

$$
p_{1}=\theta, \quad q_{1}=\frac{\theta \mu_{0}-(\theta-1) \lambda_{2}}{\lambda_{1}-\lambda_{2}}, \quad q_{2}=\theta-1-q_{1}
$$

and

$$
\begin{equation*}
\frac{(\theta-1) \lambda_{2}-\theta \mu_{0}}{\left(\lambda_{1}-\alpha\right)\left(\lambda_{2}-\alpha\right)}=\frac{1-\theta}{\lambda_{2}-\alpha}+\frac{1}{\alpha}+\frac{\theta}{\mu_{0}-\alpha} \tag{2.57}
\end{equation*}
$$

which determines the speed $c$. Now (2.57) can be simplified to

$$
\begin{equation*}
\theta \mu_{0}^{2}-\mu_{0}\left[\theta\left(\lambda_{1}+\lambda_{2}\right)-\frac{1}{\alpha} \lambda_{1} \lambda_{2}\right]-(1-\theta) \lambda_{1} \lambda_{2}=0 . \tag{2.58}
\end{equation*}
$$

Once again we use

$$
\sigma_{1}=\lambda_{1}+\lambda_{2}, \quad \sigma_{2}=\lambda_{1} \lambda_{2}
$$

and the symmetric parameterization (2.30). We rewrite (2.58) in terms of $\sigma_{1}$ and $\sigma_{2}$ as

$$
\mu_{0}^{2}-\mu_{0}\left[\sigma_{1}-\frac{1}{\alpha \theta} \sigma_{2}\right]-\frac{1-\theta}{\theta} \sigma_{2}=0
$$

and then in terms of $s$ using the parametric dependencies, giving

$$
s \mu_{0}^{2}-\mu_{0}\left[h_{0}-\frac{1}{\alpha \theta}\right]-\frac{1-\theta}{\theta}=0 .
$$

We solve the equation for $\mu_{0}$ to obtain

$$
\mu_{0}(s)=\frac{1}{2 s}\left[h_{0}(s)-\frac{1}{\alpha \theta}-\sqrt{\left(h_{0}(s)-\frac{1}{\alpha \theta}\right)^{2}+4 s \frac{1-\theta}{\theta}}\right] .
$$

Finally, (2.52) gives

$$
\begin{equation*}
|A|(s)=\mu_{0}^{2}(s)+c \mu_{0}(s) \tag{2.59}
\end{equation*}
$$

Using (2.30), we can thus obtain the propagation speed as a function of $|A|$, where $\alpha$ and $\theta$ are fixed.


Figure 2.7. Propagation speed in the bistable case as a function of $|A|$. Here $\theta=0.5$. The dashed curve is the speed for the local problem. The solid curves are the speed for nonlocal problem with an increasing range of $\alpha$ values (left to right: $2^{2}$ through $2^{-2}$ ).

In Figure 2.7 we show the propagation speed as a function of $|A|$ for $\theta=0.5$ and a range of $\alpha$ values. Notice that as $\alpha$ increases, the propagation speed approaches that of the local problem, as it should. On the other hand, as $\alpha$ decreases - as the extent of the nonlocality becomes greater - the propagation speed increases. It is perhaps better to say instead that the propagation speed becomes more positive, meaning that the $u=1$ state is more readily displacing the $u=0$ state. Upon increasing the value of $\theta$ (not pictured), we find that the propagation speed again decreases, as in the monostable case.

Of particular interest is the case $c=0$. Here (2.30) implies $s=1 / \alpha$, so that

$$
h_{0}(s)=\sqrt{1+\frac{2}{\alpha}}, \quad \mu_{0}=\frac{\alpha}{2}\left[\sqrt{1+\frac{2}{\alpha}}-\frac{1}{\alpha \theta}-\sqrt{\left(\sqrt{1+\frac{2}{\alpha}}-\frac{1}{\alpha \theta}\right)^{2}+\frac{4}{\alpha} \frac{1-\theta}{\theta}}\right],
$$

and, after some manipulations,

$$
\begin{equation*}
|A|_{c r}=\frac{(1-\theta)^{2}}{\theta^{2}}\left[\frac{1}{2} \sqrt{1+\frac{2}{\alpha}}-\frac{1}{2 \alpha \theta}+\sqrt{\left(\frac{1}{2} \sqrt{1+\frac{2}{\alpha}}-\frac{1}{2 \alpha \theta}\right)^{2}+\frac{1}{\alpha} \frac{1-\theta}{\theta}}\right]^{-2} \tag{2.60}
\end{equation*}
$$

For all values of $\alpha,|A|_{c r}(\alpha)$ is greater than the critical value $|A|_{c r}(\infty)$ in the local case, since the last factor on the right-hand side of (2.60) is greater than one.

An interesting observation is that if $c<0$ then for any $\alpha$ there is a range of $c$ such that $\lambda_{1}$ and $\lambda_{2}$ are complex (see Appendix A), so that there is no monotone wave in this case. This is different from the solution of the local problem, which can have monotonic solutions for any value of $|A|$. For the value $\alpha=3$, for example, this range is $-4.2<c<-1.25$.

### 2.5.3. Nonlocal Equation with Asymmetric Kernel $\Phi$

We now consider the nonlocal, bistable equation with the asymmetric kernel defined by (2.15). We proceed as in the symmetric case and find a solution of the form (2.55), where

$$
p_{1}=\theta, \quad q_{1}=\frac{\theta \mu_{0}-(\theta-1) \lambda_{2}}{\lambda_{1}-\lambda_{2}}, \quad q_{2}=\theta-1-q_{1}
$$

and

$$
\begin{equation*}
\frac{(\theta-1) \lambda_{2}-\theta \mu_{0}}{\left(\lambda_{1}-\alpha_{\ell}\right)\left(\lambda_{2}-\alpha_{\ell}\right)}=\frac{1-\theta}{\lambda_{2}-\alpha_{\ell}}+\frac{1}{\alpha_{\ell}}+\frac{\theta}{\mu_{0}-\alpha_{\ell}} \tag{2.61}
\end{equation*}
$$

which determines the speed $c$. When we reintroduce the parameter $s$, then

$$
\mu_{0}(s)=\frac{1}{2 s}\left[h(s)-\frac{1}{\alpha_{\ell} \theta}-\sqrt{\left(h(s)-\frac{1}{\alpha_{\ell} \theta}\right)^{2}+4 s \frac{1-\theta}{\theta}}\right]
$$

with

$$
\begin{equation*}
|A|(s)=\mu_{0}^{2}(s)+c \mu_{0}(s) \tag{2.62}
\end{equation*}
$$

This, along with the asymmetric parameterization (2.38a)-(2.38c) (which we can use since the eigenvalues $\lambda$ are again solutions of (2.36)), gives a parameterization for the propagation speed as a function of $|A|$.

We see this parameterization in Figure 2.8 for $\theta=0.5, \alpha_{\ell}=1$, and a range of $\alpha_{r}$ values. In the monostable case, Section 2.4.3.2, we saw that as the extent of the nonlocality in the positive $x$ direction became diminished (as $\alpha_{r}$ became larger), the minimum speed for small $A$ increased. We see in Figure 2.8 that the asymmetry has a similar effect in the bistable case - as the extent of the nonlocality in the positive $x$ direction became diminished, the propagation speed became more positive and the $u=1$ state more readily displaced the $u=0$ state. In fact, for fixed values of $|A|$ and $\alpha_{\ell}$, changing $\alpha_{r}$ can even change the direction of propagation. Again we find that increasing the value of $\theta$ (not pictured) decreases the propagation speed in all cases.
2.5.3.1. Effects of Asymmetry on Propagation Speed. We examine the effect of the asymmetry on the propagation speed. To do this, we will consider the near-local limit, $\alpha_{\ell}, \alpha_{r} \rightarrow \infty$.

We begin by seeking asymptotic expansions of the eigenvalues. From the near-local results in Section 2.4.2.2, we expect to see one eigenvalue near $\lambda_{1} \sim \alpha_{\ell}$, and the other eigenvalue $\lambda_{2}=O(1)$. In this asymmetric case, to find the first eigenvalue we take

$$
\lambda_{1}=(1-\epsilon) \alpha_{\ell}, \quad \epsilon \ll 1
$$



Figure 2.8. Propagation speed in the bistable case as a function of $|A|$. Here $\theta=0.5$. The dashed curve is the speed for the local problem. The solid curves are the speed for nonlocal problem with $\alpha_{\ell}=1$ and an increasing range of $\alpha_{r}$ values (left to right: $2^{-2}$ through $2^{2}$ ). The dotted curve is the symmetric case where $\alpha_{r}=\alpha_{\ell}=1$.

We insert these into (2.36) to get

$$
\epsilon(1-\epsilon) \alpha_{\ell}\left[\alpha_{\ell}(1-\epsilon)+c\right]\left(1+(1-\epsilon) \frac{\alpha_{\ell}}{\alpha_{r}}\right)=1
$$

Since $\epsilon \ll 1$, at leading order we find that

$$
\epsilon \sim \frac{\alpha_{r}}{\alpha_{\ell}\left(\alpha_{\ell}+c\right)\left(\alpha_{\ell}+\alpha_{r}\right)},
$$

and the first eigenvalue is

$$
\begin{equation*}
\lambda_{1} \sim \alpha_{\ell}\left(1-\frac{\alpha_{r}}{\alpha_{\ell}\left(\alpha_{\ell}+c\right)\left(\alpha_{\ell}+\alpha_{r}\right)}\right) \tag{2.63}
\end{equation*}
$$

uniformly in $\alpha_{r}$ and c. In the symmetric case where $\alpha_{\ell}=\alpha_{r}=\alpha$, (2.63) recovers the expansion from Section 2.4.2.2. To find the $O(1)$ root $\lambda_{2}$, we take

$$
\alpha_{\ell}=\frac{1}{\tilde{\epsilon}}, \quad \tilde{\epsilon} \ll 1, \quad \frac{\alpha_{r}}{\alpha_{\ell}}=O(1) .
$$

The asymptotic expansion for $\lambda_{2}$ is then

$$
\begin{equation*}
\lambda_{2} \sim \lambda_{0}+\frac{\lambda_{0}}{c+2 \lambda_{0}}\left(\frac{\alpha_{r}-\alpha_{\ell}}{\alpha_{\ell} \alpha_{r}}\right) \tag{2.64}
\end{equation*}
$$

where $\lambda_{0}$ is again the positive solution of

$$
\lambda_{0}^{2}+c \lambda_{0}=1, \quad \Longrightarrow \quad \lambda_{0}=-\frac{c}{2}+\sqrt{\frac{c^{2}}{4}+1}
$$

Again we see that the symmetric case where $\alpha_{\ell}=\alpha_{r}=\alpha$ recovers the expansion from Section 2.4.2.2. We now return to (2.61), which allowed us to solve for the propagation speed $c$, and seek an asymptotic expansion for $c$. We again take

$$
\alpha_{\ell}=\frac{1}{\tilde{\epsilon}}, \quad \tilde{\epsilon} \ll 1, \quad \frac{\alpha_{r}}{\alpha_{\ell}}=O(1)
$$

and obtain

$$
\begin{equation*}
c \sim c_{0}+\frac{\alpha_{r}-\alpha_{\ell}}{\alpha_{r} \alpha_{\ell}}\left[\frac{(1-\theta)\left(\sqrt{4+c_{0}^{2}}-c_{0}\right) \sqrt{4|A|+c_{0}^{2}}}{\sqrt{4+c_{0}^{2}} \sqrt{4|A|+c_{0}^{2}}+c_{0}(\theta-1) \sqrt{4|A|+c_{0}^{2}}+c_{0} \theta \sqrt{4+c_{0}^{2}}}\right], \tag{2.65}
\end{equation*}
$$

where $c_{0}$ is the propagation speed for the local case given by (2.53). It can be shown that the expression in brackets is always positive, and so the correction to the local speed $c_{0}$ is proportional to $\left(\alpha_{r}-\alpha_{\ell}\right)$. We see that as the region behind the front becomes more local ( $\alpha_{\ell}$ increases) the propagation speed decreases, and as the region ahead of the
front becomes more local ( $\alpha_{r}$ increases) the speed increases. This is surprising since we had concluded in the symmetric case that increasing the extent of the nonlocality led to increased speeds.
2.5.3.2. Hump Conditions. We begin with the conditions for a single 'hump', the same as in the monostable case, described in (2.43), (2.44). Following the same analysis as in the monostable case, we arrive at the condition

$$
q_{2}=\frac{(1-\theta) \lambda_{1}+\theta \mu_{0}}{\lambda_{2}-\lambda_{1}}>0 .
$$

In order for a hump solution to exist, we require that $\lambda_{1}, \lambda_{2}$ are real, and take $\lambda_{2}<\lambda_{1}$. Hence the condition reduces to

$$
\mu_{0}<-\frac{1-\theta}{\theta} \lambda_{1} .
$$

We use (2.52) to obtain

$$
\begin{equation*}
|A|(s)=\mu_{0}^{2}(s)+c \mu_{0}(s) \tag{2.66}
\end{equation*}
$$

This gives us the parametric dependence for the boundary as (2.38a)-(2.38c) along with

$$
\begin{equation*}
\lambda_{1}=\frac{1}{2 s}\left[h+\sqrt{h^{2}-4 s}\right], \quad \mu_{0}=-\frac{1-\theta}{\theta} \lambda_{1}, \quad|A|=\mu_{0}^{2}(s)+c \mu_{0}(s) . \tag{2.67}
\end{equation*}
$$

We notice that all hump solutions will exist above this boundary in the $(|A|, c)$ plane. Along with this condition, there is the additional requirement that the speed must equal the propagation speed described by (2.62), (2.38a)-(2.38c).

We also note that it is necessary that the eigenvalues be real. To find the range of $|A|$ values corresponding to real eigenvalues for fixed values of $\alpha_{\ell}, \alpha_{r}$, and $\theta$, we use the boundary for complex eigenvalues described by (2.39a)-(2.39b), and solve for $s$. We can do this numerically, and then use (2.62) to find the bounds on $|A|$.


Figure 2.9. A typical graph showing the regions of existence of different solution types for the bistable case. Monotonic solutions exist below the dashed curved and outside the dotted lines, solutions with exponentially decaying oscillatory tails exist between the dotted lines, and hump solutions exist above the dashed curve and outside the dotted lines. All solutions lie on the solid curve, and so a solution type will only be observed if the solid curve enters the corresponding region. This figure shows the specific case where $\theta=0.5$ and $\alpha_{\ell}=\alpha_{r}=5$. Altering the values of $\theta, \alpha_{\ell}$, and $\alpha_{r}$ will move the solid curve as well as shift the different regions, but does not qualitatively change the figure - except for the case of sufficiently small $\alpha_{\ell}$ which pushes the left dotted line beyond the $|A|=0$ axis, disallowing monotonic solutions entirely. The solid solution curve never entered the regions labeled (Not Observed) for any range of parameters $\theta, \alpha_{\ell}$, and $\alpha_{r}$ that were considered. This means that, for example, right traveling hump solutions for smaller values of $|A|$ were never actually observed.

Figure 2.9 shows an example of the regions of existence of the different solutions in the bistable case. While this figure only shows one choice of parameters $\theta, \alpha_{\ell}$, and $\alpha_{r}$, altering these values does not qualitatively change the figure - except for the case of sufficiently
small $\alpha_{\ell}$ which pushes the left dotted line beyond the $|A|=0$ axis, disallowing monotonic solutions entirely.

We make several observations from Figure 2.9 (along with the graphs from varying the values of $\theta, \alpha_{\ell}$, and $\alpha_{r}$ that are not pictured here): (i) It seems that there is a critical value of $|A|$, obtained from the upper bound for complex eigenvalues (the right-most vertical line), above which there appears to always be a hump solution. (ii) We see that there are no hump solutions below this critical value of $|A|$. (iii) We see that hump solutions can only occur for negative propagation speeds. (iv) Even in the case of strong asymmetry, which we noted previously can change the direction of propagation of the front, we see only negative propagation speeds for hump solutions. (v) $\theta$ no longer needs to be close to 1 , as it did in the monostable case, for hump solutions to exist.

In summary, we saw a number of different possible behaviors of the traveling waves for the bistable problem. Figure 2.9 includes most of these possible solutions. For very small values of $|A|$, the solution is a right-propagating, monotonic wave. For slightly larger values of $|A|$, there is a left-propagating, monotonic wave. There are left-propagating waves with exponentially decaying oscillatory tails for intermediate values of $|A|$, and left-propagating waves with humps for very large values of $|A|$. Not pictured in Figure 2.9 are the right-propagating waves with an exponentially decaying oscillatory tail for small values of $|A|$ that can occur when $\alpha_{\ell}$ is sufficiently small. The only type of solution we never found for the bistable problem is a right-propagating wave with a hump.

### 2.6. Model Validation

We have validated the results of this chapter by numerically solving the time dependent problem (2.1) with the piecewise linear source term (2.13). We imposed no other assumptions on the model, and examined the behavior of the wavefront. To compare these numerical solutions to the results in this chapter, we defined our moving frame's $x=0$ to be the location $z^{*}>0$ where $u\left(z^{*}\right)=\theta$, interpolating between collocation points where necessary. By tracking the location of $z^{*}$ over time, we were able to compute the speed $c$ of the traveling waves.

- We first note that for the time dependent problem, we saw that the solutions adhered to Assumption 2, that $u(x)<\theta$ for $x>0$ and $u(x)>\theta$ for $x<0$, despite this assumption not being imposed, validating our use of this assumption throughout the chapter.
- For several fixed values of $\alpha_{\ell}, \alpha_{r}$, and $\theta$, and a range of $A$ values, we verified the minimum speed in the monostable case from Section 2.4.3.2, noting that the traveling waves always propagated at the minimum speed.
- We verified, for a range of $\alpha_{\ell}$ values, the boundary between real and complex $\lambda$ from Section 2.4.3.1.
- We then fixed $\theta=0.99$ and considered several sets of parameters $\alpha_{\ell}, \alpha_{r}$, and $A$ for which we expected hump solutions based on the results of Section 2.4.3.3. We verified the existence of the hump solutions as well as the location and size of the hump.
- We then considered the bistable case, where we chose a range of $\alpha_{\ell}, \alpha_{r}$, and $A<0$ values and found the propagation speed, allowing us to verify the results of Section 2.5.3.
- Lastly, we considered several sets of parameters for which we expected a hump solution in the bistable case, based on the results of Section 2.5.3.2. We were again able to verify the existence of the hump solutions along with the location and size of the humps.


### 2.7. Conclusion and Summary

We have considered a piecewise linear reaction-diffusion model for population growth, and examined the possibility of traveling wave solutions. We looked at both the monostable version of the problem where the $u=0$ extinction state is unstable, and the bistable version of the problem where the extinction state becomes stable - which models the Allee Effect. In both versions of the problem, we looked at the propagation speed of the traveling waves as well as their monotonicity. We examined how the local net birth rate $(A)$, the extent of the nonlocality $(\alpha)$, and the strength of the asymmetry ( $\alpha_{\ell}$, and $\alpha_{r}$ ) affected the speed and shape of the waves.

## Monostable Case

- For the monostable version of the problem, we found that there are traveling wave solutions for any wave speed greater than some minimum speed $c_{m i n}$. When $A$ was larger than some critical value we saw that $c_{\text {min }}=c_{\mathrm{KPP}}$. But when $A$ fell below this critical value, $c_{\text {min }}>c_{\text {KPP }}$ for both the local and nonlocal problems.
- The asymmetric problem showed that as the positive $x$ direction - the direction of propagation for the monostable case - became more local, $c_{\text {min }}$ increased.
- We looked at the near-local, large $\alpha$ limit and were able to recover the local solution with a small correction. This meant that as $\alpha$ increased, i.e., as the extent of the nonlocality decreased, we had monotonic waves as in the local problem.
- We found that as $\alpha$ decreased, we would lose this monotonicity and instead would see exponentially decaying oscillatory tails for the $x<0$ region.
- We saw a third wave-shape in the hump solution, which became possible when $\theta$ was very close to 1 , and we found the region of existence in parameter space for these hump solutions. We saw that as the positive $x$ direction became more local, the parameter range giving these hump solutions increased.


## Bistable Case

- For the bistable version of the problem, we saw that the propagation speed for a given set of parameters was uniquely determined, and that it could take on negative values when the local net birth rate, $A$, became sufficiently negative.
- We saw that increasing the extent of the nonlocality in the symmetric case led to a more positive propagation speed - meaning that the $u=1$ state would more readily displace the $u=0$ state.
- We also found that diminishing the extent of the nonlocality in the positive $x$ direction in the asymmetric case also led to a more positive propagation speed. Diminishing the extent of the nonlocality in the negative $x$ direction led to a more negative propagation speed.
- When we looked at the shape of the traveling wave solutions for the bistable version, we saw a wide variety of possibilities:
- For small values of $|A|$ there could be both left-traveling and right-traveling monotonic waves.
- For small to intermediate values of $|A|$, there could be both left-traveling and right-traveling waves with exponentially decaying oscillatory tails.
- For sufficiently large values of $|A|$, we saw only left-traveling waves with humps - even when $\theta$ was not close to 1 , as was required for humps in the monostable case.
- Monotonicity in the bistable case was lost for all but small local net birth rates.


## CHAPTER 3

## Ratio-Dependent Predation

We now turn our attention to the second project included in this work, which is centered on a three species foodchain system. The paper resulting from this project is presented in Chapter 4. The foodchain in question is composed of species $u, v$, and $w$, where the species $u$ is at the bottom of the foodchain and is preyed upon by species $v$, which in turn is preyed upon by species $w$. This gives two predator-prey pairs: $w-v$ and $v-u$. In this chapter, we discuss how these predator-prey interaction enter the equations governing the system and how those so called functional responses may be derived, as well as address the controversy surrounding the particular ratio-dependent responses used in the project and their relation to nonlocality.

### 3.1. Functional Responses to Predation

The terms governing the response of a predator-prey system to a predation event between the two species are referred to as the numerical response, and depend on the predator and prey densities. The most common form of a numerical response is one that depends on the predator density multiplied by what is called the functional response, a function of both predator and prey densities that represents the rate at which an individual predator consumes prey, i.e., letting $u$ be the prey density and $v$ the predator density,
then

$$
\begin{equation*}
n(u, v)=v f(u, v) \tag{3.1}
\end{equation*}
$$

where $n$ is the numerical response and $f$ is the functional response.
It is often assumed, for what are call prey-dependent responses, that the functional response depends solely on the density of the prey species. The most common of these is the Holling type II response

$$
\begin{equation*}
f(u, v)=h(u)=\frac{a u}{u+b} \tag{3.2}
\end{equation*}
$$

where $a$ and $b$ are parameters depending on the predator-prey encounter rate and handling time per prey item.

In [25], Arditi and Ginzburg put forward the idea that the function response should depend on the ratio of the prey to the predator, rather than just on the prey species alone. Applying this idea to the Holling (II) response gave the typical ratio-dependent response that we use in Chapter 4,

$$
\begin{equation*}
f(u, v)=h(u / v)=\frac{a u / v}{u / v+b}=\frac{a u}{u+b v} \tag{3.3}
\end{equation*}
$$

This form of functional response has proven to be controversial, however, and so we discuss a potential derivation in Section 3.2, and address the controversy directly in Section 3.3.

### 3.2. Derivation of Functional Responses

Here we provide a brief discussion of how different functional responses can be obtained from different predator or prey behaviors. We note that these described behaviors
are not an exhaustive list of potential mechanisms that produce the related functional responses, but rather are fairly general, plausible mechanisms that can shed light on both the controversy of ratio-dependent predation and its relation to nonlocality. More detailed derivations are presented in [26]. We first rely on [27], which gives a general form for the functional response

$$
\begin{equation*}
f(u, v)=\frac{C E / v}{1+h C E / v} \tag{3.4}
\end{equation*}
$$

The parameters here are:

- $u=$ prey density
- $v=$ predator density
- $C=$ fraction of a prey item killed per predator per encounter
- $h=$ handling time per prey item
- $E=$ total encounter rate between predators and prey per unit time.

The parameter $C$ becomes relevant when multiple predators share in the consumption of a single prey item, with $C=1$ if no sharing occurs.

The key difference between the derivation for the Holling type II response and the ratio-dependent response is the spatial organization of the predators or prey, which in turn affects the encounter rate $E$. If both the prey and predator densities are assumed to be uniform, at least on a spatial scale smaller than that over which diffusion occurs, the law of mass action would give an encounter rate $E=e_{0} u v$, for some constant $e_{0}$. In this case, (3.4) gives the standard Holling type II response. This response could also be obtained if, for example, the prey were uniformly distributed and the predators hunted in a line, without aggregation upon encountering prey.

Meanwhile, in [26], two mechanisms are described that give rise to the ratio-dependent response. The first of these occurs when prey are uniformly distributed while predators hunt in tight packs, idealized as a point mass. In this case, the encounter rate would depend only on the prey density, $E=e_{1} N$, since the addition of more predators would not change the encounter rate, and this gives the ratio-dependent response. The second mechanism occurs when predators are uniformly distributed while the prey are in point mass clusters which are also uniformly distributed. This would result in the typical mass action encounter rate $E=e_{0} u v$. Two additional assumptions are considered: that predators share the encountered clusters, so $C=C_{0} / v$, and that the handling time $h$ is constant no matter how many predators share a cluster, which could result from predator interference. Combined, these assumptions again give the ratio-dependent response.

The behaviors described above that gave rise to the Holling type II response or the ratio-dependent response are clearly idealized behaviors, and both of these responses can be viewed as limiting cases of more realistic behaviors. If some of the assumptions that gave these responses are relaxed, the derivations break down and more complicated, though also more realistic, functional responses are obtained, such as the Hassel-Varley [28] or DeAngelis [29] type. For example, if the predators hunt in loose packs and are neither uniformly distributed nor in point mass groups, the Hassel-Varley type response is obtained instead of either the Holling type II or ratio-dependent responses.

### 3.3. Controversy Surrounding Ratio-Dependent Responses

There has been a lot of controversy surrounding the use of ratio-dependent models over the last few decades. Here we will present a brief overview of the arguments for and
against their use in general. A thorough summary of the controversy can be found in [30], while a more detailed history can be found in [31].

In their 1989 article [25], Arditi and Ginzburg first introduced the ratio-dependent functional response. Following this, in a series of papers in the early 1990s, Arditi et. al. performed experiments and cited field studies that they argued supported this idea of ratio-dependence [32-34]. This prompted a response by Abrams in 1994 [35], that lead to a back and forth between the two groups in the 1990s [35-37], which ultimately culminated in the 2000 collaboration summarizing the dispute [30]. This paper concluded that the current field studies and experiments were simply not enough to properly identify under what conditions each response would work best. Even in 2015 Abrams claimed that more studies needed to be done [31], though we note that a more recent experimental study found yet more evidence supporting the ratio-dependent response [38].

An original argument put forward in [25], and cited often in the following papers, is the idea that the functional response should be viewed on the reproductive timescale rather than on the much smaller timescale of individual predation events. Instead of viewing the functional response as the result of random encounters between prey and predators, the argument is that the functional response should in some way reflect changes in both predator and prey abundances on the reproductive timescale. Specifically, that the consumption rate should be a function of prey abundance per capita, and so yield the ratio-dependent response. This argument has proven contentious, with detractors arguing that differential equations model the instantaneous rate of change of the populations, and so the shorter behavioral timescale should be used [35], while supporters respond that the
shortest timescale over which population changes can be modeled on is the much slower reproductive timescale [36].

Arguments against ratio-dependent models tend to focus on the underlying assumptions, and specifically, on when these assumptions break down. A key assumption for ratio-dependent functional response is that predators interfere with each other and end up sharing the prey when averaged over the reproductive timescale [35,36]. It is this interference and prey sharing that gives rise to the ratio-dependent response, and so this response breaks down when interference is not present in the system. When predator densities fall far enough these key assumptions break down. The biological explanation is that interference cannot occur if predators are separated by sufficiently great distances, as would happen when predator densities are sufficiently low.

On the other hand, the arguments for ratio-dependent models tend to point at experimentally observed phenomena that correspond to behaviors observed in models with ratio-dependent responses, but that cannot occur in models with the more standard preydependent responses. There are three main behaviors cited as justification for ratiodependent responses. The first two are related and are referred to as the paradoxes of enrichment and biological control.

The paradox of enrichment focuses on how the populations at all trophic levels in a foodchain respond to changes in the carrying capacity of the lowest prey species. Ratiodependent models predict that all levels respond proportionally to the change, while prey-dependent models predict responses that differ based on the specific trophic level or the number of total trophic levels. Supporters of ratio-dependent models [36, 39] argue that the prey-dependent predictions are unrealistic and often cite [40] and [41] as the
origin of this paradox of enrichment. Meanwhile, the paradox of biological control states that prey-dependent models cannot have both a low and stable prey equilibrium. In reality, there are examples of successful biological control where the prey were maintained at densities of less that $2 \%$ of their carrying capacities $[39,42,43]$.

Detractors of the ratio-dependent response argue that prey-dependent models can correctly predict the response to enrichment in some cases: when there are multiple species at each trophic level; when the form of the predator dependence in the numerical response is altered while the functional response is kept prey-dependent; when the system undergoes population fluctuations; or when there is a class of invulnerable, or at least less edible, prey $[\mathbf{3 0}, \mathbf{3 7}]$. Supporters of ratio-dependence argue that these fixes occur either under very limiting assumptions, and the fact that the predictions change so drastically based on the organization of the trophic levels make prey-dependent models much less desirable [36].

The third behavior cited by supporters of the ratio-dependent response, and the most relevant to the project presented in Chapter 4, is the complete system collapse, where both the predator and prey species deterministically die off. This behavior has been observed in experiments [44], and is correctly predicted by ratio-dependent models. It cannot, however, occur in prey-dependent models. While this system collapse behavior might be 'pathological' in the mathematical sense, it is realistic in the biological sense, which tends to support the idea of ratio-dependence $[\mathbf{3 6}, \mathbf{3 9}]$. If viewed from a prey-dependent approach, experiments that show system collapse are explained through stochastic effects that kill off the populations when they reach low levels [45]. It is important to note that system collapse can be problematic for ratio-dependent models because, as discussed
earlier, these models break down when the predator populations become sufficiently small. Although there is an argument to be made that once predator populations drop low enough to cause this breakdown of the ratio-dependent assumptions, any continuous model would be insufficient [36].

This system collapse behavior is particularly relevant for biological control, where a predator species is introduced into an environment in an attempt to kill off a pest species. In this situation, the optimal outcome would be the complete collapse of the system, where both the predator and prey are driven to extinction. For the project in Chapter 4, we are concerned with the behavior of a three species foodchain comprised of species $u, v$, and $w$. We consider biological control in this context, where $u$ is a valuable crop species, $v$ is the pest, and $w$ is the predator introduced to eliminate the pest. Completely successful biological control in this context then would be the extinction of both species $v$ and $w$, i.e., the extinction of the $w-v$ predator-prey pair. This can only occur if the ratio-dependent, as opposed to prey-dependent, response is used.

Both the ratio-dependent and prey-dependent models suffer from a number of flaws. The consensus is that both responses are idealized, limiting cases of more realistic models [30]. Two responses that are considered more realistic throughout the cited literature are the DeAngelis type response

$$
g(u, v)=\frac{a u}{b+u+c v}, \quad p(u, v)=\frac{a u v}{b+u+c v},
$$

from [29], and the Hassell-Varley type response

$$
g(u, v)=g\left(\frac{u}{v^{m}}\right)
$$

from [28]. We can see that in the DeAngelis type response, as parameter $b \rightarrow 0$, we arrive at the ratio-dependent response, and as $c \rightarrow 0$, we arrive at the prey-dependent Holling (II) response. For the Hassell-Varley response, $m \rightarrow 0$ corresponds to prey-dependent and $m \rightarrow 1$ corresponds to ratio-dependent. Once these models are introduced into the argument, the discussion becomes more philosophical about the relative merits of preydependent versus ratio-dependent models as useful, more tractable, simplifications [30], and we note that the ratio-dependent response is more relevant when considering biological control.

### 3.4. Ratio-Dependent Predation and Nonlocality

It is important to note that the discussion so far of the ratio-dependent responses has been for ODE models without explicit spatial dependence, and that it was in this context that this response was proposed and debated. At the same time, a number of explanations for this ratio-dependence relied on the mobility of the species involved. It is therefore necessary for us to consider the relationship between explicit spatial dependence and nonlocality to justify its use.

We first address the question of considering an explicit spatial dependence by adding diffusion to an ODE model with a ratio-dependent functional response (as we do to the model from [39]). As noted above, spatial heterogeneity is often cited as a justification for the use of ratio-dependent models. So it would be reasonable to question whether they should be used when the model already incorporates explicit spatial dependence. To answer this question, we note that the behaviors described in [26] are on the spatial scale of individual or small groups of predators. Our introduced spatial dependence is on the
much larger diffusive scale of the population as a whole. So we can argue that at each 'location' on the diffusive scale, the individual behaviors of the predators and prey can still give rise to ratio-dependent responses.

To consider the relationship between nonlocality and ratio-dependent responses, we turn to [46], which discusses the impact of predator density and the size of the predators' 'home ranges' on predator interference, and hence on the ratio-dependent nature of the responses. They argue that even if predator densities are low, if the predators' 'home ranges' are large enough to overlap, then the predators will still likely interfere with each other. So in the case of large 'home ranges', even low predator densities can see ratiodependent behaviors. A reasonable example of nonlocal behavior in predators is that of large hunting grounds, i.e. where predators live at a specific location on relatively small spatial scale, but are mobile enough to hunt over an area on the larger diffusive spatial scale. This can lead to overlapping hunting grounds where predators that live at different locations may still compete for the same prey. We can see then that this sort of nonlocality corresponds to predator interference over large distances, and so can justify the use of ratio-dependent responses for even low predator densities.

## CHAPTER 4

## Biological Control with Nonlocal Interactions

In this chapter, we consider a three-species food chain model with ratio-dependent predation, where species $u$ is preyed upon by species $v$, which in turn is preyed upon by species $w$. Our primary focus is on biological control, where the bottom species $u$ is an important crop, and $v$ is a pest that has infested the crop. The superpredator $w$ is introduced into this pest-infested environment in an attempt to restore the system to a pest-free state. We assume that the species can behave nonlocally, where individuals will interact over a distance, and incorporate this nonlocality into the model. For this model, we consider two types of nonlocality: one where the crop species $u$ competes nonlocally with itself, and the other where the superpredator $w$ is assumed to be highly mobile and therefore preys upon the pest $v$ in a nonlocal fashion. We examine how biological control can prove to be highly susceptible to noise, and can fail outright if the pest species is highly diffusive. We show, however, that control can be restored if the superpredator is sufficiently diffusive, and that robust partial control can occur if the superpredator behaves nonlocally. Since the superpredator is generally introduced artificially, our results point to properties of the superpredator which can lead to successful control.

### 4.1. Introduction

Biological invasions are currently regarded as a major threat to biodiversity and agriculture all over the world, often resulting in huge economic losses. Biological control aims
to control or even prevent the invasion of a pest infesting a valuable species via the introduction of a so-called superpredator which devours the pest but not the desirable species. One such example is gypsy moth infestation of deciduous hardwood trees [47]. In this case the role of the superpredator is played by a virus (Nuclear Polyhedrosis Virus or NPV) which preys on gypsy moth larvae. Thus, at a minimum there are three species involved: the valuable crop species, $u$, which is preyed upon by the pest, $v$, and the superpredator, $w$, which preys on $v$ but not on $u$. The interaction of $u$ and $v$ without the superpredator would be a two-species predator-prey system. With the introduction of the superpredator $w$, the pest species $v$ becomes both prey (to $w$ ) and predator (to $u$ ). The three species $u$, $v$, and $w$ then form the components of a food chain model, where the variables $u, v$, and $w$ correspond to the biomass of their respective species.

In this chapter we develop a three-species model for biological control, accounting for species mobility, i.e., diffusion, as well as nonlocal interactions between the different species involved. Our focus will be on the invasion problem, whereby a superpredator is introduced into a small interval inside of an already infested two species (crop and pest) region so that an invasion wave of the superpredator aims to eliminate the pest and restore the ecological system to one in which the valuable crop is fully or partially recovered. We analyze this model both analytically and computationally, focusing on the roles of nonlocality and diffusion in promoting robust biological control.

In Section 4.2, we introduce the food chain model considered in this chapter. We discuss the incorporation of nonlocality in Section 4.2.1, our initial and boundary conditions in Section 4.2.2, and the code we use for numerical simulation in Section 4.2.3. Section 4.3 addresses the stability of the different equilibrium states for both the local
and nonlocal problems. We obtain predictions for the propagation speeds of various fronts and numerically validate these predictions in Section 4.4. In Section 4.5, we consider the biological control problem directly and discuss the robustness of control. Specifically we address how small truncation errors, small stochastic perturbations, and diffusion driven effects can lead to a resurgence of the pest, as well as how a highly diffusive or highly nonlocal superpredator can overcome these resurgences. Finally, we provide a summary of our results in Section 4.6.

### 4.2. Model

A suitably nondimensionalized two-species predator-prey model without nonlocal interactions can be written as
(4.1a) $u_{t}=u_{x x}+u\left(1-u-\frac{a_{1} v}{u+v}\right)$,

$$
\begin{equation*}
v_{t}=\mu_{2} v_{x x}+v\left(-d_{1}+\frac{m_{1} u}{u+v}\right) \tag{4.1b}
\end{equation*}
$$

where $a_{1}, d_{1}, m_{1}$ are kinetic constants and $\mu_{2}$ is the diffusion coefficient of species $v$, all positive. Note that it is assumed that the population of the prey $u$ can be sustained in the absence of the predator $v$ (the logistic term in (4.1a)), while the predator will die out without sustenance from the prey (the linear term in (4.1b)).

The other nonlinear terms in the differential equations describe the interactions between the two species. The form of these terms is due to our choice of a ratio-dependent functional response (specifically, the Arditi-Ginzburg type II response function [25]). Various other choices are also possible and have been extensively discussed in the literature.

A comprehensive discussion of ratio-dependent response functions is given in $[\mathbf{3 0}, \mathbf{3 1}]$. We note that a study fitting different response functions against observations in a freshwater microcosm showed that our chosen function gave the best fit to observational data [38].

Upon introducing a superpredator $w$, assuming the same type of response function for the $w-v$ predation pair as for the $v-u$ pair, we arrive at the model

$$
\begin{align*}
& u_{t}=u_{x x}+u\left(1-u-\frac{a_{1} v}{u+v}\right)  \tag{4.2a}\\
& v_{t}=\mu_{2} v_{x x}+v\left(-d_{1}+\frac{m_{1} u}{u+v}-\frac{a_{2} w}{v+w}\right)  \tag{4.2~b}\\
& w_{t}=\mu_{3} w_{x x}+w\left(-d_{2}+\frac{m_{2} v}{v+w}\right)
\end{align*}
$$

This system was introduced and studied in [39] as an ODE system (i.e., without any spatial dependencies).

The system (4.2) only makes physical sense if the dependent variables $u, v$ and $w$ are nonnegative. Furthermore, there is a singularity in the system when either or both of the combinations $(u, v)=(0,0)$ or $(v, w)=(0,0)$ holds. This singularity is removable in the sense that the terms $u v /(u+v)$ and $v w /(v+w)$ can be continuously extended (from the physical region $u, v, w>0$ ) to be zero at these points. However, this extension is not differentiable and is at the boundary of the physical region. This means that a conventional linear stability analysis at these points cannot be performed. One might think that a simple regularization, i.e., adding a small number $\epsilon$ to the denominators in (4.2), would overcome this difficulty. It is easy to see, however, that such a regularization would change the stability properties of the pest free state $(u, v, w)=(1,0,0)$. Specifically, it
forces this state to become unstable to an open set of perturbations. This is unacceptable since the original model cannot then be obtained as a limit of this regularized system.

We next consider uniform equilibrium states of (4.2). We note that this system exhibits the domino effect in that if one species becomes extinct, then all species higher up on the food chain will also be extinct, and so we characterize the equilibria according to the number of nonzero species. The zero-state, extinction equilibrium $E_{0}$ is $(u, v, w)=$ $(0,0,0)$. The one-state, pest free equilibrium $E_{1}$ is $(u, v, w)=(1,0,0)$, and we note that for the purposes of biological control this is the desired state. A two-state, pest infested equilibrium $E_{2},(\bar{u}, \bar{v}, 0)$ exists, where

$$
\begin{equation*}
\bar{u}=1-a_{1}\left(1-\eta_{1}\right), \quad \bar{v}=\bar{u} \frac{1-\eta_{1}}{\eta_{1}}, \quad \eta_{1} \equiv \frac{d_{1}}{m_{1}} \tag{4.3}
\end{equation*}
$$

but is only physical in the restricted parameter region $0<1-\eta_{1}<1 / a_{1}$. It is easy to see that when physical, we will always have $\bar{u}<1$ so that the presence of the pest, $\bar{v}$, reduces the population of the desirable species $u$. Similarly, a physical three-state, partial restoration equilibrium $E_{3},\left(u_{c}, v_{c}, w_{c}\right)$, exists, where

$$
\begin{equation*}
u_{c}=1-a_{1}(1-A), \quad v_{c}=u_{c} \frac{1-A}{A}, \quad w_{c}=v_{c} \frac{1-\eta_{2}}{\eta_{2}} \tag{4.4}
\end{equation*}
$$

with

$$
\eta_{2} \equiv \frac{d_{2}}{m_{2}}, \quad A \equiv \eta_{1}+\frac{a_{2}}{m_{1}}\left(1-\eta_{2}\right)
$$

but only in a restricted parameter regime $0<\eta_{2}<1$ and $0<1-A<1 / a_{1}$. We call this state the partial restoration state because it is always true that $\bar{u}<u_{c}<1$, and so the
presence of species $w$ in this $E_{3}$ state allows for an increase in the population of the crop $u$ above its infested levels.

We refrain from calling $E_{0}$ and $E_{1}$ critical points because the system (4.2) is not differentiable at these points, and indeed, a standard linear stability analysis about these equilibria gives nonlinear equations. $E_{2}$ and $E_{3}$ are critical points as there are no singularities at these points.

### 4.2.1. Nonlocality

It has long been recognized that competition and predation, as well as other species interaction phenomena, are often nonlocal in either space or time. In this chapter we focus on spatial nonlocality. Nonlocality results when terms in the equation (say at a point $x^{*}$ ) are assumed to depend not on pointwise values of the population, but rather on a weighted average of the population in a neighborhood of $x^{*}$. When the weighting is independent of $x^{*}$, the result is a convolution integral against a specified nonnegative kernel function describing the weighting. Thus, the nonlocality is modeled by a system of integro-partial differential equations. Nonlocal competition effects have been extensively studied for single, isolated populations described by scalar equations, e.g., $[\mathbf{1 , 9}, \mathbf{1 0}, \mathbf{4 8}-\mathbf{5 2}]$. Nonlocality for systems, mainly systems of competing populations, has also been studied, e.g., $[9,53-56]$, primarily for pattern formation. Nonlocality for predator-prey systems was studied in [57-60]. Nonlocality can introduce complex spatial and temporal patterns which dramatically alter the nature of the solution, and, in particular, the biological and ecological inferences drawn from the computed solution.

In this chapter we consider two specific manifestations of nonlocality appropriate for the three species model (4.2), while using a stepfunction kernel function

$$
\varphi(x)=\left\{\begin{array}{cl}
\frac{1}{2 \delta}, & |x|<\delta  \tag{4.5}\\
0, & |x|>\delta
\end{array}\right.
$$

throughout. The parameter $\delta$ controls the width of the kernel function, and thereby the extent of the nonlocality. For the stability analyses presented in Section 4.3, we will need the Fourier transform of this kernel, which is

$$
\begin{equation*}
\hat{\varphi}(k)=\frac{\sin (\delta k)}{\delta k} \tag{4.6}
\end{equation*}
$$

$C$-type Nonlocality: What we will refer to as the $C$-type nonlocality arises when the crop species $u$ competes nonlocally with itself. This results in a convolution integral appearing in the logistic term of the equation for species $u$, giving the system

$$
\begin{align*}
& \text { (4.7a) } u_{t}=u_{x x}+u\left(1-(\varphi * u)-\frac{a_{1} v}{u+v}\right),  \tag{4.7a}\\
& \text { (4.7b) } v_{t}=\mu_{2} v_{x x}+v\left(-d_{1}+\frac{m_{1} u}{u+v}-\frac{a_{2} w}{v+w}\right. \\
& \text { (4.7c) } w_{t}=\mu_{3} w_{x x}+w\left(-d_{2}+\frac{m_{2} v}{v+w}\right) .
\end{align*}
$$

Here the convolution is given by

$$
\varphi * u=\int_{-\infty}^{\infty} \varphi(y-x) u(y) d y
$$

This commonly considered $C$-type nonlocality is often explained as a mobile species $u$ competing for some scarce, vital resource, with this scarcity forcing the species to range over a wide area. As individuals of the species will have overlapping ranges, this will create competition between the individuals despite the fact that they actually reside in different locales. If $u$ is a plant species, then this type of nonlocality could arise due to, for example, extensive root systems or a shared water table.
$P_{w}$-type Nonlocality: What we will refer to as the $P_{w}$-type nonlocality arises when we consider a superpredator $w$ which nonlocally preys upon the pest $v$, corresponding to a superpredator with large hunting grounds. So we would expect that in this case, we will have convolution integrals appearing in the $w-v$ predation terms.

To see exactly how this type of nonlocality manifests itself in the food chain system, we consider the origin of the ratio-dependent predation terms. The $w-v$ predation terms in equations (4.2b) and (4.2c) take the form $n(v, w) \equiv w f(v, w)$, where $n(v, w)$ is called the numerical response, and $f(v, w)$ is called the functional response, which describes the rate at which a predator encounters its prey. The ratio-dependent terms in this chapter are so called because the functional response depends on the ratio of the prey to the predator, i.e., if we apply this ratio-dependence to the standard Holling II functional response we obtain

$$
f(v, w)=\frac{v / w}{v / w+1}=\frac{v}{v+w}
$$

A species behaving nonlocally as predator or prey should then only affect the encounter rate, i.e., the functional response. The numerical response, and hence the terms that appear in the full system, should depend on the product of the local predator density
with the nonlocal encounter rate. In this ratio-dependent context, a mobile species $w$ will give predation terms of the form

$$
n(v, w)=w \frac{v}{v+\varphi * w}
$$

This gives the $P_{w}$-type system

$$
\begin{align*}
& \text { (4.8a) } u_{t}=u_{x x}+u\left(1-u-\frac{a_{1} v}{u+v}\right)  \tag{4.8a}\\
& \text { (4.8b) } v_{t}=\mu_{2} v_{x x}+v\left(-d_{1}+\frac{m_{1} u}{u+v}-\frac{a_{2} w}{v+\varphi * w}\right), \\
& \text { (4.8c) } w_{t}=\mu_{3} w_{x x}+w\left(-d_{2}+\frac{m_{2} v}{v+\varphi * w}\right) .
\end{align*}
$$

$P_{v}$-type Nonlocalities: We mention that it is possible to consider a highly mobile pest species $v$, which nonlocally preys upon the crop $u$ and is nonlocally preyed upon by the superpredator $w$. The analysis for this type of nonlocality can be performed by following the same procedures as those presented for the $P_{w}$-type nonlocality, and suffers from the same difficulties. We forgo this analysis since, aside from the potential for the formation of cellular patterns, we have found that this nonlocality does not have a large effect.

### 4.2.2. Invasion Waves - Initial and Boundary Conditions

In this chapter our primary interest is the invasion problem where the superpredator $w$ is introduced into a pest infested region of large extent, mathematically infinite. For practical purposes, we numerically simulate the systems (4.2), (4.7), and (4.8) taking
periodic boundary conditions, while ensuring that the spatial domain is large enough so that the relevant parts of the simulation, specifically the wave fronts of interest, do not come in contact with the periodic boundaries.

We consider two types of initial conditions. The first type corresponds to one equilibrium state invading another with a linear connection between them initially. We set $\vec{u}=(u, v, w)$, and define the initial conditions

$$
\vec{u}= \begin{cases}\overrightarrow{s_{1}}, & |x|<x_{1},  \tag{4.9}\\ \left.\frac{x-x_{1}}{x_{2}-x_{1}} \overrightarrow{s_{2}}-\overrightarrow{s_{1}}\right)+\overrightarrow{s_{1}}, & x_{1}<|x|<x_{2}, \\ \overrightarrow{s_{2}}, & x_{2}<|x|,\end{cases}
$$

where $\overrightarrow{s_{1}}$ and $\overrightarrow{s_{2}}$ are the two equilibrium states. The second type of initial condition corresponds directly to the invasion problem of primary interest: a pulse of species $w$ introduced into a region inhabited by a given equilibrium state $\left(s_{1}, s_{2}, s_{3}\right)$. This type of initial condition is then defined by
(4.10a) $u=s_{1}, \quad v=s_{2}$,
(4.10b) $w= \begin{cases}W, & |x|<x_{1}, \\ \frac{x-x_{1}}{x_{2}-x_{1}}\left(s_{3}-W\right)+W, & x_{1}<|x|<x_{2}, \\ s_{3}, & x_{2}<|x|,\end{cases}$
where $W$ is the height of the initial pulse of $w$ released into the environment.
Note that we do not explicitly impose symmetry about $x=0$. We, however, consider only symmetric initial conditions, and our numerical method will maintain symmetry in the absence of asymmetric computer round-off errors. We use this later in Section 4.5.2 in order to characterize non-robust behavior.

### 4.2.3. Description of Code for Numerical Simulations

To numerically simulate the systems (4.2), (4.7), and (4.8), we used a Fourier pseudospectral scheme with periodic boundary conditions and a semi-implicit predictor-corrector temporal integration, as was used in [60]. For a typical simulation, we take initial conditions (4.9) or (4.10) and consider a spatial domain of $-1800<x<1800$, with the initial pulse located between $250<x_{1}, x_{2}<1000$ with a height of $0.001<W<0.1$ (when relevant), and take 32768 collocation points and a timestep between $10^{-3}$ and $10^{-4}$. We examined finer and coarser resolutions in both space and time, and believe that our computations are fully resolved in all cases except where indicated, as will be discussed in Section 4.5.

The presence of singularities in (4.2), (4.7), and (4.8) can give rise to numerical instabilities when both populations $u$ and $v$ are close to zero or when both $v$ and $w$ are close to zero, as they are when the solution approaches the $E_{0}$ or $E_{1}$ state. We consider two different methods of preventing these small denominator errors. We again note that a more standard regularization, adding a small number $\epsilon$ to the denominators in (4.2), (4.7), and (4.8), is not appropriate as it would change the stability of the $E_{1}$ state.

Explicit Zero Denominator Checks: A problem that arises from the ratiodependent terms is that small errors can cause a population near zero to become negative. In simulations, these errors were on the order of machine epsilon and proved to be almost entirely inconsequential, but they could cause divide-by-zero errors if they ever allowed $u+v=0$ or $v+w=0$. To deal with this possibility, we explicitly check if $u+v=0$ or $v+w=0$, and set the respective ratio-dependent terms to zero if necessary.

Numerical Cutoff: We also employed a numerical cutoff, applied at each timestep, to attempt to prevent small errors near the $E_{0}$ and $E_{1}$ states. At the end of each timestep, we check the value of each species at each location in space and set the respective population to exactly zero if

$$
|u|,|v|,|w|<\text { cutoff. }
$$

We employ a cutoff value of $2 \times 10^{-15}$ in all simulations unless otherwise stated.

### 4.3. Stability

The four equilibrium states $E_{0}, E_{1}, E_{2}$ and $E_{3}$ are also equilibrium states of the nonlocal models (4.7) and (4.8). An understanding of the stability of these states is necessary for determining the feasibility of biological control for this model. In this chapter we consider primarily $E_{1}, E_{2}$, and $E_{3}$ since these are most relevant to biological control, representing complete control, pest infestation, and partial control, respectively. Specifically, we consider the case where $E_{2}$ is stable in the $u v$-plane (when there are no perturbations in $w$ ), while $E_{1}$ or $E_{3}$ is stable in the presence of species $w$. The stability of $E_{1}$ or $E_{3}$ guarantees the potential for complete or partial biological control, while the stability of $E_{2}$ in the $u v$-plane is necessary for the pest infested state to actually be observed. For some parameter sets, the $E_{2}$ state can lose stability to a Hopf bifurcation in the $u v$-plane, resulting in a stable limit cycle [39]. We do not consider these parameter regimes as the limit cycle does not qualitatively affect the results presented below.

As there is no singularity for the $E_{2}$ and $E_{3}$ states, the linear stability of both can be analyzed for the full spatially dependent nonlocal models using standard techniques,
while the analysis for the $E_{1}$ state requires other analytic methods due to the singularity. In general the analysis is considerably more algebraically complicated than for two species systems, rendering closed form expressions for the stability bounds impractical even when obtainable. We instead outline an algorithmic procedure to determine these stability bounds, and validate these procedures through numerical computation of the full nonlocal, nonlinear problems (4.7) and (4.8).

### 4.3.1. Stability of $E_{1}$ for the ODE Model

We first briefly consider the $w$-free problem (4.1). Suppressing the spatial dependence and linearizing about the $(u, v)=(1,0)$ state gives the two eigenvalues $\lambda_{1}=-1$ and $\lambda_{2}=m_{1}-d_{1}$. Thus the $E_{1}$ state is a saddle in the $u v$-plane if and only if $m_{1}>d_{1}$. For the $E_{2}$ state to be physical, however, it must be that $m_{1}>d_{1}$. Hence for all parameter regimes relevant to biological control, i.e., when the pest infested $E_{2}$ state is physical, the $E_{1}$ state is a saddle in the $u v$-plane. This will become important when we later consider diffusion driven instabilities of the $E_{1}$ state. We now turn to the full food chain model.

We start by discussing the stability of the $E_{1}$ state for the ODE system, i.e., with no spatial dependence. We will present two methods for determining conditions on the stability of $E_{1}$. The first method follows, and extends, the stability analysis presented in [39]. We present the second method because it becomes necessary when we consider nonlocality.

Method 1: Our first approach will be to follow the analysis in [39], introduce the new variable $R=v / w$, and consider the $(u, v, R)$ system,
(4.11a) $u_{t}=u(1-u)-\frac{a_{1} u v}{u+v}$,

$$
v_{t}=\frac{m_{1} u v}{u+v}-d_{1} v-\frac{a_{2} v}{R+1},
$$

$$
\begin{equation*}
R_{t}=R\left[\frac{m_{1} u}{u+v}+d_{2}-d_{1}-\frac{a_{2}+m_{2} R}{R+1}\right] \tag{4.11c}
\end{equation*}
$$

This system has two equilibrium points. The first point is $(u, v, R)=(1,0,0)$, what we will refer to as the $R=0$ point, which corresponds to the case where $v=o(w)$ as $t \rightarrow \infty$. The second is $\left(1,0, R^{*}\right)$, where the constant $R^{*}$ is the solution to

$$
\begin{equation*}
m_{1}-d_{1}+d_{2}=\frac{a_{2}+m_{2} R^{*}}{R^{*}+1} \tag{4.12}
\end{equation*}
$$

which corresponds to the case where $v \sim R^{*} w$ as $t \rightarrow \infty$. Due to the domino effect in this food chain, if either of these states is stable, then the fact that $v \rightarrow 0$ will result in $w \rightarrow 0$, and so imply the stability of the $E_{1}$ state.

We note that (4.11) is examined in [39], where it is concluded that the $R=0$ point is stable if and only if

$$
\begin{equation*}
m_{1}+d_{2}<d_{1}+a_{2} \tag{4.13}
\end{equation*}
$$

and that the $\left(1,0, R^{*}\right)$ point is stable if and only if

$$
\begin{equation*}
\left(m_{2}-d_{2}\right) a_{2}>\left(m_{1}-d_{1}\right) m_{2}, \quad a_{2}<m_{1}-d_{1}+d_{2}<m_{2} \tag{4.14}
\end{equation*}
$$

Thus if condition (4.13) holds, then the $E_{1}$ state is stable with $v=o(w)$ as $t \rightarrow \infty$, and if (4.14) holds, then the $E_{1}$ state is stable with $v \sim R^{*} w$ as $t \rightarrow \infty$.

In [39] a third condition is found after introducing the transformation $Q=u / v$, $R=v / w$, and considering the $(Q, v, R)$ system. The condition is

$$
m_{2}>d_{2}, \quad m_{1}<\min \left\{1+d_{1}, d_{1}+a_{2}-d_{2}\right\} .
$$

Here we note that this condition is more restrictive than (4.13), because $m_{1}+d_{2}<d_{1}+a_{2}$ is always true if $m_{1}<\min \left\{1+d_{1}, d_{1}+a_{2}-d_{2}\right\}$. Hence, in the $v=o(w)$ regime, the condition that $m_{2}>d_{2}$ is not necessary for stability. Nor is the condition that $m_{1}<1+d_{1}$ when $1+d_{1}<d_{1}+a_{2}-d_{2}$, since $m_{1}<d_{1}+a_{2}-d_{2}$ implies stability even when $m_{1}>1+d_{1}$.

The analysis in [39] does not consider the case where $w=o(v)$ as $t \rightarrow \infty$. This case can be examined by considering the transformation $Q=w / v$ and linearizing about the $Q=0$ critical state. Here we instead let

$$
v \sim e^{-\alpha t}, \quad w \sim e^{-\beta t}, \quad \beta>\alpha .
$$

This means that as $t \rightarrow \infty$,

$$
\frac{u}{u+v} \rightarrow 1, \quad \frac{w}{v+w} \rightarrow 0, \quad \frac{v}{v+w} \rightarrow 1
$$

and so the equations for $v$ and $w$ are equivalent to

$$
-\alpha=m_{1}-d_{1}, \quad-\beta=m_{2}-d_{2}
$$

When we require that

$$
\alpha, \beta>0, \quad \beta>\alpha
$$

we arrive at the condition

$$
\begin{equation*}
d_{2}-m_{2}>d_{1}-m_{1}>0 \tag{4.15}
\end{equation*}
$$

If condition (4.15) holds, then the $E_{1}$ state is stable with $w=o(v)$ as $t \rightarrow \infty$.
We note that the three conditions (4.13), (4.14), and (4.15) are mutually exclusive. Thus we can conclude that $E_{1}$ is stable if any one of these conditions is satisfied, and the specific condition that is satisfied determines the long time relative behavior of $v$ and $w$.

Method 2: We perturb the full $(u, v, w)$ system about the $E_{1}$ state by considering solutions where $u$ is close to 1 while $v$ and $w$ are small. This can be written in the form

$$
u \sim 1+\epsilon \tilde{u}+\mathcal{O}\left(\epsilon^{2}\right), \quad v \sim \epsilon \tilde{v}+\mathcal{O}\left(\epsilon^{2}\right), \quad w \sim \epsilon \tilde{w}+\mathcal{O}\left(\epsilon^{2}\right)
$$

where $\epsilon \ll 1$. We substitute these expansions and keep only terms that are linear in $\epsilon$. This linear stability analysis gives the nonlinear equations
(4.16a) $\tilde{u}_{t}=-\tilde{u}-a_{1} \tilde{v}$,
(4.16b) $\tilde{v}_{t}=\left(m_{1}-d_{1}\right) \tilde{v}-\frac{a_{2} \tilde{v} \tilde{w}}{\tilde{v}+\tilde{w}}$,
(4.16c) $\tilde{w}_{t}=-d_{2} \tilde{w}+\frac{m_{2} \tilde{v} \tilde{w}}{\tilde{v}+\tilde{w}}$.

Note that (4.16b) and (4.16c) decouple from (4.16a), and so they can be considered first. The system $(4.16 \mathrm{~b}),(4.16 \mathrm{c})$ can be solved since it admits two first integrals. This analysis is presented in Appendix D. The results agree with those from the first method. Specifically, when $v=o(w)$, we arrive at (4.13), and obtain the long time behavior of $v$
and $w$ as

$$
\begin{equation*}
v \sim e^{\left(m_{1}-d_{1}-a_{2}\right) t}, \quad w \sim e^{-d_{2} t} . \tag{4.17}
\end{equation*}
$$

When $v \sim C w$ (where $C$ is a nonzero constant that will be exactly $R^{*}$ from (4.12)), we arrive at (4.14), and obtain the long time behaviors

$$
\begin{equation*}
v, w \sim \exp \left(\frac{\left(m_{2}-d_{2}\right) a_{2}-\left(m_{1}-d_{1}\right) m_{2}}{a_{2}-m_{2}} t\right) \tag{4.18}
\end{equation*}
$$

When $w=o(v)$, we arrive at (4.15), and obtain the long time behaviors

$$
\begin{equation*}
v \sim e^{\left(m_{1}-d_{1}\right) t}, \quad w \sim e^{\left(m_{2}-d_{2}\right) t} . \tag{4.19}
\end{equation*}
$$

### 4.3.2. Stability of $E_{1}$ for the Nonlocal Problems

We now extend the second method to examine the stability of the $E_{1}$ state for the full nonlocal problems. We consider perturbations of the form

$$
u \sim 1+\epsilon \tilde{u}(x, t), \quad v \sim \epsilon \tilde{v}(x, t), \quad w \sim \epsilon \tilde{w}(x, t), \quad \epsilon \ll 1 .
$$

For the local problem, this gives
(4.20a) $\tilde{u}_{t}=\tilde{u}_{x x}-\tilde{u}-a_{1} \tilde{v}$,
(4.20b) $\tilde{v}_{t}=\mu_{2} \tilde{v}_{x x}+\left(m_{1}-d_{1}\right) \tilde{v}-\frac{a_{2} \tilde{v} \tilde{w}}{\tilde{v}+\tilde{w}}$,
(4.20c) $\tilde{w}_{t}=\mu_{3} \tilde{w}_{x x}-d_{2} \tilde{w}+\frac{m_{2} \tilde{v} \tilde{w}}{\tilde{v}+\tilde{w}}$.

We could now consider the standard ansatz that $\tilde{u}, \tilde{v}, \tilde{w} \sim e^{i k x}$, and again follow the second method from Section 4.3.1, but the results would not identify a critical condition for stability in general. Since the evolution equations for the $(\tilde{v}, \tilde{w})$ system are nonlinear, we lose the principle of superposition, and so the analysis can only tell us about the instability of the $E_{1}$ state to a single, given value of $k$. If only a single value of $k$ is considered, however, then the ansatz that $\tilde{v}, \tilde{w} \sim e^{i k x}$ is nonphysical as it allows for negative populations. Therefore this method does not allow for any analysis, and so we will have to turn to numerics to discuss any diffusion driven instabilities of the $E_{1}$ state. This will be discussed further in Section 4.5.2.
$C$-type Nonlocality: The $C$-type nonlocal problem yields the evolution equation for $\tilde{u}$

$$
\begin{equation*}
\tilde{u}_{t}=\tilde{u}_{x x}-\varphi * \tilde{u}-a_{1} \tilde{v}, \tag{4.21}
\end{equation*}
$$

while the equations for $\tilde{v}$ and $\tilde{w}$ are given by (4.20b) and (4.20c) respectively. The equation for $\tilde{u}$, (4.21), decouples from the other equations, and the nonlocality only affects this equation. Since we are seeking to describe the instability due to the nonlocality, we will make the assumption that the spatially uniform $E_{1}$ state is stable for the local problem. Then we can conclude that $\tilde{v}, \tilde{w} \rightarrow 0$ for this $C$-type nonlocal problem as well. This means that the only instability that can arise due to this type of nonlocality comes from the linear equation for $\tilde{u}$. We can now make the ansatz that $\tilde{u} \sim e^{i k x}$, and consider the long time problem where $\tilde{v}, \tilde{w}=0$. This gives us a linear equation

$$
\tilde{u}_{t}=-\left(k^{2}+\hat{\varphi}\right) \tilde{u},
$$

where $\hat{\varphi}$ is the Fourier transform of the kernel given by (4.6), and so the principal of superposition allows us to determine the condition for stability

$$
\begin{equation*}
\hat{\varphi}>-k^{2} \quad \Longrightarrow \quad \frac{\sin (\delta k)}{\delta k}>-k^{2} \tag{4.22}
\end{equation*}
$$

This is the condition for stability from the nonlocal Fisher's equation [50]. We now introduce a new variable $\beta=\delta k$ so that the critical condition for stability is

$$
\frac{\sin (\beta)}{\beta}=\frac{-\beta^{2}}{\delta^{2}}
$$

Solving then for the critical value of $\delta$ gives us

$$
\begin{equation*}
\delta_{c}=\sqrt{\frac{-\beta_{c}^{3}}{\sin \left(\beta_{c}\right)}} \tag{4.23}
\end{equation*}
$$

where the critical $\delta_{c}, \beta_{c}$ pair can be found by minimizing this expression with respect to $\beta$, which gives $\delta_{c} \sim 9.18$.
$P_{w}$-type Nonlocalities: While the $C$-type nonlocality altered only the linear evolution equation (4.21) for the perturbation in $u$ and allowed for an analysis, the $P_{w}$-type nonlocality will alter the evolution equations for $\tilde{v},(4.20 \mathrm{~b})$, and $\tilde{w},(4.20 \mathrm{c})$. The altered equations are still nonlinear, and so we again lose the principal of superposition, and must turn to numerics. We will discuss instabilities due to this $P_{w}$-type nonlocality in Sections 4.5.2 and 4.5.3.

### 4.3.3. Stability of $E_{2}$ for the Nonlocal Problems

Here we examine the stability of the $E_{2}$ state given by (4.3). We seek solutions of the form

$$
u \sim \bar{u}+\epsilon \tilde{u} e^{\lambda t} e^{i k x}, \quad v \sim \bar{v}+\epsilon \tilde{v} e^{\lambda t} e^{i k x}, \quad w \sim \epsilon \tilde{w} e^{\lambda t} e^{i k x} .
$$

In the local case, we arrive at the Jacobian

$$
J_{2}=\left[\begin{array}{ccc}
-k^{2}+\eta_{1}(1-\bar{u})-\bar{u} & -a_{1} \eta_{1}^{2} & 0  \tag{4.24}\\
\frac{\left(m_{1}-d_{1}\right)^{2}}{m_{1}} & -\eta_{1}\left(m_{1}-d_{1}\right)-\mu_{2} k^{2} & -a_{2} \\
0 & 0 & m_{2}-d_{2}-\mu_{3} k^{2}
\end{array}\right]
$$

Two of the eigenvalues of $J_{2}$ are the same as those of the two species, $w$-free problem, while the third eigenvalue is $m_{2}-d_{2}-\mu_{3} k^{2}$. This eigenvalue corresponds to the only eigenvector with nonzero $w$ component. For the $C$-type nonlocality, only the $w$-free problem is affected by the nonlocality, and this third eigenvalue remains unchanged. So for this nonlocality, we need only consider the two species problem (4.1) to look for cellular instabilities.
$C$-type Nonlocality: When we consider the $C$-type nonlocality, the Jacobian for the $w$-free system becomes

$$
\tilde{J}_{2}=\left[\begin{array}{cc}
-k^{2}+\eta_{1}(1-\bar{u})-\bar{u} \hat{\varphi} & -a_{1} \eta_{1}^{2}  \tag{4.25}\\
\frac{\left(m_{1}-d_{1}\right)^{2}}{m_{1}} & -\eta_{1}\left(m_{1}-d_{1}\right)-\mu_{2} k^{2}
\end{array}\right]
$$

Stability requires that the determinant of $\tilde{J}_{2}$ be positive. This gives us the condition

$$
\begin{equation*}
\frac{\sin (\delta k)}{\delta k}>\frac{a_{1}}{\bar{u} m_{1}}\left(\frac{\eta_{1}\left(m_{1}-d_{1}\right) \mu_{2} k^{2}}{\eta_{1}\left(m_{1}-d_{1}\right)+\mu_{2} k^{2}}\right)-\frac{k^{2}}{\bar{u}} \tag{4.26}
\end{equation*}
$$

We rewrite (4.26) using $\beta=\delta k$ and $D=1 / \delta^{2}$ to obtain the critical condition

$$
F_{C}(\beta, D)=0
$$

where

$$
\begin{align*}
& F_{C}(\beta, D) \equiv  \tag{4.27}\\
& \mu_{2} \beta^{4} D^{2}+\left[\eta_{1}\left(m_{1}-d_{1}\right)+\eta_{1} \mu_{2}(\bar{u}-1)+\mu_{2} \bar{u} \frac{\sin (\beta)}{\beta}\right] \beta^{2} D+\eta_{1}\left(m_{1}-d_{1}\right) \bar{u} \frac{\sin (\beta)}{\beta} .
\end{align*}
$$

We seek the critical value for $D$ such that there is exactly one value of $\beta$ that gives instability. This critical pair can be found in two ways, described in Appendix E.

We do not present the similar condition on the trace of $\tilde{J}_{2}$ since there were no observed oscillatory instabilities for the parameters considered in this chapter, and indeed, the determinant condition proved to be more restrictive for all of those parameters.
$P_{w}$ Nonlocality: For the $P_{w}$ nonlocality, we must consider the full three species system. However, we find that the Jacobian is unchanged from that of the local problem (4.24), and so the $P_{w}$ nonlocality does not affect the $E_{2}$ state.

### 4.3.4. Stability of $E_{3}$ for the Nonlocal Problems

We begin by examining the stability of the $E_{3}$ state, given by (4.4), for the local problem. Here we seek solutions of the form

$$
\begin{aligned}
& u \sim u_{c}+\epsilon \tilde{u} e^{\lambda t} e^{i k x}, \quad v \sim v_{c}+\epsilon \tilde{v} e^{\lambda t} e^{i k x}, \\
& w \sim w_{c}+\epsilon \tilde{w} e^{\lambda t} e^{i k x} .
\end{aligned}
$$

From this expansion, we obtain the Jacobian
(4.28) $J_{3}=\left[\begin{array}{ccc}j_{11} & j_{12} & 0 \\ j_{21} & j_{22} & j_{23} \\ 0 & j_{32} & j_{33}\end{array}\right]$,
where
(4.29a) $j_{11}=1-k^{2}-2 u_{c}-\frac{a_{1} v_{c}^{2}}{\left(u_{c}+v_{c}\right)^{2}}$,
(4.29b) $j_{22}=-d_{1}-\mu_{2} k^{2}+\frac{m_{1} u_{c}^{2}}{\left(u_{c}+v_{c}\right)^{2}}-\frac{a_{2} w_{c}^{2}}{\left(v_{c}+w_{c}\right)^{2}}$,
(4.29c) $j_{33}=-d_{2}-\mu_{3} k^{2}+\frac{m_{2} v_{c}^{2}}{\left(v_{c}+w_{c}\right)^{2}}$,
(4.29d) $j_{12}=-\frac{a_{1} u_{c}^{2}}{\left(u_{c}+v_{c}\right)^{2}}, \quad j_{21}=\frac{m_{1} v_{c}^{2}}{\left(u_{c}+v_{c}\right)^{2}}$,
(4.29e) $\quad j_{23}=-\frac{a_{2} v_{c}^{2}}{\left(v_{c}+w_{c}\right)^{2}}, \quad j_{32}=\frac{m_{2} w_{c}^{2}}{\left(v_{c}+w_{c}\right)^{2}}$.

We note that the eigenvalues $\lambda$ of $J_{3}$ satisfy the equation
(4.30) $\lambda^{3}+A_{1} \lambda^{2}+A_{2} \lambda+A_{3}=0$,
where
(4.31a) $A_{1}=-j_{11}-j_{22}-j_{33}$,
(4.31b) $A_{2}=j_{22} j_{33}+j_{11} j_{22}+j_{11} j_{33}-j_{12} j_{21}-j_{23} j_{32}$,
(4.31c) $\quad A_{3}=j_{12} j_{21} j_{33}+j_{11} j_{23} j_{32}-j_{11} j_{22} j_{33}$.

From the Routh-Hurwitz criterion for stability, we have that $E_{3}$ will be asymptotically stable if and only if

$$
\begin{equation*}
F \equiv A_{1}>0, \quad G \equiv A_{3}>0, \quad H \equiv A_{1} A_{2}-A_{3}>0 \tag{4.32}
\end{equation*}
$$

C-type Nonlocality: For the $C$-type nonlocality, the Jacobian of the system linearized about $E_{3}$ is the same as (4.28), (4.29), except that now

$$
\begin{equation*}
j_{11}=1-k^{2}-(1+\hat{\varphi}) u_{c}-\frac{a_{1} v_{c}^{2}}{\left(u_{c}+v_{c}\right)^{2}} \tag{4.33}
\end{equation*}
$$

We now consider the three conditions for stability from (4.32). We can again use the variables $\beta=\delta k$ and $D=\delta^{-2}$ to write these conditions as functions of $D$ and $\beta$. The critical $D$ and $\beta$ values can then be found following the procedure described in Appendix F.
$P_{w}$-type Nonlocality: Here we again follow the same analysis as for the $C$-type nonlocality. The Jacobian is the same as (4.28), (4.29), except that now

$$
\begin{align*}
& \text { (4.34a) } j_{23}=-\frac{a_{2} v_{c}^{2}}{\left(v_{c}+w_{c}\right)^{2}}-\frac{a_{2} v_{c} w_{c}(1-\hat{\varphi})}{\left(v_{c}+w_{c}\right)^{2}}  \tag{4.34a}\\
& \text { (4.34b) } j_{33}=-d_{2}-\mu_{3} k^{2}+\frac{m_{2} v_{c}^{2}}{\left(v_{c}+w_{c}\right)^{2}}+\frac{a_{2} v_{c} w_{c}(1-\hat{\varphi})}{\left(v_{c}+w_{c}\right)^{2}} .
\end{align*}
$$

The critical conditions (4.32) are again either linear or cubic in $D$, and so finding the critical $D_{c}$ and $\beta_{c}$ pair employs the same method as before.

### 4.3.5. Numerical Validation

To validate these procedures for finding the critical value of $\delta$, we will present results for two different sets of parameters. The first set is

$$
\begin{equation*}
a_{1}=0.9, \quad m_{1}=1.0, \quad d_{1}=0.9, a_{2}=2.0, \quad m_{2}=1.1, \quad d_{2}=1.0 \tag{4.35}
\end{equation*}
$$

This parameter set was chosen because it ensures that $E_{2}$ is stable in the $u v$-plane, while $E_{1}$ is stable in the presence of the superpredator $w$, i.e., it corresponds to a situation where we would expect to see complete biological control from the introduction of the superpredator. For this parameter set, the $E_{3}$ state is nonphysical.

The second parameter set gives a stable $E_{3}$ state in the presence of species $w$, corresponding to partial biological control. This parameter set is

$$
\begin{equation*}
a_{1}=0.5, \quad m_{1}=1.5, \quad d_{1}=1.0, a_{2}=0.5, \quad m_{2}=2.0, \quad d_{2}=1.0 \tag{4.36}
\end{equation*}
$$

Along with these parameter sets, we will take the diffusivities to be $\mu_{2}=\mu_{3}=1$.
Table 4.1 gives the predicted critical $\delta$ values and the range over which the critical transition was observed in numerical simulations. For the $C$-type nonlocality, the observed transitions were sharp and showed agreement with the predicted values, validating our procedures for all three states $E_{1}, E_{2}$, and $E_{3}$.

For the $P_{w}$ case presented in Table 4.1, the observed transition also shows agreement with the analysis. The range of $\delta$ values considered for this transition is much larger
(though still roughly $\pm 10 \%$ of the critical value). This was because taking a value of $\delta$ below, but close to the critical threshold would lead to the formation of transient cells that ultimately decayed in time. For values of $\delta$ that were too close to the critical threshold, the time required for these patterns to noticeably decay, along with a necessarily restricted timestep, made simulation impractical.

Finally we make an important observation about the procedures for determining $\delta_{c}$ we have presented in this chapter: it is possible that the maximum value of $D$ is not positive, and so there is no critical $\delta_{c}$, i.e., the given state is stable for all values of $\delta$. This occurs for the $E_{2}$ state when considering the $P_{w}$-type nonlocality for both parameter sets (4.35) and (4.36). In these cases, we considered values up to $\delta=200$ and did not observe the formation of any cellular patterns, as the analysis predicts.

| Parameters | Nonlocality | State | $\delta_{c}$ | Range |
| :---: | :---: | :---: | :---: | :---: |
| $(4.35)$ | $C$-type | $E_{1}$ | 9.18 | $9-10$ |
| $(4.35)$ | $C$-type | $E_{2}$ | 8.33 | $7.5-8.5$ |
| $(4.36)$ | $C$-type | $E_{1}$ | 9.18 | $9-10$ |
| $(4.36)$ | $C$-type | $E_{2}$ | 8.96 | $8.5-9.5$ |
| $(4.36)$ | $C$-type | $E_{3}$ | 8.84 | $8-9$ |
| $(4.36)$ | $P_{w}$-type | $E_{3}$ | 66.3 | $60-73$ |

Table 4.1. Table of predicted critical $\delta$ values and numerically observed critical transitions. The column labeled range was obtained through numerical simulation: the lower number is the largest value of $\delta$ considered for which the given state was stable; the higher number is the smallest value of $\delta$ considered for which cellular patterns formed and persisted.

### 4.4. Front Speeds

We obtain estimates of the speeds of the different fronts we have observed through simulation. We follow an analysis similar to that presented in $[\mathbf{6 0}, \mathbf{6 1}]$, where it is assumed
that the fronts are pulled fronts, i.e., that the propagation of the front is determined by the behavior of the system ahead of the front. We do this by considering the problem linearized about the unstable state ahead of the front. It is important to note that these results will not be correct when the fronts are not pulled. However, it appears that the fronts of interest in this chapter are pulled fronts, and so the following gives accurate predictions of the propagation speeds in all cases for which the analysis is applicable.

### 4.4.1. Analytic Predictions of Front Speeds

In this chapter we are primarily concerned with biological control, so that the fronts of interest are
(1) The original invasion of the pest species $v$ into a region inhabited only by the crop species $u$, corresponding to the pest infested $E_{2}$ state displacing the $E_{1}$ state with $w \equiv 0$.
(2) Partial control where a pulse of species $w$ introduced into an infested region restores some, but not all, of the crop $u$ (since $\bar{u}<u_{c}<1$ ). This corresponds to the partial restoration $E_{3}$ state displacing the pest infested $E_{2}$ state.
(3) Complete control where a pulse of species $w$ introduced into an infested region removes all of the pest $v$. This corresponds to the pest free $E_{1}$ state displacing the pest infested $E_{2}$ state.

For the first of these fronts, the $E_{1}$ state is the unstable state being displaced. For the second and third fronts, the $E_{2}$ state is the unstable state being displaced. Thus we will linearize (4.2) about each of these two states using the methodology of $[\mathbf{6 0}, \mathbf{6 1}]$ to determine the propagation speeds of the fronts that displace them.

Propagation into the $E_{1}$ State: We first note that the front we are primarily concerned with, that propagates into the $E_{1}$ state (front 1 ), only occurs when $w \equiv 0$. So we can consider the $w$-free problem (4.1). We now linearize (4.1) about the $(1,0)$ state, since there is now no singularity for the $w$-free problem, seeking solutions of the form

$$
u \sim 1+\epsilon \tilde{u} e^{-K\left(x-\frac{\Lambda}{K} t\right)}, \quad v \sim \epsilon \tilde{v} e^{-K\left(x-\frac{\Lambda}{K} t\right)}
$$

and noting that this would correspond to a front with propagation speed $c=\Lambda / K$. This gives us two eigenvalues

$$
\Lambda_{1}=K^{2}-1, \quad \Lambda_{2}=m_{1}-d_{1}+\mu_{2} K^{2}
$$

We note that the eigenvector corresponding to $\Lambda_{1}$ has a zero $v$ component, and so only $\Lambda_{2}$ is relevant for this case where the $E_{2}$ state displaces the $E_{1}$ state. When we consider $\Lambda_{2}$, we see that the propagation speed is given by

$$
c=\frac{\Lambda_{2}}{K}=\frac{m_{1}-d_{1}}{K}+\mu_{2} K .
$$

We can then minimize this speed with respect to $K$ to obtain an expression for the minimal speed, which is the expected speed of propagation after the initial conditions evolve into the propagating front [61]. This minimal speed is given by

$$
\begin{equation*}
c_{\min }=2 \sqrt{\mu_{2}\left(m_{1}-d_{1}\right)} \tag{4.37}
\end{equation*}
$$

Propagation into the $E_{2}$ State: Here we must consider the full system linearized about the unstable $E_{2}$ state. There is again no singularity, so we seek solutions of the
form

$$
\begin{aligned}
& u \sim \bar{u}+\epsilon \tilde{u} e^{-K\left(x-\frac{\Lambda}{K} t\right)}, \quad v \sim \bar{v}+\epsilon \tilde{v} e^{-K\left(x-\frac{\Lambda}{K} t\right)}, \\
& w \sim \epsilon \tilde{w} e^{-K\left(x-\frac{\Lambda}{K} t\right)}
\end{aligned}
$$

which corresponds to a front with propagation speed $c=\Lambda / K$. We obtain the Jacobian

$$
\hat{J}_{2}=\left[\begin{array}{ccc}
\eta_{1}(1-\bar{u})-\bar{u}+K^{2} & -\frac{a_{1} d_{1}^{2}}{m_{1}^{2}} & 0  \tag{4.38}\\
\frac{\left(m_{1}-d_{1}\right)^{2}}{m_{1}} & -\eta_{1}\left(m_{1}-d_{1}\right)+\mu_{2} K^{2} & -a_{2} \\
0 & 0 & m_{2}-d_{2}+\mu_{3} K^{2}
\end{array}\right]
$$

We now observe that two of the eigenvalues of $\hat{J}_{2}$ come from the $w$-free problem linearized about the $(\bar{u}, \bar{v})$ state. As we are concerned with scenarios where this state is stable in the absence of species $w$, both of these eigenvalues will be negative. Therefore the only positive eigenvalue to consider is given by

$$
\Lambda_{3}=m_{2}-d_{2}+\mu_{3} K^{2}
$$

which gives the speed

$$
c=\frac{\Lambda_{3}}{K}=\frac{m_{2}-d_{2}}{K}+\mu_{3} K
$$

and the minimal speed is then given by

$$
\begin{equation*}
c_{\min }=2 \sqrt{\mu_{3}\left(m_{2}-d_{2}\right)} \tag{4.39}
\end{equation*}
$$

### 4.4.2. Numerical Validation of Front Speeds

To validate our front speed predictions, we will consider parameter sets (4.35) and (4.36), along with a third set

$$
\begin{equation*}
a_{1}=0.9, \quad m_{1}=1.0, \quad d_{1}=0.9, a_{2}=1.2, \quad m_{2}=1.1, \quad d_{2}=1.0 \tag{4.40}
\end{equation*}
$$

The stability of the equilibrium states in the ODE system is the same for both parameter sets (4.35) and (4.40), i.e., $E_{2}$ is stable in the $u v$-plane, while $E_{1}$ is stable in the presence of $w$.

We consider these parameter sets along with several values for the diffusivities and compare the observed front speeds with the analytically predicted speeds (4.37) and (4.39) in Tables 4.2, 4.3, 4.4, and 4.5.

Table 4.2 shows speeds for fronts of type 1, representing the original pest infestation of the pest free state, i.e., fronts where the $E_{2}$ state displaces the $E_{1}$ state and the predicted speed is given by (4.37). For these fronts, we take the initial condition (4.9) with $E_{2}$ and $E_{1}$ as the equilibrium states $\overrightarrow{s_{1}}$ and $\overrightarrow{s_{2}}$ respectively. We note that all of the observed speeds agree well with the analytical predictions.

Table 4.3 shows front speeds for parameter set (4.36), where the partial restoration $E_{3}$ state is asymptotically stable. Here we consider partial control fronts of type 2, where the partial restoration $E_{3}$ state displaces the pest infested $E_{2}$ state after a pulse of the superpredator $w$ is introduced into a pest infested region, corresponding to initial condition (4.10) where $E_{2}$ is the invaded uniform state $\left(s_{1}, s_{2}, s_{3}\right)$. For these cases, the predicted speed (4.39) and the observed speeds also agree well.

| $\mu_{2}$ | $\mu_{3}$ | Parameters | Predicted | Observed |
| :---: | :---: | :---: | :---: | :---: |
| 1 | 1 | $(4.35)$ | 0.6325 | 0.6251 |
| 1 | 1 | $(4.40)$ | 0.6325 | 0.6251 |
| 1 | 4 | $(4.35)$ | 0.6325 | 0.6251 |
| 1 | 4 | $(4.40)$ | 0.6325 | 0.6251 |
| $1 / 4$ | 1 | $(4.35)$ | 0.3162 | 0.3131 |
| $1 / 4$ | 1 | $(4.40)$ | 0.3162 | 0.3131 |
| 1 | $1 / 4$ | $(4.35)$ | 0.6325 | 0.6317 |
| 1 | $1 / 4$ | $(4.40)$ | 0.6325 | 0.6306 |
| 4 | 1 | $(4.35)$ | 1.2649 | 1.2635 |
| 4 | 1 | $(4.40)$ | 1.2649 | 1.2613 |

Table 4.2. Table of front propagation speeds for the original pest infestation of the pest free state.

| $\mu_{2}$ | $\mu_{3}$ | Parameters | Predicted | Observed |
| :---: | :---: | :---: | :---: | :---: |
| 1 | 1 | $(4.36)$ | 2 | 1.9776 |
| 1 | 4 | $(4.36)$ | 4 | 3.9552 |
| $1 / 4$ | 1 | $(4.36)$ | 2 | 1.9776 |
| 1 | $1 / 4$ | $(4.36)$ | 1 | 0.9888 |
| 4 | 1 | $(4.36)$ | 2 | 1.9776 |

Table 4.3. Table of front propagation speeds for the partial control of an infestation, where the partial restoration $E_{3}$ state displaces the pest infested state $E_{2}$ state.

Table 4.4 again shows front speeds for parameter set (4.36), taking the same parameter values as in Table 4.3, but with a different initial condition. For these cases, we consider an initial condition given by (4.9) where the invading state $\overrightarrow{s_{1}}$ is the partial restoration $E_{3}$ state, and the displaced state $\overrightarrow{s_{2}}$ is the pest free state $E_{1}$. This represents a kind of infestation where the pest is accompanied by the superpredator as it invades. With this initial setup, we observed two different behaviors.

The first behavior observed, corresponding to the single starred entries in Table 4.4, was where a front formed between the $E_{3}$ state and the $E_{1}$ state. For this behavior, the observed speeds were quite different from the speeds given by (4.37). This does not,

| $\mu_{2}$ | $\mu_{3}$ | Parameters | Predicted | Observed |
| :---: | :---: | :---: | :---: | :---: |
| 1 | 1 | $(4.36)$ | 1.4142 | $1.1470^{*}$ |
| 1 | 4 | $(4.36)$ | 1.4142 | $0.8262^{*}$ |
| $1 / 4$ | 1 | $(4.36)$ | 0.7071 | $0.4131^{*}$ |
| 1 | $1 / 4$ | $(4.36)$ | 1.4142 | $1.4019^{* *}$ |
| 4 | 1 | $(4.36)$ | 2.8284 | $2.8038^{* *}$ |

Table 4.4. Table of front propagation speeds involving invasion fronts that result when $E_{3}$ is initially set to invade the $E_{1}$ state. The single starred entries are the cases where the speeds do not agree, and correspond to the cases where $E_{3}$ directly displaces $E_{1}$. The double starred entries are the cases where the initial front splits, and the speeds recorded are for the pest invasion where $E_{2}$ displaces $E_{1}$.
however, represent a failure of the analysis presented in Section 4.4.1, but rather it reflects the fact that this analysis is not applicable in these cases. We obtained the predicted speed (4.37) by considering the instability of the $E_{1}$ state in the $u v$-plane, i.e. for the $w$-free problem. Thus this analysis can only be applied in the absence of species $w$. Any invasion involving the $E_{3}$ state, however, must involve species $w$, thereby rendering the analysis inapplicable for these cases.

The second behavior observed, corresponding to the double starred entries in Table 4.4, was where the initial 'front' connecting $E_{3}$ to $E_{1}$ split, with the $E_{2}$ state forming between the two states. This behavior can be seen in Figure 4.1. Once the $E_{2}$ state has formed, we can see two distinct fronts: the $E_{3}$ state displacing the $E_{2}$ state on the left, which follows the $E_{2}$ state displacing the $E_{1}$ state on the right. We calculated the observed speeds for each of these fronts separately. The rightmost fronts, where $E_{2}$ displaces $E_{1}$ are recorded in of Table 4.4, and show good agreement with the predicted speeds for these cases, given by (4.37). We note that the leftmost fronts, where $E_{3}$ displaces $E_{2}$, correspond to the fronts considered at the bottom of Table 4.3, and gave nearly the same

(a) Space-Time Plot of $u$

(b) Space-Time Plot of $v$

(d) Profile of the Split Fronts

$$
4
$$


(c) Space-Time Plot of $w$

Figure 4.1. Typical splitting behavior of the 'front' connecting the $E_{3}$ state to the $E_{1}$ state. We can see that the $E_{2}$ state forms between the original two states. Here we use the parameters (4.36) with $\mu_{2}=4$ and $\mu_{3}=1$.
observed speeds. This splitting behavior only occurred when the speed at which the $E_{2}$ state displaced the $E_{1}$ state was larger than the speed at which the $E_{3}$ state displaced the $E_{2}$ state, i.e. when the speed (4.37) was larger than (4.39).

Table 4.5 shows the speeds for control fronts of type 3 where a pulse of the superpredator $w$ is introduced into a pest infested region, corresponding to initial condition (4.10) where $E_{2}$ is the invaded uniform state $\left(s_{1}, s_{2}, s_{3}\right)$. This creates a front where the pest free $E_{1}$ state displaces the $E_{2}$ state. In this case, the predicted speed is given by (4.39). We note that again all of the observed speeds agree well with the analytical predictions. The final four cases considered in Table 4.5 produced a resurgent behavior in the pest species $v$, where the pest infested $E_{2}$ state would reemerge behind the control front, as discussed in Section 4.5.

| $\mu_{2}$ | $\mu_{3}$ | Parameters | Predicted | Observed |
| :---: | :---: | :---: | :---: | :---: |
| 1 | 1 | $(4.35)$ | 0.6325 | 0.6229 |
| 1 | 1 | $(4.40)$ | 0.6325 | 0.6229 |
| 1 | 4 | $(4.35)$ | 1.2649 | 1.2470 |
| 1 | 4 | $(4.40)$ | 1.2649 | 1.2459 |
| $1 / 4$ | 1 | $(4.35)$ | 0.6325 | 0.6229 |
| $1 / 4$ | 1 | $(4.40)$ | 0.6325 | 0.6251 |
| 1 | $1 / 4$ | $(4.35)$ | 0.3162 | 0.3208 |
| 1 | $1 / 4$ | $(4.40)$ | 0.3162 | 0.3153 |
| 4 | 1 | $(4.35)$ | 0.6325 | 0.6504 |
| 4 | 1 | $(4.40)$ | 0.6325 | 0.6339 |

Table 4.5. Table of front propagation speeds for the control fronts. The final four entries correspond to parameter values that saw deterministic resurgences of the pest $v$.

### 4.5. Robustness of Control

We describe simulations using parameter sets (4.35) and (4.40). For these parameters, the $E_{1}$ state is stable for the ODE model, and so we might expect that in this case complete biological control is the result expected from introducing the superpredator $w$ into a pest infested region. In numerical simulations, we do observe control fronts where an introduction of species $w$ completely removes the pest $v$, as discussed in Section 4.5.1. We find, however, that this is not always the case.

Recall that when the pest infested state $E_{2}$ is physical, the $E_{1}$ state is necessarily a saddle in the $u v$-plane for the $w$-free, two species problem (4.1). This means that small perturbations in $v$, that maintain $w \equiv 0$, can send the system back to the $E_{2}$ state even after biological control has been achieved. We have observed numerous simulations where control failed due to this resurgent behavior of the pest $v$, and we have identified several triggering mechanisms for these resurgences. It is important to note that even small computer round-off errors can act as a triggering mechanism, as they can lead
to perturbations in $v$. We will refer to the resurgences resulting from these errors as 'nondeterministic,' but we note here that the resurgent behavior itself is deterministic and it is instead the triggering mechanism that is not robust. We will discuss these truncation errors along with the other triggering mechanisms further in Section 4.5.2.

We were also able to identify two restorative mechanisms that can counteract these triggers and result in robust control. These mechanisms are related solely to traits of species $w$, and so are especially appealing since the superpredator is generally artificially introduced. The first of these restorative mechanisms is a high diffusivity of species $w$ relative to species $v$, counteracting directly the trigger caused by the diffusion of the pest $v$, which we will discuss further when we examine this type of triggering mechanism in Section 4.5.2. The second of these restorative mechanisms is the nonlocal behavior of $w$ when it is of large enough extent. This leads to what we consider the most robust type of control, where propagating cells of species $w$ eliminate the pest as if the superpredator were being periodically reintroduced. We discuss this further in Section 4.5.3.

### 4.5.1. Complete Biological Control

We first present examples of control fronts, where a pulse of species $w$ introduced into a pest infested region restores the system to the pest free state. For these examples, we use the parameter set (4.35) and set $\mu_{2}=\mu_{3}=1$. This type of front for the local problem can be seen in Figure 4.2, where we see a front in $u$ that connects $u=1$ to $u=\bar{u}$, a front in $v$ that connects $v=0$ to $v=\bar{v}$, and a traveling pulse of species $w$ that exists only around the front.


Figure 4.2. Typical behavior of the $E_{1}$ state displacing the $E_{2}$ state for the local problem. Figure 4.2 d provides a closer view of the structure of the front at a fixed time.

The behavior of the controlling front with the $C$-type nonlocality is shown in Figure 4.3. By taking $\delta=10$, we have exceeded the critical threshold for cellular instabilities in both the pest free $(\delta \sim 9.18)$ and pest infested $(\delta \sim 8.33)$ states. This leads to the formation of cells in each region. We note that for species $u$, the cells in the pest infested region have different amplitude and period than those in the pest free region.

### 4.5.2. Triggering Mechanisms of Resurgence

Here we discuss several triggering mechanisms of the resurgent behavior in $v$. We emphasize two important points about these triggers. First, while a specific triggering mechanism (such as round-off error) may itself be non-robust, once the triggering has occurred, the


Figure 4.3. Typical behavior of the $E_{1}$ state displacing the $E_{2}$ state with the $C$-type nonlocality, and with $\delta=10$. Figure 4.3 d shows a closer view of the cellular patterns in $u$ that form in both the pest free and pest infested regions.
resulting resurgence is deterministic and robust to changes in spatial or temporal resolutions, i.e., is stable under grid refinement. Second, these triggering mechanisms are not mutually exclusive, and it is not only possible, but is in fact common, for multiple triggers to occur in a single simulation. In particular, resurgences caused by round-off errors occur in almost every simulation if run for a sufficiently long time, with the only exception being cases where the $P_{w}$-type nonlocality is considered with a sufficiently large $\delta$ (see Section 4.5.3).

Round-off Errors and Stochasticity: Due to the presence of singularities in the systems (4.2), (4.7), and (4.8), the $E_{1}$ state is particularly prone to small errors in species $v$ and $w$ as their populations approach zero. We observed in many simulations involving
the $E_{1}$ state a nondeterministic resurgence of species $v$ where the solution would tend towards the $E_{2}$ state.

We attribute these nondeterministic resurgences to truncation errors for two reasons. First, they broke the spatial symmetry of the solution. Our initial conditions (4.9) and (4.10) are both symmetric about $x=0$, and while we do not explicitly impose symmetry, our numerical method will maintain symmetry in the absence of round-off error. Second, the locations and times at which these resurgences occurred would change, for the exact same set of parameters and initial conditions, when run on different processors or with different temporal or spatial resolutions. These nondeterministic resurgences indicate that the stability of the $E_{1}$ state is highly susceptible to small perturbations.

This suggests that if stochasticity were added to the system, we would see resurgences of the pest and a failure of biological control. Indeed, we considered numerical simulations with low levels of noise and observed resurgences for even very high spatial resolutions and restrictive timesteps. This susceptibility to even very low levels of noise makes the $E_{1}$ state effectively unstable despite the (limited) stability results. Thus our focus will shift from methods of control that seek to obtain this effectively unstable pest free state, to methods that provide a partial control which is robust to noise, and therefore more sustainable.

Diffusion-driven Resurgences: A resurgence of the pest $v$ can also occur due to non-stochastic, deterministic triggers. One such trigger is enhanced mobility of the pest species. When the diffusivity of species $v$ is sufficiently large relative to that of species $w$, we see a resurgence of the pest that returns the system to the pest infested $E_{2}$ state after the control front has passed. In simulations, we observe these resurgences once the
ratio of the diffusivity of species $v$ to that of species $w$ becomes larger than some critical threshold. Call this ratio

$$
\begin{equation*}
\mu=\frac{\mu_{2}}{\mu_{3}} \tag{4.41}
\end{equation*}
$$

These resurgences are not the result of numerical errors, are robust to changes in resolution, and maintain the symmetry of the solution.

Figure 4.4 shows a space-time plot of a typical diffusion-driven resurgence. For this simulation, we have taken $\mu_{2}=4$ and $\mu_{3}=1$, so that $\mu=4$. To understand this figure, it is important to note that: (i) Figures 4.4 b and 4.4 c are plotted on a $\log$ scale, while Figure 4.4a is not; and (ii) the fronts in these figures are not sharp, and so the labels serve only an illustrative purpose to highlight the demarcation between the different regions of interest. It is for these reasons that the regions in Figure 4.4a do not appear to align with those in Figures 4.4b and 4.4c, as the latter two plots show variations in the populations that are too small to see without the $\log$ scale. Indeed, a plot of $\log (1-u)$ would be nearly indistinguishable from Figure 4.4b. With this understanding of Figure 4.4, we discuss the specific highlighted fronts.

We begin with the front labeled A. This front is the original control front that forms due to the introduction of species $w$, and represents the pest free $E_{1}$ state displacing the pest infested $E_{2}$ state. The speed of this front is given by (4.39), which depends only on parameters related to species $w$, i.e., the speed of the control front is not dependent on the pest species $v$. In Figure 4.4c, we see the full traveling pulse of species $w$ that characterizes this type of control front.


Figure 4.4. Typical resurgence behavior for the local problem. Here we use parameter set (4.35) with $\mu=4$. Figure 4.4a shows species $u$ with the different regions labeled according to which state inhabits them. Figure 4.4 b shows species $v$ on a $\log$ scale for the same simulation, and Figure 4.4c shows species $w$ on a log scale.

The difference between front A in Figure 4.4 and the control front from Figure 4.2 is the formation of the labeled front B. This is the resurgence front that sees the pest free $E_{1}$ state revert to the pest infested $E_{2}$ state. The speed of this front is given by (4.37). In Figure 4.4a, it appears as though this front originates at some distance behind control front A, but the $\log$ scale in Figure 4.4b shows that this resurgence originates directly at the rear of the control front A. From this image, we see that a small amount of species $v$ has escaped the superpredator $w$ and repopulates the region behind the control front. We note that this front B cannot be seen in the plot of species $w$ in Figure 4.4c since the front does not involve the presence of species $w$.

In Figure 4.4c, we see the formation of a secondary control front, labeled as front C. This front originates immediately following the resurgence front $B$, where now the superpredator chases the pests that escaped, corresponding to the pest free $E_{1}$ state once again displacing the pest infested $E_{2}$ state. The speed of this front is given by (4.39), which is the same as front A, though now traveling in the opposite direction. Figure 4.4c
again shows the full traveling pulse of species $w$ that characterizes this type of control front.

The last highlighted feature of Figure 4.4 is labeled D. It would be incorrect to call this a front as it does not connect two equilibrium states. The region ahead of this feature D (corresponding to the region between the highlighted lines for feature D and front A ) is not inhabited by an equilibrium state. This feature corresponds to the formation of a resurgence following the control front C , much as the resurgence front B follows the control front A. Now, however, the feature D immediately hits the rear of control front A, and so a full resurgence does not occur. It is interesting to note that another (unlabeled) resurgence forms once the feature D has fully collided with front A and the region behind the control front A is occupied by the pest free $E_{1}$ state, corresponding again to a small amount of the pest escaping from the superpredator.

We now make an important observation about Figure 4.4 that holds for all of the resurgent cases we have found: when there is a resurgence, the resurgent front B always travels faster than the control front C. This suggests that comparing the propagation speeds of these fronts should give a critical condition for the existence of a resurgence. Indeed, if the control wave is faster than the resurgent wave, we would expect that no diffusion-driven resurgence is possible. From Section 4.4, the speed of the control wave is given by (4.39) and the speed of the resurgent wave is given by (4.37), making the critical ratio of diffusivities

$$
\begin{equation*}
\mu_{c}=\frac{m_{2}-d_{2}}{m_{1}-d_{1}} \tag{4.42}
\end{equation*}
$$

with a ratio $\mu>\mu_{c}$ resulting in a deterministic triggering of a resurgence. For the parameter set (4.35), $\mu_{c}=1$.

It is interesting to note that the critical ratio (4.42) is the same for the splitting behavior discussed in Section 4.4.2 and shown in Figure 4.1, i.e., when $\mu>\mu_{c}$ this spitting behavior will occur. For both the splitting behavior and the diffusion-driven resurgence behavior, the front where species $v$ displaces the $E_{1}$ state travels faster than the front where species $w$ displaces the $E_{2}$ state. In Figure 4.1, this results in the $E_{2}$ state forming between regions inhabited by the $E_{1}$ and $E_{3}$ states. In the resurgent case, however, this difference in speeds results in the $E_{2}$ state forming between regions inhabited by the $E_{1}$ state.

In order to validate (4.42), we consider the parameter set (4.35). For this parameter set, we numerically found a critical ratio of about $2.5<\mu_{c}<2.7$, as opposed to the predicted $\mu_{c}=1$ from (4.42). This observed value, however, depended on the size of the cutoff used in the simulations, which suggests that the reason we do not observe the predicted value is that we cannot fully resolve the resurgence when $\mu$ is too close to $\mu_{c}$.

To examine this, we turn to Figure 4.5, which shows the profile of species $v$ on a $\log$ scale as a resurgence forms for two cases. In the first case, shown in Figure 4.5a, we take $\mu_{2}=4$ and $\mu_{3}=1$ so that $\mu=4$. We can see that in this case, the value of $v$ at the resurgence is roughly $10^{-8}$. In the second case, shown in Figure 4.5b, we instead take $\mu_{2}=2.7$ and $\mu_{3}=1$ so that $\mu=2.7$, and now observe that the value of $v$ at the resurgence is roughly $10^{-12}$. Typically, we consider a numerical cutoff, discussed in Section 4.2.3, of $2 \times 10^{-15}$. With this cutoff, we see a resurgence in this $\mu=2.7$ case, and would conclude that $\mu_{c}<2.7$. If we were to increase the cutoff to $10^{-12}$, however, the resurgence would
not occur and we would incorrectly conclude $\mu_{c}>2.7$, i.e., we would have failed to resolve the resurgence. As we continue to decrease $\mu$, the value of $v$ at the resurgence continues to decrease. Thus we expect that if we were able to continue decreasing the cutoff, we would find smaller values for $\mu_{c}$, approaching the predicted value of $\mu_{c}=1$. Note that even if we could decrease the cutoff further without instabilities forming, machine epsilon would still prevent us from seeing a critical ratio as low as was analytically predicted.


Figure 4.5. The formation of the resurgence front for two different cases, shown by $v$ plotted on a semi-log scale. Figure 4.5 a has $\mu_{2}=4$, and Figure 4.5b has $\mu_{2}=2.7$.

To observe a critical ratio near this analytically predicted ratio, we recall an important result from the analysis in Section 4.3.1: when $v=o(w)$, the long time behavior is $v \sim e^{\left(m_{1}-d_{1}-a_{2}\right) t}$, from (4.17). Since we want to leave the predicted $\mu_{c}=1$ unchanged, we decrease $a_{2}$ while leaving all other parameters constant, so that $v$ decays more slowly. When we take $a_{2}=1.2$, as in parameter set (4.40), we are able to numerically observe $1.1<\mu_{c}<1.2$. When we further considered $a_{2}=1.15$, we were able to numerically observe $\mu_{c}<1.1$. This suggests that the comparison of the propagation speeds that led to (4.42) is likely correct.

An important implication of the critical ratio (4.42) is that increasing $\mu_{3}$, the diffusivity of the superpredator $w$, can prevent these deterministic, diffusion-driven instabilities. In biological control, the superpredator is generally artificially introduced. This means that the particular species chosen as the controlling agent is selected specifically for this task of eliminating the pest $v$. These results suggest that selecting a highly mobile, highly diffusive superpredator would be best for biological control.

Resurgence from the $P_{w}$-type Nonlocality with Small and Intermediate $\delta$ : Here we discuss resurgent behavior triggered by the $P_{w}$-type nonlocality. We consider initial conditions given by (4.10), where a pulse of species $w$, centered at the origin, invades the pest infested $E_{2}$ state. This corresponds to the release of the top predator into the middle of a pest-infested region in an attempt at biological control.

For small values of $\delta$, we observe no difference from the local case. In this regime, there is a small controlling pulse of species $w$ that invades the $E_{2}$ state, returning the system to $E_{1}$ behind the front as in Figure 4.2. We note that, as in the local case, simulations in this regime are very sensitive to truncation errors, and the $E_{1}$ state remains highly susceptible to noise.

For intermediate values of $\delta$, deterministic resurgence type behavior is observed. Figure 4.6 shows a typical simulation in this regime. Figures 4.6a-4.6c show space-time plots of $u, v$, and $w$. We can see the original control front on the right in each image, where the $E_{2}$ state is displaced. Behind this control front, we see a resurgence form and move to the left. While it appears that this resurgence originates in the interior of the $E_{1}$ region, the resurgence actually originates directly at the rear of the intial control front as in Figure 4.4. These images are not on a log scale, and so we simply cannot see the resurgence until
it has reached an appreciable level. We note that this resurgence is followed immediately by another control front, which returns the system to the $E_{1}$ state. In these images, we can also see a secondary resurgence that travels to the right. This resurgence originates at the rear of the secondary control front, in much the same way that the feature D forms behind the second control front C in Figure 4.4b.


Figure 4.6. Typical behavior of the $P_{w}$-type resurgence behavior for intermediate values of $\delta$. Here parameter set (4.35) is taken with $\delta=12, \mu_{2}=1$, and $\mu_{3}=1$. The initial pulse of species $w$ is taken to be within $|x|<900$.

Notice that this type of resurgence is not the same as those previously discussed, and that the diffusion-driven triggering mechanism does not carry over to this discussion. This is because the $P_{w}$-type nonlocality does not affect the analysis of the propagation speeds from Section 4.4. For Figure 4.6, we considered the case where $\mu=\mu_{c}=1$. When we considered cases where $\mu<\mu_{c}$, i.e., cases where the diffusion does not trigger a resurgence, we were still able to observe both the primary and secondary resurgences triggered by the
nonlocality. Taking a sufficiently small value of $\mu$, however, could prevent the secondary resurgence.

We speculate that these resurgences are caused by the $P_{w}$-type nonlocality creating locations of positive concavity in the solution, which promotes growth due to the diffusive terms. In more standard, scalar versions of nonlocal problems, decaying oscillations behind wavefronts are observed even when the extent of the nonlocality, $\delta$, is below the critical threshold where cellular patterns form [1]. Figure 4.6d shows decaying oscillations forming behind the wavefronts, and these oscillations give regions of positive concavity. In this image, all of the populations are traveling outward from the location $x=900$. It is interesting to observe that the peaks of species $w$ always follow the peaks of species $v$, as if these larger groups of $w$ were chasing the larger groups of their prey. We note these solutions remain very sensitive to truncation errors and require fine grids for the time interval considered.

### 4.5.3. Robust Control through the $P_{w}$-type Nonlocality

When the extent of the nonlocality, $\delta$, is sufficiently large, we observe a cellular instability of the $E_{1}$ state. As mentioned in Section 4.3.2, this type of nonlocality does not lend itself to any standard linear stability analyses, and so we rely on numerics to describe the resulting patterns. We consider the parameter set (4.35) and find that increasing $\delta$ changes the form of the resulting solutions. We again consider initial conditions given by (4.10), where a pulse of species $w$, centered at the origin, invades the pest infested $E_{2}$ state. We first consider an initial pulse extending for $|x|<200$, but will also examine how the width of this pulse affects the behavior of the system.


Figure 4.7. Typical behavior of the $P_{w}$-type traveling cellular patterns for larger values of $\delta$. Here $\delta=15$ and $\mu_{2}=\mu_{3}=1$.

For sufficiently large values of $\delta$, we observe cellular patterns that form and travel behind the front. Figure 4.7 shows typical images of these patterns for $\delta=15$. Note that we are now plotting the entire domain, including the $x<0$ region, to better display the outcome of introducing a pulse of species $w$ into a pest infested region. The cellular patterns shown form at the locations where the initial front originated (the locations of the linear connection from the initial condition (4.10), for this figure at $|x| \approx 200$ ), and propagate in both directions: outward into the pest infested $E_{2}$ state; and inwards into the pest free $E_{1}$ state, which had formed due to the initial pulse of species $w$ (similar propagating cells were observed in a nonlocal two-species, predator-prey model in [60]). These propagating cells are therefore not analogous to the stationary cellular patterns previously observed for the $C$-type nonlocality. Figure 4.7 d shows the profile of the
oscillatory resurgence patterns that form about the locations $|x|=200$. In this image, cells between $x=-200$ and $x=200$ move inward, while populations outside of $|x|=200$ move outward. We again observe that the peaks in $w$ chase the peaks in $v$, and that the peaks in $v$ chase the peaks in $u$.

The cellular patterns that form in this large $\delta$ regime are robust to the small truncation errors that afflicted the smaller $\delta$ regimes, the $C$-type nonlocal problem, and the local problem. This suggests that the introduction of a highly mobile superpredator species that behaves in a sufficiently nonlocal fashion will provide the most robust form of biological control. From a qualitative perspective, these traveling cellular patterns would be akin to the periodic reintroduction of the superpredator into the system.

We note that Figure 4.7 was generated with $\mu=1$. It is natural to ask how the diffusivities of species $v$ and $w$ affect the patterns that form. When we take $\mu>\mu_{c}$, we do indeed see a resurgence that sends the system to the $E_{2}$ state. This resurgence is short lived, however, as the cellular patterns encroach on the newly formed $E_{2}$ state and eventually occupy the entire domain. Thus in this case, the resulting solution is robust to all of the triggering mechanisms we have identified.


Figure 4.8. Typical behavior of the $P_{w}$-type traveling cellular patterns for larger values of $\delta$ when $\mu<\mu_{c}$. Here $\delta=15, \mu_{2}=1$, and $\mu_{3}=4$. The initial pulse of species $w$ is located within $|x|<500$.

When we take $\mu<\mu_{c}$, i.e., if we take the diffusivity of species $w$ to be large relative to that of species $v$, the outward traveling cells form as before, but the inward traveling cells are overtaken by species $w$ before they can fully form. This is shown in Figure 4.8, where we consider $\mu=1 / 4$ and an initial pulse located within $|x|<500$. We see that the inward traveling cells die off quickly after they form, leaving the $E_{1}$ state intact in the interior of the domain. At first, this would appear to be a positive feature of this $P_{w}$-type nonlocality, since the $E_{1}$ state is the desired, pest free state. The problem arises from the fact that while the cellular patterns do still slowly move inward to eventually occupy the whole domain, these solutions are once again susceptible to noise.

(a) Space-Time Plot of $u$

(b) Space-Time Plot of $v$

(c) Space-Time Plot of $w$

Figure 4.9. Typical behavior of the $P_{w}$-type traveling cellular patterns for larger values of $\delta$ when $\mu<\mu_{c}$, but the initial pulse is thin. Here $\delta=15$, $\mu_{2}=1$, and $\mu_{3}=4$. The initial pulse of species $w$ is located within $|x|<50$.

To address the fact that these solutions are once again susceptible to noise, we recall an observation we made about Figure 4.7: the source of the oscillatory resurgences we observe appears to be located at the edge of the initial pulse of $w$. This suggests that varying this initial width may change the behavior of the system. Indeed, Figure 4.9 considers an initial pulse located within $|x|<50$, and shows a solution that is once more robust to noise. The pulse is now thin enough that the previously short-lived inward
traveling cells collide before they are overtaken by species $w$, ensuring that species $w$ is eventually nonzero in the entire domain. Since $\mu<\mu_{c}$ in this case, these solutions are once more robust to all of the resurgence triggering mechanisms we identified.

### 4.6. Summary

In this chapter, we used the food chain model with ratio-dependent function responses given by (4.2) to examine biological control obtained via the introduction of a superpredator into a pest infested ecosystem. Specifically, in the food chain where species $u$ represents a crop species, species $v$ represents a pest species that feeds on the crop, and species $w$ represents the superpredator that hunts the pest, we considered the behavior of the system when species $w$ was introduced in an attempt to either drive species $v$ to collapse, or at least preserve more of the crop species $u$.

In the spatially independent version of the problem, the ODE system admits four equilibrium states: extinction $E_{0}=(0,0,0)$, pest free $E_{1}=(1,0,0)$, pest infested $E_{2}=$ $(\bar{u}, \bar{v}, 0)$, and the partial restoration $E_{3}=\left(u_{c}, v_{c}, w_{c}\right)$. When we consider the invasion problem, we observe traveling waves in which one state displaces another. Of particular interest were waves involving the pest infested $E_{2}$ state in the regimes where it is stable in the absence of the superpredator $w$. This corresponds to a situation where biological control would need to be employed, i.e., where the natural system tends towards the pest infested state without the artificially introduced superpredator.

We considered the role of nonlocality in two different forms. In the $C$-type nonlocality, we modeled the more standard situation where members of the crop species $u$ competed nonlocally with each other. The $P_{w}$-type nonlocality modeled a superpredator $w$ that
nonlocally searches for its prey over a large area. We considered how the extent of the nonlocality in each of these cases affected potential cellular instabilities in each of the equilibrium states.

The primary results of this chapter are:

- We analytically determined the stability of the $E_{1}$ state in the ODE system, extending the results presented in [39].
- We analytically determined the stability of the $E_{1}$ state for the $C$-type nonlocality.
- We analytically determined a condition for the stability of the $E_{2}$ state for the $C$ type nonlocality, and described a procedure to determine the critical extent of the nonlocality for a given parameter set that would give rise to a cellular instability. We also noted that the $P_{w}$-type nonlocality would not affect the stability of the $E_{2}$ state.
- We analytically determined a set of conditions for the stability of the $E_{3}$ state for the $C$-type and $P_{w}$-type nonlocalities, and described a procedure to determine the critical extent of the nonlocality for a given parameter set.
- We numerically verified our stability analyses of each equilibrium state for a number of different parameter sets.
- We obtained expressions for the propagation speeds of fronts involving species $v$ invading the $E_{1}$ state, and of the front involving species $w$ invading the $E_{2}$ state. We were able to verify these predictions for a number of parameter values. We note that this analysis was not applicable to fronts involving species $w$ invading the $E_{1}$ state.
- We observed fronts of complete biological control where a pulse of species $w$ introduced into a pest infested region resulted in the system returning to the pest free $E_{1}$ state behind the front that formed.
- We noted that small round-off errors could trigger a resurgent behavior of species $v$, and showed that stochasticity would also trigger these resurgences. This indicates that biological control, when considered with the ratio-dependent functional responses, is very susceptible to noise in the system, and that the pest free $E_{1}$ state can be considered effectively unstable in these cases despite the (limited) stability results.
- We observed diffusion-driven resurgences of the $E_{2}$ state when the diffusivity of the pest $v$ was sufficiently large. We obtained a critical condition for the emergence of these resurgences, and used numerical simulation to support this condition.
- We observed resurgences of the $E_{2}$ state that were triggered by the $P_{w}$-type nonlocality when the extent of the nonlocality was below a threshold that could only be computed numerically. We attributed these resurgences to decaying oscillations that formed in the profile of species $v$ that resulted in the formation of locations of positive concavity in the solution.
- We numerically found an instability of the $E_{1}$ state for the $P_{w}$-type nonlocality when the extent of the nonlocality was sufficiently large. We emphasize that while we call this an instability of the pest free state, this case actually corresponds to the most robust form of biological control that we have found. These cellular patterns proved robust to both round-off errors and the introduction of stochastic
noise to the system. They ensure that species $w$ is eventually nonzero throughout the entire domain, and effectively describe an automatic periodic reintroduction of the superpredator to maintain a nearly controlled state.


## CHAPTER 5

## Conclusion

In this thesis, we presented two projects involving models of population dynamics with nonlocal interactions. Our main interests were in traveling waves, corresponding to migrations of the species involved, and in describing both the propagation speeds and front shapes of those waves.

The first project, presented in Chapter 2, was centered on a scalar equation describing the population of a single species competing with itself in a nonlocal fashion, where individuals of the species competed for resources over a large distance. The piecewise linear source term in the equation, along with the choice of kernel function, allowed us to reduce the governing integro-partial differential equation to a system of algebraic equations. This allowed for a full description of the solutions, which covered a wide range of possible behaviors observed in standard nonlinear, nonlocal equations. We considered two biologically relevant cases: monostable and bistable. For the monostable case, we determined the minimum speed for the existence of traveling wave solutions. For the bistable case, we determined the unique propagation speed. In both cases, we found conditions for the formation of decaying oscillations or a 'hump' behind the traveling fronts. We were able to describe how the propagation speed and the shape of the fronts were affected by the parameters of the model: the local net birth rate, the extent of the nonlocality, and the strength of the asymmetry in the nonlocal interactions.

The second project, presented in Chapter 4, focused on a three species foodchain, where a crop species was infested by a pest species, which was preyed upon by a superpredator species. We considered the problem of biological control, where the superpredator was introduced into a pest-infested environment with the goal of returning the system to a pest-free state. The foodchain model we considered employed ratio-dependent predation terms, the use of which was discussed in Chapter 3. We considered two types of nonlocal interactions: intraspecies competition of the crop, and nonlocal predation of the pest by the superpredator. We determined conditions for the formation of cellular patterns in the various equilibrium states of the system, as well as expression for the propagation speed of several relevant fronts. We then turned to the question of biological control, where we sought to determine conditions, particularly on properties of the typically artificially introduced superpredator, that would lead to successful biological control. We found that there were a number of mechanisms that could trigger a resurgence of the pest species and lead to a failure of biological control. But, we also determined that if the superpredator was sufficiently mobile, or if the extent of its nonlocal predation of the pest was sufficiently large, successful control could be achieved.

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## APPENDIX A

## Analysis of equations (2.36) and (2.28)

For all values of $\alpha_{\ell}$ and $\alpha_{r}>0,(2.36)$ has two roots with positive real parts, either two real positive roots or two complex conjugate roots with positive real part. This can be easily verified by assuming $\lambda$ is purely imaginary, i.e. $\lambda=i \beta$. By balancing the real and imaginary parts of the resulting equation, we obtain

$$
\begin{aligned}
& -\beta^{2}\left[\left(1+\frac{\beta^{2}}{\alpha_{\ell} \alpha_{r}}\right)+c\left(\frac{\alpha_{\ell}-\alpha_{r}}{\alpha_{\ell} \alpha_{r}}\right)\right]=1 \\
& i \beta\left[c\left(1+\frac{\beta^{2}}{\alpha_{\ell} \alpha_{r}}\right)-\beta^{2}\left(\frac{\alpha_{\ell}-\alpha_{r}}{\alpha_{\ell} \alpha_{r}}\right)\right]=0
\end{aligned}
$$

It is easily shown that this system has no solutions, and so the solutions to (2.36) cannot cross the imaginary axis. Finally, we note that taking $c=\alpha_{\ell}=\alpha_{r}=1$ clearly gives two roots in the left half plane and two roots in the right half plane. Thus (2.36) has two roots with positive real parts for all parameter values.

Below we derive a parametric solution for these two roots. We denote these roots by $\lambda_{1}$ and $\lambda_{2}$ and assume for concreteness that in the case of real roots $\lambda_{1}>\lambda_{2}$. Notice that (2.36) is just
(A.1) $k_{1} \lambda^{4}+k_{2} \lambda^{3}+k_{3} \lambda^{2}+k_{4} \lambda=1$,
with
(A.2) $\quad k_{1}=-\frac{1}{\alpha_{\ell} \alpha_{r}}, \quad k_{2}=\frac{\alpha_{\ell}-\alpha_{r}-c}{\alpha_{\ell} \alpha_{r}}, \quad k_{3}=\frac{\alpha_{\ell} \alpha_{r}+c\left(\alpha_{\ell}-\alpha_{r}\right)}{\alpha_{\ell} \alpha_{r}}, \quad k_{4}=c$.

So we have

$$
\begin{align*}
& k_{1} \lambda_{1}^{4}+k_{2} \lambda_{1}^{3}+k_{3} \lambda_{1}^{2}+k_{4} \lambda_{1}=1  \tag{A.3}\\
& k_{1} \lambda_{2}^{4}+k_{2} \lambda_{2}^{3}+k_{3} \lambda_{2}^{2}+k_{4} \lambda_{2}=1 \tag{A.4}
\end{align*}
$$

Computing the sum and the difference of (A.3) and (A.4) we obtain

$$
\begin{align*}
& k_{1}\left(\lambda_{1}^{4}-\lambda_{2}^{4}\right)+k_{2}\left(\lambda_{1}^{3}-\lambda_{2}^{3}\right)+k_{3}\left(\lambda_{1}^{2}-\lambda_{2}^{2}\right)+k_{4}\left(\lambda_{1}-\lambda_{2}\right)=0,  \tag{A.5}\\
& k_{1}\left(\lambda_{1}^{4}+\lambda_{2}^{4}\right)+k_{2}\left(\lambda_{1}^{3}+\lambda_{2}^{3}\right)+k_{3}\left(\lambda_{1}^{2}+\lambda_{2}^{2}\right)+k_{4}\left(\lambda_{1}+\lambda_{2}\right)=2 . \tag{A.6}
\end{align*}
$$

Introducing

$$
\sigma_{1}=\lambda_{1}+\lambda_{2}, \quad \sigma_{2}=\lambda_{1} \lambda_{2}
$$

and using

$$
\lambda_{1}^{2}+\lambda_{2}^{2}=\sigma_{1}^{2}-2 \sigma_{2}, \quad \lambda_{1}^{3}+\lambda_{2}^{3}=\sigma_{1}^{3}-3 \sigma_{1} \sigma_{2}, \quad \lambda_{1}^{4}+\lambda_{2}^{4}=\sigma_{1}^{4}-4 \sigma_{1}^{2} \sigma_{2}+2 \sigma_{2}^{2}
$$

we rewrite (A.5), (A.6) as

$$
\begin{equation*}
k_{1}\left(\sigma_{1}^{4}-4 \sigma_{1}^{2} \sigma_{2}+2 \sigma_{2}^{2}\right)+k_{2}\left(\sigma_{1}^{3}-3 \sigma_{1} \sigma_{2}\right)+k_{3}\left(\sigma_{1}^{2}-2 \sigma_{2}\right)+k_{4} \sigma_{1}=2 \tag{A.7}
\end{equation*}
$$

We use (A.7), (A.8) to express $c$ and $\sigma_{1}$ in terms of $\sigma_{2}, \alpha_{\ell}$, and $\alpha_{r}$. Specifically, multiplying (A.7) by $\sigma_{1}$ and subtracting the result from (A.8), we obtain (A.9) $\quad-k_{1}\left(\sigma_{1}^{2}-\sigma_{2}\right)-k_{2} \sigma_{1}-k_{3}=\frac{1}{\sigma_{2}}$. Multiplying (A.9) by $\sigma_{1}$ and adding to (A.7) we get (A.10) $-k_{1} \sigma_{1} \sigma_{2}-k_{2} \sigma_{2}+k_{4}=\frac{\sigma_{1}}{\sigma_{2}}$.

We can use (A.9) and (A.10) along with the definitions of the coefficients $k_{1}, k_{2}, k_{3}$, and $k_{4}$ from (A.2) to solve for the speed $c$ in terms of $\sigma_{1}, \sigma_{2}, \alpha_{\ell}$, and $\alpha_{r}$. We get

$$
\begin{aligned}
c & =\frac{\alpha_{\ell} \alpha_{r}}{\sigma_{1}-\alpha_{\ell}+\alpha_{r}}\left[\frac{1}{\sigma_{2}}+1-\frac{1}{\alpha_{\ell} \alpha_{r}}\left(\sigma_{1}^{2}-\sigma_{2}\right)+\frac{\alpha_{\ell}-\alpha_{r}}{\alpha_{\ell} \alpha_{r}} \sigma_{1}\right] \\
& =\frac{\sigma_{1}\left(\frac{1}{\sigma_{2}^{2}}-\frac{1}{\alpha_{\ell} \alpha_{r}}\right)+\frac{\alpha_{\ell}-\alpha_{r}}{\alpha_{\ell} \alpha_{r}}}{\frac{1}{\sigma_{2}}+\frac{1}{\alpha_{\ell} \alpha_{r}}} .
\end{aligned}
$$

From these equations, solving for $\sigma_{1}$ in terms of $\sigma_{2}$ and expressing $c$ in terms of $\sigma_{2}$, we get the parametric dependence seen in (2.38a)-(2.38c). Notice that in the symmetric case, where $\alpha_{\ell}=\alpha_{r}=\alpha$, (2.36) reduces to (2.28) and the definitions in (2.38a)-(2.38c) reduce to (2.30).

## APPENDIX B

## Reduction of the Nonlocal Problem to Local Equations

Consider the nonlocal problem (2.12), (2.13). For the $u>\theta, x<0$ region, we have the equation

$$
\begin{equation*}
u^{\prime \prime}+c u^{\prime}+1-\phi_{\alpha} * u=0 \tag{B.1}
\end{equation*}
$$

This equation can be reduced to a local problem. Consider the convolution integral

$$
w_{0}(x)=\phi_{\alpha} * u
$$

When we have the kernel function (2.14),

$$
\begin{aligned}
& w_{0}(x)=\frac{\alpha}{2} \int_{-\infty}^{\infty} e^{-\alpha|x-y|} u(y) d y=\frac{\alpha}{2} \int_{-\infty}^{x} e^{-\alpha(x-y)} u(y) d y+\frac{\alpha}{2} \int_{x}^{\infty} e^{\alpha(x-y)} u(y) d y \\
& \frac{d w_{0}}{d x}=\frac{\alpha}{2}\left(u(x)-\alpha \int_{-\infty}^{x} e^{-\alpha(x-y)} u(y) d y-u(x)+\alpha \int_{x}^{\infty} e^{\alpha(x-y)} u(y) d y\right) \\
& \frac{d^{2} w_{0}}{d x^{2}}=\frac{\alpha}{2}\left(-\alpha u(x)+\alpha^{2} \int_{-\infty}^{x} e^{-\alpha(x-y)} u(y) d y-\alpha u(x)+\alpha^{2} \int_{x}^{\infty} e^{\alpha(x-y)} u(y) d y\right),
\end{aligned}
$$

so that

$$
\begin{equation*}
\frac{d^{2} w_{0}}{d x^{2}}=\alpha^{2}\left[w_{0}(x)-u(x)\right] \tag{B.2}
\end{equation*}
$$

Thus, the nonlocal equation (B.1) can be reduced to a system of local equations consisting of the equations

$$
u^{\prime \prime}+c u^{\prime}+1-w_{0}=0
$$

and (B.2).
A similar reduction to local problems can be done for some other kernels as well. Denote

$$
\phi_{\alpha, n}(x) \equiv \frac{\alpha^{n+1}}{2 n!}|x|^{n} e^{-\alpha|x|}, \quad \alpha>0, \quad n=0,1,2, \ldots
$$

and

$$
w_{n}(x)=\phi_{\alpha, n} * u
$$

Then a calculation similar to that for $w_{0}$ yields
(B.3) $\frac{d^{2} w_{1}}{d x^{2}}=\alpha^{2}\left[w_{1}(x)-2 w_{0}(x)+u(x)\right]$,

$$
\begin{equation*}
\frac{d^{2} w_{j}}{d x^{2}}=\alpha^{2}\left[w_{j}(x)-2 w_{j-1}(x)+w_{j-2}(x)\right], \quad j=2,3, \ldots, n \tag{B.4}
\end{equation*}
$$

Thus, the nonlocal equation

$$
\begin{equation*}
u^{\prime \prime}+c u^{\prime}+1-\phi_{\alpha, n} * u=0 \tag{B.5}
\end{equation*}
$$

can be replaced by the local system consisting of
(B.6) $u^{\prime \prime}+c u^{\prime}+1-w_{n}=0$
and (B.2)-(B.4).
Since the nonlocal equation (B.1) is reduced to a linear system of differential equations with constant coefficients we can easily find its solution, rather than assuming the form of the solution beforehand. Seeking the solution of (B.2)-(B.4), (B.6) in the form

$$
\begin{aligned}
& u=1+k e^{\lambda z}, \\
& w_{j}=1+k_{j} e^{\lambda z}, \quad j=0,1, \ldots, n
\end{aligned}
$$

we obtain

$$
\begin{aligned}
& k_{0} \lambda^{2}=\alpha^{2}\left(k_{0}-k\right) \\
& k_{1} \lambda^{2}=\alpha^{2}\left(k_{1}-2 k_{0}+k\right) \\
& k_{j} \lambda^{2}=\alpha^{2}\left(k_{j}-2 k_{j-1}+k_{j-2}\right), \quad j=2,3, \ldots, n
\end{aligned}
$$

Solving the above equations for $k_{0}, k_{1}$ and $k_{2}$ in terms of $k$, we obtain

$$
k_{0}=\frac{1}{1-p^{2}} k, \quad k_{1}=\frac{1+p^{2}}{\left(1-p^{2}\right)^{2}} k, \quad k_{2}=\frac{1+3 p^{2}}{\left(1-p^{2}\right)^{3}} k
$$

where $p=\lambda / \alpha$. In general, the recurrence formula can be written as

$$
\left(1-p^{2}\right) k_{j}-2 k_{j-1}+k_{j-2}=0, j=2,3, \ldots, n
$$

The solutions $k_{j}$ can be taken in the form $k_{j} \sim a^{j}$, from which

$$
a^{2}\left(1-p^{2}\right)-2 a+1=0
$$

We get

$$
a=\frac{1}{1-p}, \quad a=\frac{1}{1+p}
$$

so that

$$
k_{j}=\frac{C_{1}}{(1-p)^{j}}+\frac{C_{2}}{(1+p)^{j}}, \quad j=2,3, \ldots, n
$$

Using the expressions for $k_{1}$ and $k_{2}$ to determine the constants $C_{1}$ and $C_{2}$ we obtain

$$
k_{j}=\left[\frac{1}{(1-p)^{j+1}}+\frac{1}{(1+p)^{j+1}}\right] \frac{k}{2}, \quad j=0,1,2,3, \ldots, n
$$

Finally, (B.6) gives an equation for $\lambda$

$$
\begin{equation*}
\lambda^{2}+c \lambda=\frac{1}{2}\left[\frac{1}{(1-p)^{j+1}}+\frac{1}{(1+p)^{j+1}}\right], \quad p=\frac{\lambda}{\alpha} \tag{B.7}
\end{equation*}
$$

We now make two comments regarding this process. First, this approach tells us that we are not missing any solutions when seeking solutions in the form (2.25). Second, it has to be noted that the system (B.2), (B.5) is not equivalent to the nonlocal equation (B.1) the convolution integral is a particular solution of the equations for $w$, so that by solving the local system we can get extraneous solutions $w$ in the form of the convolution integral plus a homogeneous solution. These homogeneous solutions are removed by imposing an additional condition, i.e., setting (2.27c) equal to zero.

## APPENDIX C

## Solving via Laplace Transformation

Consider equation (B.1) with a general kernel $\phi$. We first define

$$
u(x)=1+v(x)
$$

The equation for $v$ is now
(C.1) $\quad v^{\prime \prime}+c v^{\prime}-\phi *_{x} v=0, \quad x<0$.

We transform to a reversed variable $\xi=-x$, with $v(x)=\tilde{v}(-x)=\tilde{v}(\xi)$, to get the equation
(C.2) $\quad \tilde{v}^{\prime \prime}-c \tilde{v}^{\prime}-\psi_{\alpha} *_{\xi} \tilde{v}=0, \quad \xi>0$,
where $\psi(x)=\phi(-x)$. Note here that

$$
\phi *_{x} v=\int_{-\infty}^{\infty} \phi(y) v(x-y) d y, \quad \text { and } \quad \psi *_{\xi} \tilde{v}=\int_{-\infty}^{\infty} \psi(x) \tilde{v}(\xi-x) d x .
$$

Now we apply the Laplace Transform,

$$
\mathscr{L}\{v(\xi)\}(p)=\int_{0}^{\infty} v(\xi) e^{-p \xi} d \xi,
$$

to Equation C. 2 to get
(C.3) $\bar{v}=\frac{v^{\prime}(0)+(p-c) v(0)}{p^{2}-c p-\bar{\psi}(p)-\bar{\phi}(-p)}$,
where $\bar{v}=\mathscr{L}\{v\}$. Now we can invert the transform using a Bromwhich Integral, which will give us the sum of the residuals of $\bar{v} e^{p \xi}$ at each of its poles in the $p$-plane. Notice now that if the kernel is of the form

$$
\phi(x)= \begin{cases}\phi_{+}(x), & x>0 \\ \phi_{-}(x), & x<0\end{cases}
$$

then we have
(C.4) $\quad \bar{v}=\frac{v^{\prime}(0)+(p-c) v(0)}{p^{2}-c p-\bar{\phi}_{-}(p)-\bar{\phi}_{+}(-p)}$.

Now consider the kernel defined in (2.14). In this case we get
(C.5) $\bar{v}=\frac{\left[v^{\prime}(0)+(p-c) v(0)\right]\left(p^{2}-\alpha^{2}\right)}{p^{4}-c p^{3}-\alpha^{2} p^{2}+c \alpha^{2} p+\alpha^{2}}$.

Then the exponentials in our solution $v(\xi)$ will be the negative roots of the polynomial
(C.6) $\quad p^{4}-c p^{3}-\alpha^{2} p^{2}+c \alpha^{2} p+\alpha^{2}=0$.

If we define $\lambda=-p$, then we seek the positive roots of
(C.7) $\quad \lambda^{4}+c \lambda^{3}-\alpha^{2} \lambda^{2}-c \alpha^{2} \lambda+\alpha^{2}=0$.

Notice that this equation (C.7) is exactly equation (2.28).

## APPENDIX D

## Stability of the $E_{1}$ State: Method 2

We linearize the full $(u, v, w)$ system about the $E_{1}$ state by considering solutions where $u$ is close to 1 while $v$ and $w$ are small. This can be written in the form

$$
u \sim 1+\epsilon \tilde{u}+\mathcal{O}\left(\epsilon^{2}\right), \quad v \sim \epsilon \tilde{v}+\mathcal{O}\left(\epsilon^{2}\right), \quad w \sim \epsilon \tilde{w}+\mathcal{O}\left(\epsilon^{2}\right)
$$

Substituting these expansions into (4.2) gives equations (4.16). Specifically, we consider the equations for $\tilde{v},(4.16 \mathrm{~b})$, and $\tilde{w},(4.16 \mathrm{c})$, that decouple from the equation for $\tilde{u}$, and define

$$
\alpha=d_{1}-m_{1} .
$$

This gives the $(\tilde{v}, \tilde{w})$ system

$$
\begin{equation*}
\frac{d \tilde{v}}{d t}=-\alpha \tilde{v}-a_{2} \frac{\tilde{v} \tilde{w}}{\tilde{v}+\tilde{w}}, \quad \frac{d \tilde{w}}{d t}=-d_{2} \tilde{w}+m_{2} \frac{\tilde{v} \tilde{w}}{\tilde{v}+\tilde{w}} \tag{D.1}
\end{equation*}
$$

which can be solved since it admits two first integrals. To derive one of them, we rewrite (D.1) as

$$
\begin{aligned}
& \frac{m_{2}}{\tilde{v}} \frac{d \tilde{v}}{d t}=-\alpha m_{2}-a_{2} m_{2} \frac{\tilde{w}}{\tilde{v}+\tilde{w}}, \\
& \frac{a_{2}}{\tilde{w}} \frac{d \tilde{w}}{d t}=-d_{2} a_{2}+a_{2} m_{2} \frac{\tilde{v}}{\tilde{v}+\tilde{w}},
\end{aligned}
$$

and subtract to obtain

$$
\frac{a_{2}}{\tilde{w}} \frac{d \tilde{w}}{d t}-\frac{m_{2}}{\tilde{v}} \frac{d \tilde{v}}{d t}=-d_{2} a_{2}+\alpha m_{2}+a_{2} m_{2}
$$

Integrating gives one first integral as
(D.2) $\frac{\tilde{w}^{a_{2}}}{\tilde{v}^{m_{2}}}=c_{1} e^{K t}$,
where $K=-d_{2} a_{2}+\alpha m_{2}+a_{2} m_{2}$.
To derive the other first integral, we reduce the system (D.1) to a single phase plane equation

$$
\frac{d \tilde{v}}{d \tilde{w}}=\frac{-\alpha \tilde{v}(\tilde{v}+\tilde{w})-a_{2} \tilde{v} \tilde{w}}{-d_{2} \tilde{w}(\tilde{v}+\tilde{w})+m_{2} \tilde{v} \tilde{w}}
$$

We now make the change of variables $\tilde{v}(\tilde{w})=\tilde{w} z(\tilde{w})$, to arrive at the separable equation

$$
z+\tilde{w} \frac{d z}{d \tilde{w}}=-\frac{\alpha z(z+1)+a_{2} z}{-d_{2}(z+1)+m_{2} z} \quad \Rightarrow \quad \frac{d_{2}(z+1)-m_{2} z}{z\left[\left(\alpha-d_{2}\right)(z+1)+m_{2} z+a_{2}\right]} d z=\frac{d \tilde{w}}{\tilde{w}} .
$$

Using the decomposition

$$
\frac{d_{2}(z+1)-m_{2} z}{z\left[\left(\alpha-d_{2}\right)(z+1)+m_{2} z+a_{2}\right]}=\frac{A}{z}+\frac{B}{\left(\alpha-d_{2}\right)(z+1)+m_{2} z+a_{2}},
$$

where

$$
A=\frac{d_{2}}{\alpha-d_{2}+a_{2}}, \quad B=\frac{d_{2} a_{2}-\alpha m_{2}-a_{2} m_{2}}{\alpha-d_{2}+a_{2}}=\frac{-K}{\alpha-d_{2}+a_{2}},
$$

and integrating, we obtain one more first integral

$$
z^{A}\left[\left(\alpha-d_{2}\right)(z+1)+m_{2} z+a_{2}\right]^{\frac{B}{\alpha-d_{2}+m_{2}}}=c_{2} \tilde{w},
$$

which can be written as
(D.3) $z^{A}[p z+1]^{\frac{B}{\alpha-d_{2}+m_{2}}}=c_{3} \tilde{w}, \quad p=\frac{\alpha-d_{2}+m_{2}}{\alpha-d_{2}+a_{2}}$.

Using (D.2) and $z=\tilde{v} / \tilde{w}$, we can rewrite (D.3) as

$$
\begin{equation*}
p z+1+c_{7}\left[z e^{\left(\alpha-d_{2}+a_{2}\right) t}\right]^{\frac{\alpha-d_{2}+m_{2}}{m_{2}-a_{2}}}=0 \tag{D.4}
\end{equation*}
$$

Different terms in (D.4) may be of different magnitudes as $t \rightarrow \infty$.
Case I: Consider the case where the second and third terms are the two largest.
Balancing these terms implies

$$
\begin{equation*}
z \sim e^{-\left(\alpha-d_{2}+a_{2}\right) t} \quad \Rightarrow \quad \tilde{v} \sim e^{-\left(\alpha+a_{2}\right) t}=e^{\left(m_{1}-d_{1}-a_{2}\right) t}, \quad \tilde{w} \sim e^{-d_{2} t}, \tag{D.5}
\end{equation*}
$$

which is the scaling for $v=o(w),(4.17)$. Now the condition that the first term be smaller, i.e., $p z \ll 1$, requires $\alpha-d_{2}+a_{2}>0$. Thus the stability conditions are

$$
\begin{equation*}
\alpha-d_{2}+a_{2}>0, \quad \alpha+a_{2}>0, \quad d_{2}>0 \quad \Rightarrow \quad m_{1}+d_{2}<d_{1}+a_{2} \tag{D.6}
\end{equation*}
$$

which is the condition (4.13).

Case II: Consider the case when the first and second terms are the two largest terms. Balancing these terms implies

$$
\begin{equation*}
z \sim 1 \Rightarrow \tilde{v}, \tilde{w} \sim e^{\frac{K}{a_{2}-m_{2}} t}=\exp \left(\frac{\left(m_{2}-d_{2}\right) a_{2}-\left(m_{1}-d_{1}\right) m_{2}}{a_{2}-m_{2}} t\right) \tag{D.7}
\end{equation*}
$$

which is the scaling (4.18) for $v \sim C w$ (where $C$ is a nonzero constant that will be exactly $R^{*}$ from (4.12)). Now the condition that the third term be smaller requires

$$
\left(\alpha-d_{2}+a_{2}\right) \frac{\alpha-d_{2}+m_{2}}{m_{2}-a_{2}}<0
$$

In order for the first two terms to balance, they must be of different signs, and so $p<0$, and
(D.8) $\quad \alpha-d_{2}+a_{2}<0, \quad \alpha-d_{2}+m_{2}>0, \quad m_{2}>a_{2} \quad \Rightarrow \quad a_{2}<m_{1}-d_{1}+d_{2}<m_{2}$.

From the scaling for $v$ and $w$ in (D.7), the stability conditions are
(D.9) $\frac{K}{a_{2}-m_{2}}<0 \Rightarrow K>0 \Rightarrow\left(m_{2}-d_{2}\right) a_{2}>\left(m_{1}-d_{1}\right) m_{2}$.

Taken together, (D.8) and (D.9) lead to (4.14).
Case III: Consider the case when the first and third terms are the two largest terms.
Balancing these terms implies
(D.10) $z \sim e^{-\left(\alpha-d_{2}+m_{2}\right) t} \Rightarrow \tilde{v} \sim e^{-\alpha t}=e^{\left(m_{1}-d_{1}\right) t}, \quad \tilde{w} \sim e^{\left(m_{2}-d_{2}\right) t}$,
which is the scaling for $w=o(v),(4.19)$. Now the condition that the second term be smaller, i.e., $p z \gg 1$, requires $\alpha-d_{2}+m_{2}<0$. Thus the stability conditions are
(D.11) $\alpha-d_{2}+m_{2}<0, \quad m_{1}-d_{1}<0, \quad m_{2}-d_{2}<0 \quad \Rightarrow \quad 0<d_{1}-m_{1}<d_{2}-m_{2}$,
which is the condition (4.15).

## APPENDIX E

## Methods of Finding Critical $D, \beta$ Pair for the $E_{2}$ State

Method 1: We are searching for a critical pair of $D$ and $\beta$ values where (4.27) is zero for exactly one value of $\beta$. This means that we are trying to simultaneously solve the equations

$$
\begin{equation*}
F_{C}\left(\beta_{c}, D_{c}\right)=0, \quad \frac{\partial F_{C}}{\partial \beta}\left(\beta_{c}, D_{c}\right)=0 \tag{E.1}
\end{equation*}
$$

We note that both $F_{C}$ and $\frac{\partial F_{C}}{\partial \beta}$ are quadratic functions in $D$. We can find $\beta_{c}$ such that equations (E.1) are satisfied by solving both expressions for $D(\beta)$ and equating the results. This will give us four equations for $\beta_{c}$. Any solutions of these equations are potential critical values of $\beta$, and so we choose the critical value of $\beta$ that corresponds to the smallest critical value of $\delta$.

Method 2: A difficulty in using the first method to find the critical $D$ and $\beta$ values is that we cannot specify a range of $\beta$ values where the critical value must occur. To deal with this problem, we again make use of the fact that $F_{C}(\beta, D)=0$ is a quadratic equation in $D$. We first note that for a fixed value of $\beta$, the resulting parabola opens upwards, and so the larger root of this equation will correspond to the larger $D$, and hence the smallest $\delta$ value. We will call this larger expression $D_{c}(\beta)$, which will correspond to the critical value of $D$ when maximized over $\beta$.

We now note that if we define another function $\tilde{F}_{C}(\beta, D)<F_{C}(\beta, D)$ that is also quadratic in $D$, then the larger root of $\tilde{F}_{C}$ for a fixed value of $\beta$ will provide an upper bound on $D_{c}(\beta)$ for the same $\beta$. We can create this new function by bounding every occurrence of the fraction $\sin (\beta) / \beta$ by 1 or -1 , whichever makes the whole expression more negative. This gives us

$$
\begin{equation*}
\tilde{F}_{C}(\beta, D) \equiv \mu_{2} \beta^{4} D^{2}-\eta_{1}\left(m_{1}-d_{1}\right) \bar{u}+\left[\eta_{1}\left(m_{1}-d_{1}\right)+\eta_{1} \mu_{2}(\bar{u}-1)-\mu_{2} \bar{u}\right] \beta^{2} D=0 \tag{E.2}
\end{equation*}
$$

We can see that $\tilde{F}_{C}$ is actually a quadratic in $\beta^{2} D$, and has no other dependence on $\beta$. So the expressions for what we will call $\tilde{D}(\beta)$, obtained from solving $\tilde{F}_{C}=0$ for $D$, will decay with $\beta^{-2}$, and will otherwise not depend on $\beta$. This means that the larger of these expressions is an upper bound on the critical $D_{c}$, and is a monotonically decreasing function of $\beta$. This gives us a procedure to find the critical $D_{c}$ and $\beta_{c}$ pair.

We first find the explicit expression for $D_{c}(\beta)$ by solving $F_{C}=0$ for $D$. We then find the maximum of this function over some preset range in $\beta$, ignoring any values of $\beta$ that give complex $D$. Call this maximum $D^{*}$. It is possible that $D^{*}$ is nonpositive for a given range of $\beta$. In this case, the preset range must be extended. If $D^{*}$ remains nonpositive for all preset ranges practically considered, the conclusion is that there is no $\delta_{c}$, and so the $E_{2}$ state is stable for all values of $\delta$.

Once we have obtained a positive value for $D^{*}$, we use the expression for $\tilde{D}(\beta)$, obtained from $\tilde{F}_{C}$. We solve $\tilde{D}(\beta)=D^{*}$ for $\beta$, noting that $D_{c}(\beta)<D^{*}$ for all $\beta$ larger than this value we have found. Hence we have obtained a new range for $\beta$ in which we are guaranteed that $D_{c}(\beta)$ must attain its maximum value.

## APPENDIX F

## Method of Finding Critical $D, \beta$ Pair for the $E_{3}$ State

We consider the three conditions for stability from (4.32), introducing the variables $\beta=\delta k$ and $D=\delta^{-2}$ to write these conditions as functions of $D$ and $\beta$. We note now that $F(\beta, D)$ is linear in $D$, while both $G(\beta, D)$ and $H(\beta, D)$ are cubic in $D$. As we are seeking the critical value of $D$ such that there is exactly one value of $\beta$ that gives instability, we will simultaneously solve each of the pairs of equations
(F.1a) $\quad F\left(\beta_{c}, D_{c}\right)=0, \quad \frac{\partial F}{\partial \beta}\left(\beta_{c}, D_{c}\right)=0$,
(F.1b) $\quad G\left(\beta_{c}, D_{c}\right)=0, \quad \frac{\partial G}{\partial \beta}\left(\beta_{c}, D_{c}\right)=0$,
(F.1c) $\quad H\left(\beta_{c}, D_{c}\right)=0, \quad \frac{\partial H}{\partial \beta}\left(\beta_{c}, D_{c}\right)=0$.

We can do this by noting that (F.1a) are both linear in $D$, while (F.1b) are both cubic in $D$, as are (F.1c). So we can solve each of these six equations for $D(\beta)$ and equate the resulting expressions for each pair - (F.1a), (F.1b), and (F.1c) - to find any potential values of the $D_{c}$ and $\beta_{c}$ pair. This process gives us nineteen equations for potential critical values of $\beta_{c}$ - one from (F.1a), and nine each from (F.1b) and (F.1c). Since we are looking for a minimum critical value of the parameter $\delta$, we will keep only the maximum value of $D_{c}$ we find. It is important to note that since several of these conditions are cubic in $D$, this process cannot be automated in a similar way to what was done in Appendix E.

Instead, the range of $\beta$ values over which to search for $D_{c}$ and $\beta_{c}$ pairs must be manually determined for each set of parameter values considered.

