12-2015

Spreading speeds and traveling waves in some population models.

Quancheng Meng
University of Louisville

Recommended Citation

Meng, Quancheng, "Spreading speeds and traveling waves in some population models." (2015). *Electronic Theses and Dissertations.* Paper 2297.
https://doi.org/10.18297/etd/2297

SPREADING SPEEDS AND TRAVELING WAVES IN SOME POPULATION MODELS

By

Quancheng Meng
B.S., University of Science and Technology Beijing, 2009
M.A., University of Louisville, 2011

A Dissertation
Submitted to the Faculty of the
College of Arts and Sciences of the University of Louisville
in Partial Fulfillment of the Requirements
for the Degree of

Doctor of Philosophy
in Applied and Industrial Mathematics

Department of Mathematics
University of Louisville
Louisville, Kentucky

December 2015

SPREADING SPEEDS AND TRAVELING WAVES IN SOME POPULATION MODELS

Submitted by

Quancheng Meng

A Dissertation Approved on

November 20, 2015

by the Following Dissertation Committee:

Bingtuan Li, Dissertation Director

Jiaxu Li

Ryan Gill

Changbing Hu

Wei Song

ACKNOWLEDGMENTS

First and foremost I would like to thank my dissertation advisor, Dr. Bingtuan Li, for his guidance, patience, help and encouragement during my Ph.D. study. What I have benefited from him are not only his contributions to the problems in this dissertation, but also his diligence, insights, and dedication to the intellectual and personal growth of his graduate students.

I would like to thank all my committee members, Dr. Jiaxu Li, Dr. Ryan Gill, Dr. Changbing Hu and Dr. Wei Song for their continual support, advice, encouragement and the time they contributed in reviewing my work.

I specially thank my loving family for providing me with unconditional love and unsurpassed support no matter where we are. In particular, I thank my mom, Guohua Liu, for her always being so supportive on not only my study but also my life and dream. I thank my dad, Zhaorui Meng, for showing me the way to pursue my goal with my passion and diligence. I thank my sister, Nan Meng, for being my best friend and always believing in me.

ABSTRACT

SPREADING SPEEDS AND TRAVELING WAVES IN SOME POPULATION MODELS

Quancheng Meng

November 20, 2015

Virtually every ecosystem has been invaded by exotic organisms with potentially drastic consequences for the native fauna or flora. Studying the forms and rates of invading species has been an important topic in spatial ecology. We investigate two two-species competition models with Allee effects in the forms of reaction-diffusion equations and integro-difference equations. We discuss the spatial transitions from a mono-culture equilibrium to a coexistence equilibrium or a different mono-culture equilibrium in these models. We provide formulas for the spreading speeds based on the linear determinacy and show the results on the existence of traveling waves. We also study a two-sex stage-structured model. We carry out initial analysis for the spreading speed and conduct numerical simulations on the traveling waves and spreading speeds in the two-sex model.

TABLE OF CONTENTS

ACKNOWLEDGMENTS iii

ABSTRACT iv

LIST OF TABLES vii

LIST OF FIGURES ix

CHAPTER

1. INTRODUCTION AND BACKGROUND 1
   1.1 Introduction 1
   1.2 Reaction-Diffusion Equations 5
   1.3 Integro-Difference Equations 7
   1.4 The Spreading Speed 8
   1.5 Traveling Wave Solutions 14
2. TWO-SPECIES REACTION-DIFFUSION COMPETITION MODEL WITH ALLEE EFFECT 16
   2.1 The Model 16
   2.2 Local Stability 18
   2.3 Global Stability 23
   2.4 Spreading Speed and Linear Determinacy 27
   2.5 Existence of Traveling Waves 34
3. TWO-SPECIES DISCRETE-TIME SPATIO-TEMPORAL COMPETITION MODEL WITH ALLEE EFFECT 38
   3.1 The Model 38

3.2 Local Stability 40
3.3 Global Stability 42
3.4 Spreading Speed and Linear Determinacy 49
3.5 Existence of Traveling Waves 54
4. TWO-SEX STAGE-STRUCTURED COMPETITION MODEL . . . 57
4.1 Model Formulation 57
4.2 The Linearization 59
4.3 Spreading Speed of the Linearized System 66
5. NUMERICAL SIMULATION 69
6. CONCLUSION AND FUTURE DIRECTIONS 75
6.1 Conclusion 75
6.2 Future Directions 77
REFERENCES 79
CURRICULUM VITAE 89

LIST OF TABLES

TABLE PAGE

2.1 Model (2.1) Parameter Descriptions 17

2.2 Summary of Existence and Local Stability Criteria of Equilibria in Model (2.1) 22

3.1 Summary of Existence and Local Stability Criteria of Equilibria in Model (3.1) 42

4.1 Two-Sex Model Parameter Descriptions 60

5.1 Two-Sex Model Parameter Values 71

5.2 Comparison of ${c_m}^*$ and ${c_f}^*$ when $\tau = 0.3$ 72

5.3 Comparison of ${c_f}^*$ and $\bar{c}$ when $\tau = 0.3$ 73

LIST OF FIGURES

FIGURE PAGE

1.1 The population profiliation rate when there is (a) no Allee effect (b) weak Allee effect (c) strong Allee effect. 3

2.1 Equilibria and spatial transitions in the reaction-diffusion system before and after the change of variables $p = u, q = 1 - v$: (a) Before the change of variables, when the two coexistence equilibria exist, the spatial transition is from $(0, 1)$ to E_2^*; when the coexistence equilibria do not exist, the spatial transition is from $(0, 1)$ to $(k, 0)$. (b) After the change of variables, when the two coexistence equilibria exist, the spatial transition is from $(0, 0)$ to $\hat{E}_2^*$; when the coexistence equilibria do not exist, the spatial tansition is from $(0, 0)$ to $(k, 1)$. 29

3.1 Equilibria and spatial transitions in the integro-difference system before and after the change of variables $u_n = p_n, v_n = 1 - q_n$: (a) Before the change of variables, when the two coexistence equilibria exist, the spatial transition is from $(0, 1)$ to E_1^*; when the coexistence equilibria do not exist, the spatial transition is from $(0, 1)$ to $(1, 0)$. (b) After the change of variables, when the two coexistence equilibria exist, the spatial transition is from $(0, 0)$ to $\hat{E}_1^*$; when the coexistence equilibria do not exist, the spatial tansition is from $(0, 0)$ to $(1, 1)$. 50

5.1 Traveling wave solutions of female and male populations at the end of year $1, 5, 10, 15, 20, 25, 30, 35, 40$, given $\lambda = 15$ and $\tau = 0.3$, with the initial condition $u(0,x) = v(0,x) = \frac{1}{2}\sin(x)$. . 74

CHAPTER 1
INTRODUCTION AND BACKGROUND

1.1 Introduction

The ecology of invasions by animals and plants has received more and more attention in recent years, chiefly because nearly every ecosystem has been invaded by exotic organisms with potentially drastic consequences for the native fauna or flora [22]. For example, Butomus umbellatus, which is also known as flowering rush or grass rush in North America, has now become a serious invasive weed in the Great Lakes area. The Asian tiger mosquito originally came from Southeast Asia, has spread to Europe, the Americas, the Caribbean, Africa, and the Middle East, and it is now one of the most invasive alien species in the world according to the Global Invasive Species Database [1]. And there is a clear historical record of the grey squirrel Sciurus carolinensis out-competing and replacing the local red squirrel Sciurus vulgaris in the United Kingdom [50].

Biological invasions can be described as the study of how certain animals or plant species spread across the globe [30]. Mathematical models that attempt to describe or predict the fate of some particular invasions have long been central to the development of spatial theory in ecology [15, 47, 48, 49, 50, 51, 52, 53]. One crucial measure of mathematically analyzing the invasiveness of a species is to investigate the form and rate of its spread when it enters a new environment [14, 22]. The early attempt can be traced back to 1937, when R.A. Fisher was interested in the spatial spread of new genes that appeared in a population. He proposed the famous Fisher-KPP equation in [45]:

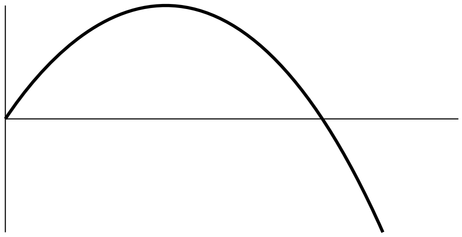
$$\frac{\partial u}{\partial t} = ru(K-u) + D\frac{\partial^2 u}{\partial x^2}, \tag{1.1}$$

where x denotes the position, t denotes the time and $u = u(x,t)$ is the local population density. In this model, population expansion arises from a balance between the local growth with maximum population density or carrying capacity K and the linear growth rate rK, and the diffusion of individuals in space with the coefficient of diffusion D [31]. Fisher used this model to describe the spatial spread of an advantageous allele within a spatially extended population and explored its traveling wave solutions. Later that same year, the model was used independently by Kolmogorov, Petrovsky and Piskunov to describe the general growth and diffusion processes [46, 31], and in 1951 by Skellam in the ecological context of the invasion of the new territory by a colonizing species [47, 31].

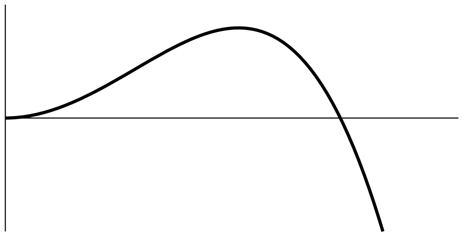
The Allee Effect

In recent years, much attention has been paid to the Allee effect, simply because it is extremely important for the control of invasive species. Allee effect was originally proposed as a phenomenon associated with a paucity of reproductive opportunities at low population densities. The name "Allee effect" comes from W.C. Allee's work on the cooperative behavior of animals [22, 25, 32]. Allee effect can be caused by many factors such as difficulties in finding mates when population density is low, social dysfunction at small population sizes, less efficient feeding at low densities, and inbreeding depression.

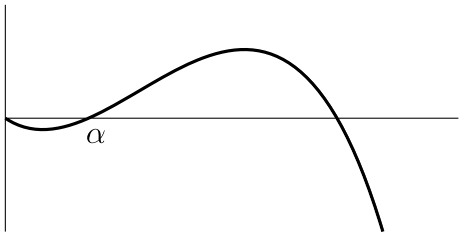
Strong Allee effect occurs when there exists a critical threshold below which the population growth is negative, and it may lead to the extinction of a species. By contrast, there is no such critical threshold that the population must surpass to reproduce and grow when weak Allee effect occurs [24].



(a) No Allee Effect



(b) Weak Allee Effect



(c) Strong Allee Effect

FIGURE 1.1 – The population profiliation rate when there is (a) no Allee effect (b) weak Allee effect (c) strong Allee effect.

Figure 1.1 illustrates the density dependent population profiliation rate in three different cases. It has been shown in some literatures that Allee effect may reduce the traveling wave speed and thus lead to a slower asymptotic rate of spread of an invasive species [10, 17, 22, 24]. In addition, the patterns of range expansion may also be changed by Allee effect [41]. In this dissertation, we will investigate the spreading speeds and traveling waves in two two-species competition models with Allee effect.

Two-Sex Invasions

Most of the currently available models for biological invasions explicitly track densities of only one sex. One-sex models are well suited to asexual or hermaphroditic species, including some fish and most plants. However, the application of one-sex invasion theory to dioecious species is more complicated due to the fact that dispersal may be sex biased, with males and females moving different distance [39].

In a two-sex invasion model, one should take gender-related factors into consideration, such as mating formation, that are central to the study of the life history of real populations [34]. Kendall [21] and Goodman [35] explored a number of specific hypotheses on how the birth rate depends on the male and female populations, for example:

$$\Lambda(M,F) = MF,\ (MF)^{\frac{1}{2}},\ \frac{1}{2}(M+F),\ \min(M,F),$$

where F and M are the numbers of females and males respectively. Many two-sex models concentrate on the evolutionary stability of specific traits such as sex ratio [82, 83, 84], but give little or no attention to population dynamics. Those models addressing dynamical issues are primarily concerned with the two-sex problem of appropriately mating, or pair formation between genders [21, 85, 86, 87]. Ashih et al. [40] constructed a two-sex single-species model of population dynamics incorporating the fertilizaiton state of females and studied the spreading speed and traveling waves. Miller et al. [39] established a two-sex integro-difference equation model and derived an explicit formula for the invasion speed and used it to show that sex-biased dispersal may significantly increase or decrease the invasion speed by skewing the operational sex ratio at the invasion's low-density leading edge.

1.2 Reaction-Diffusion Equations

Reaction-diffusion equations often yield elegantly tractable and compact models of spread and persistence, they stand on the assumptions that the dispersal and growth take place continuously in both space and time, and that the dispersal is conducted by random diffusion [15]. A large portion of mathematical literatures on spread and persistence rely on reaction-diffusion equations, and noteworthy success has been made by reaction-diffusion equations in explaining the rates at which species have invaded new environments as well as spatial patterns that species have had established in bounded-patch habitats. It has been well documented that the spatial theory about species spread and persistence matches the field observations well in a large number of cases [15, 48, 51, 52, 53].

Reaction-diffusion equations are used to model the intrinsic reaction activities of a species, such as birth, death, the interactions with other species, and the movement of a species in a bounded or unbounded domain. A typical reaction-diffusion equation comprises a reaction term and a diffusion term as shown below:

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + R(u). \tag{1.2}$$

Here $u = u(x,t)$ is a state variable and describes the population density at position x at time t. $D\frac{\partial^2 u}{\partial x^2}$ is the diffusion term with the coefficient of diffusion D and $R(u)$ denotes the reaction term which describes the net population change from birth and death. Examples of some typical reaction terms are

1. Exponential growth:

$$R(u) = ru.$$

2. Logistic growth:

$$R(u) = ru(1 - \frac{u}{K}),$$

where K is a carrying capacity, which serves as the limitation of growth.

3. Strong Allee effect:

$$R(u) = ru(u - \alpha)(1 - u),$$

where $0 < \alpha < 1$. The basis of this model approach is still exponential growth, but if the population is too low, i.e. $0 < u < \alpha$, extinction may occur.

The diffusion process can be considered as an ensemble of particles takes random walk from a starting point to somewhere with a random direction. Fick's laws of diffusion were derived to describe this process by Adolf Fick in 1855. It can be used to solve for the coefficient of diffusion D. In particular, Fick's first law postulates that the flux goes from regions of high concentration to regions of lower concentration, and Fick's second law predicts how diffusion would lead to the concentration change over time [73].

Impulsive Reaction-Diffusion Models

When population dynamics contain growth and dispersal, as well as continuous and discrete components, traditional reaction-diffusion equations will not be suitable to describe the spread and persistence of such population. For example, many fish and large mammal populations exhibit a birth pulse growth pattern, which was originally proposed by Caughley in 1977 [75]. That is, reproduction takes place in a relatively short period each year. Mortality takes its toll in between these birth pulses, which leads to a decrease in population size. The dynamics of such populations usually consist of two stages: within-season stage and between-season stage. Population mortality is continuous within a season, while between seasons population growth is discrete [15]. Semi-discrete models are often used to model populations in a birth pulse growth pattern, that is when both discrete and continuous components need to be incorporated into one single model [76, 77]. Especially, impulsive reaction-diffusion equations give a natural depiction of such spatial dynamics of the population. Lewis and Li [15] built such a model with a single species:

$$\begin{aligned} &\tfrac{\partial u}{\partial t} = d\tfrac{\partial u}{\partial x^2} + \alpha u - \gamma u^2, \\ &u(x,0) = g(N_n(x)), \\ &N_{n+1}(x) = u(x,1). \end{aligned} \tag{1.3}$$

They provided an explicit formula for the spreading speed and showed that the spreading speed can be characterized as the slowest speed of class of traveling wave solutions.

In this dissertation, the formulation of the two-sex stage-structured model is inspired by the model (1.3).

1.3 Integro-Difference Equations

When it comes to univoltine populations such as many arthropod and annual plant species, which have discrete time dynamics and is distributed in a continuous spatial habitat, reaction-diffusion equations are not a reasonable choice for modeling such population dynamics. Instead, integro-difference equations have been used broadly in literatures for such modeling purposes, especially for modeling the invading organisms [24]. They can, like reaction-diffusion equations, generate constant-speed traveling waves [3, 4, 5, 8, 9]. In addition, integro-difference equations can generate continually accelerating solutions with asympototically infinite speeds [10, 11, 12]. They can, in other words, account for invasions in which spread rates increase with time.

To formulate an integro-difference equation, we assume there is a sedentary stage at which the population grows, and a dispersal stage at which the population migrates. These stages are assumed to occur independently with the growth occuring in discrete-time intervals and the migration occuring in continuous one dimensional space.

The population density at location x and time $n+1$ is given by the sum of the contributions from all other locations y in the form of an **integro-difference equation**:

$$u_{n+1}(x) = \int_{-\infty}^{\infty} k(x-y) f(u_n(y)) dy. \tag{1.4}$$

We use equation (1.4) to model the dispersal and growth of populations. $u_n(x)$ is the population size or density at location x, $f(u_n(y))$ describes the density dependent local population growth at location y, and $k(x-y)$ is the probability of the population moving from location y to x, which is often referred to as the dispersal kernel. Since $k(x)$ is a probability distribution function, we have that $k(x)$ must be nonnegative and $\int_{-\infty}^{\infty} k(x)dx = 1$.

Note that integro-difference equations can be used to model multivoltine populations as well, as long as the organism has non-overlapping generations. In this case, t is not measured in years, but rather the time increment between broods [78].

1.4 The Spreading Speed

One crucial measure of mathematically analyzing invasions is to investigate the speed at which the invasive species spreads into a new environment. Aronson and Weinberger [79, 80, 81] introduced the conception of **spreading speed** as a mechanism to quantify the spread, that is, to consider the asymptotic behavior of the solution as x approaches infinity.

We introduce the precise definition of the spreading speed in reaction-diffusion equations and integro-difference equations respectively. For the classic reaction-diffusion equation (1.2), the spreading speed c_1^* is defined in the following sense:

1. If $0 \leq u(x,0) < 1$ and $u(x,0) \equiv 0$ for all sufficiently large x, then for any positive ϵ,
$$\lim_{x\to\infty}\left\{\max_{|x|\geq(c_1^*+\epsilon)t} u(x,t)\right\} = 0. \tag{1.5}$$
2. For every positive number σ there exists a positive number r_σ such that if $0 \leq u(x,0) \leq 1$, and if $u(x,0) \geq \sigma$ on an interval of length r_σ, then for any positive ϵ,
$$\lim_{x\to\infty}\left\{\sup_{|x|\leq(c_1^*-\epsilon)t} (1-u(x,t))\right\} = 0. \tag{1.6}$$

As for the integro-difference equation (1.4), we suppose there exists a positive steady-state γ of the recursion. Then c_2^* is defined to be the spreading speed in the following sense:

1. If $u_n(x)$ is a solution of the recursion (1.4) with $0 \leq u_0(x) < \gamma$ uniformly in x and $u_0(x) = 0$ for all sufficiently large x, then for any positive ϵ,
$$\lim_{n\to\infty}\left\{\sup_{|x|\geq(c_2^*+\epsilon)n} u_n(x)\right\} = 0. \tag{1.7}$$
2. For every $0 < \sigma < 1$ there exists a positive number r_σ such that if u_n is a solution of (1.4) and if $0 \leq u_0(x) < \gamma$ and $u_0(x) \geq \sigma\gamma$ on an interval of length r_σ, then for any positive ϵ,
$$\lim_{n\to\infty}\left\{\sup_{|x|\leq(c_2^*-\epsilon)n} (\gamma-u_n(x))\right\} = 0. \tag{1.8}$$

Equation (1.5) states that c_1^* is the upper bound for the spreading speed of (1.2). In other words, if an observer were to move faster than the rate of spread of the population, he or she should always be in front of the advancing population.

On the other hand, equation (1.6) states that c_1^* is a lower bound for the spreading speed. If an observer always moves more slowly than the population ($|x| \leq (c_1^* - \epsilon)t$), then he or she should always be behind the leading edge of the advancing population.

Together, it follows that c_1^* is the asymptotic rate of spread of the solutions of the reaction-diffusion equation (1.2). Similar conclusion can be made for c_2^* by combining the interpretations from equation (1.7) and (1.8).

Weinberger et al. [3, 80, 81] showed that for the reaction-diffusion equation (1.2), if $R(u)$ describes the logistic population growth, then the spreading speed is given by

$$c_1^* = 2\sqrt{DR'(0)}, \tag{1.9}$$

at which the compact initial data expands. And for the scalar recursion (1.4), under certain conditions, the spreading speed is given by

$$c_2^* = \inf_{\mu>0} \left\{ \frac{1}{\mu} ln \left(f'(0) \int_{-\infty}^{\infty} e^{\mu y} k(y) dy \right) \right\}. \tag{1.10}$$

So far we have introduced the explicit formulas for the spreading speed of a reaction-diffusion equation and an integro-difference equation respectively. However, for the general case of a nonlinear multi-species system, different spreading speeds are expected since different species can move at different speeds. Particularly, Weinberger et al. [2] showed that there exists a c^*, which is the slowest spreading speed, Li et al. [19] further showed that there exists an upper bound c_+^* for all spreading speeds.

Before proceeding, we introduce the general multi-species discrete-time, and possibly discrete-space recursions of the form

$$\mathbf{u}_{n+1}(x) = Q[\mathbf{u}_n](x), \quad n = 0, 1, 2, ... \tag{1.11}$$

Here the function $\mathbf{u}_n(x)$ is vector valued, and its components usually represent the population densities at time n of the interacting species or age classes. Such a formulation can also be applied to the reaction-diffusion systems of the form

$$\begin{aligned} &[u_i]_{,t} = d_i[u_i]_{,xx} - e_i[u_i]_{,x} + f_i(\mathbf{u}), \quad i = 1, 2, ..., k, \\ &\mathbf{u}(0, x) = \mathbf{u}_0(x) \end{aligned} \tag{1.12}$$

by letting Q be the time-one map which takes the initial values $\mathbf{u}_0(x)$ into the value $\mathbf{u}(x, 1)$ at $t = 1$ of the solution $\mathbf{u}(x, t)$ of (1.12). It has been shown that the operator Q can correspond to even more general class of models. For example, Q may be a non-linear integral operator, or (1.11) may be an explicit finite difference equation [19].

The linear operator M is defined to be **linearization** of Q at $\mathbf{0}$ if for any $\epsilon > 0$ there exists a $\delta > 0$ such that $\|\mathbf{u}\| \leq \delta$ indicates $\|Q[\mathbf{u}] - M[\mathbf{u}]\| \leq \epsilon\|\mathbf{u}\|$. And for every bounded $\mathbf{u} \geq \mathbf{0}$, we have

$$M[\mathbf{u}] = \lim_{\rho \searrow 0} \frac{Q[\rho\mathbf{u}]}{\rho}.$$

If $\mathbf{u} \geq \mathbf{v}$ implies that $Q[\mathbf{u}] \geq Q[\mathbf{v}]$, then Q is said to be **order-preserving**. It means whenever there is an increase in any species, all species will eventually benefit from that. And if this property is satisfied, then we say that the recursion (1.11) is **cooperative**.

When Q is translation and reflection invariant, then so does M. In this case, M can be represented by

$$(M[\mathbf{v}](x))_i = \sum_{j=1}^{k} \int_{-\infty}^{\infty} \mathbf{v}_j(x - y) m_{ij}(y, dy),$$

where each m_{ij} is a bounded symmetric nonnegative measure.

It is helpful to consider the $k \times k$ matrix of two-sided Laplace transforms

$$B_\mu = \left(\int_{-\infty}^{\infty} e^{\mu y} m_{ij}(y, dy) \right). \tag{1.13}$$

Note that $B_\mu \alpha = M[\alpha e^{-\mu x}]|_{x=0}$ for every constant vector α. We assume that all the matrices B_μ are in Frobenius form. It is known that any nonzero irreducible matrix with nonnegative entries has a unique positive eigenvalue, which is called the **principal eigenvalue**, with a corresponding **principal eigenvector** that has strictly positive coordinates. It has been shown that the absolute values of all the other eigenvalues are no larger than the principal eigenvalue [2].

In order to define the slowest spreading speed c^*, Weinberger et al. [2] introduced a sequence $\mathbf{a}_0(c; s) = \boldsymbol{\phi}(s)$, where $\boldsymbol{\phi}(x)$ is a continuous vector-valued functuon with the following properties:

1. $\boldsymbol{\phi}(x)$ is non-increasing in x;
2. $\boldsymbol{\phi}(x) = 0$ for all $x \geq 0$;
3. $\mathbf{0} \ll \boldsymbol{\phi}(-\infty) \ll \boldsymbol{\beta}$, where $\boldsymbol{\beta}$ is a globally stable coexistence equilibrium of the recursion (1.11).

Then the sequence $\mathbf{a}_n(c; s)$ can be defined by the recursion

$$\mathbf{a}_{n+1}(c; s) = \max\{\boldsymbol{\phi}(s), \mathbf{Q}[\mathbf{a}_n(c; x)](s + c)\}. \tag{1.14}$$

By definition, we have $\mathbf{a}_1 \geq \boldsymbol{\phi} > \mathbf{a}_0$, and induction tells us that for all n, we have $\mathbf{a}_n \leq \mathbf{a}_{n+1} \leq \boldsymbol{\beta}$. Note that $\mathbf{a}_n(c; x)$ is nonincreasing in c and x implies that the sequence $\mathbf{a}_n$ increases to a limit function $\mathbf{a}(c; x)$ which is again nonincreasing in c and x and bounded by $\boldsymbol{\beta}$. With Hypothesis 2.1 and the Comparison Lemma in [19], the slowest spreading speed can be defined as

$$c^* := \sup\{c : \ \mathbf{a}(c; \infty) = \boldsymbol{\beta}\}, \tag{1.15}$$

and the upper bounds of all spreading speeds can be defined as

$$c_+^* := \sup\{c: \ \mathbf{a}(c;\infty) \neq \mathbf{0}\}. \tag{1.16}$$

The Comparison Lemma in [19] also implies that

$$c^* \leq c_+^*.$$

However, when the nonlinear system is dominated by a linear system in the direction of the vector corresponding to the principal eigenvalue of the generating matrix, then the nonlinear system has a unique spreading speed, which is equal to that of the linear system [2]. This is known as **linear determinacy** and the spreading speed of the nonlinear system is said to be **linearly determined** in this case. For general spatio-temporal models, the belief that a certain list of properties implies the linear determinacy has been called **linear conjecture** [14].

We study the linear determinacy of a nonlinear system simply because it is much easier to find an explicit formula for the spreading speed of the corresponding linearized system. In fact, if a nonlinear system is linearly determinate then the spreading speed c^* is equal to the spreading speed $\bar{c}$ of the linearized system, which is given by

$$\bar{c} = \inf_{\mu > 0} \left\{ \frac{1}{\mu} ln \lambda_1(\mu) \right\}, \tag{1.17}$$

where λ_1 is the principal eigenvalue of the first diagonal block of the matrix B_μ defined by (1.13). In addition, if the spreading speed of a nonlinear system is linearly determined then

$$c^* = c_+^* = \bar{c}.$$

Lui [6, 7] obtained sufficient conditions for the linear determinacy of a certain class of multi-species cooperative models. Weinberger et al. [2] analyzed the linear determinacy of the continuous and discrete-time models which require a sharper set of conditions than Lui's, and gave sufficient conditions for the linear determincy of those models. Lewis et al. [14] then carried out applications of the theorems developed in [2], and obtained the parameter ranges for the linear determinacy of the two-species Lotka-Volterra competition model

$$\begin{aligned} p_t &= d_1 p_{xx} + r_1 p(1 - p - a_1 q), \\ q_t &= d_2 q_{xx} + r_2 p(1 - q - a_2 p), \end{aligned} \tag{1.18}$$

and the two-species discrete-time spatial spreading model

$$\begin{aligned} p_{n+1}(x) &= \textstyle\int_{R^1} \frac{(1+p_1)p_n(x-y)}{1+\rho_1(p_n(x-y)+\alpha_1 q_n(x-y))} k_1(y, dy), \\ q_{n+1}(x) &= \textstyle\int_{R^1} \frac{(1+p_2)q_n(x-y)}{1+\rho_2(q_n(x-y)+\alpha_2 p_n(x-y))} k_2(y, dy). \end{aligned} \tag{1.19}$$

However, neither of the above models has taken Allee effect into consideration. As an extension, we investigate two two-species competition models in the forms of reaction-diffusion equations and integro-difference equations respectively, and consider that the native species exhibit strong Allee effect. Then we discuss the spreading speeds of the spatial transitions in those models and show the existence of traveling wave solutions.

1.5 Traveling Wave Solutions

We consider the vector-valued reaction-diffusion equation system

$$\begin{aligned} &\mathbf{u}_{,t} = D\mathbf{u}_{,xx} + \mathbf{f}(\mathbf{u}), \\ &\mathbf{u}(0, x) = \mathbf{u}_0(x), \end{aligned} \tag{1.20}$$

where $D := \mathrm{diag}(d_1, d_2, ..., d_k)$ is a constant diagonal matrix. We also consider the vector-valued integro-difference equation system

$$u_{n+1}(x) = \int_{-\infty}^{\infty} \mathrm{diag}(\mathbf{k}(x-y))\mathbf{f}(\mathbf{u_n}(y))dy, \tag{1.21}$$

where $\mathbf{k}(x)$ is a diagonal matrix of dispersal kernels corresponding to the stage-specific dispersal and $\mathbf{f}(\mathbf{u})$ describes how population densities fluctuate over time.

A non-constant solution of the vector-valued reaction-diffusion system (1.20) of the form

$$\mathbf{u_t}(x) = \mathbf{w}(x - ct), \tag{1.22}$$

or for the integro-difference system (1.21),

$$\mathbf{u_n}(x) = \mathbf{w}(x - nc), \tag{1.23}$$

where c is a positive constant, is called a **traveling wave solution** with speed c.

Traveling wave solutions enable us to better understand how a species propagates in space. From (1.22) and (1.23) we notice that traveling waves can be interpreted as solutions which retain their shape but translate by a fixed length for each iteration of time. Thus over time, the solutions travel in space at a constant rate of c.

Li and Zhang [18] showed that for the discrete-time recursion (1.11), under certain hypotheses and if $c \geq c_+^*$, then there is a nonincreasing traveling wave solution $\mathbf{W}(c;\ x-nc)$ of speed c with $\mathbf{W}(c;\ \infty) = \mathbf{0}$ and $\mathbf{W}(c;\ -\infty)$ an equilibrium other than $\mathbf{0}$, and such a traveling wave does not exist if $c < c_+^*$. Similar conclusions can be applied to continuous system such as reaction-diffusion equations when considering the system as a continuous time semiflow $\{Q_t\}_{t=0}^{\infty}$.

As mentioned earlier, a multi-species system may have different spreading speeds corresponding to different species. It has been shown for cooperative systems and some almost cooperative systems, the slowest spreading speed of those all can be characterized as the minimum wave speed for a particular class of traveling wave solutions [13, 19, 20].

CHAPTER 2

TWO-SPECIES REACTION-DIFFUSION COMPETITION MODEL WITH ALLEE EFFECT

In this chapter we extend the two-species Lotka-Volterra competition model (1.18), such that the native species exhibits strong Allee effect. We demonstrate the local stability of each equilibrium, as well as the global stability of a coexistence equilibrium and a mono-culture equilibrium. We will discuss the spatial transitions from a mono-culture equilibrium to a coexistence equilibrium or a different mono-culture equilibrium. With certain assumptions, we provide sufficient conditions for the linear determinacy of the model, and a formula for the spreading speed of the spatial transitions based on the linear determinacy. We will also show the existence of traveling waves based on the spatial transitions mentioned above.

2.1 The Model

We reconstruct the two-species reaction-diffusion competition model (1.18) as the following:

$$\begin{aligned} u_t &= d_1 u_{xx} + r_1 u(1 - \tfrac{u}{k} - a_1 v), \\ v_t &= d_2 v_{xx} + r_2 v\left((v - \alpha)(1 - v) - a_2 u\right), \end{aligned} \tag{2.1}$$

given that all parameters are positive and $0 < \alpha < 1$, and that the population densities u and v are required to be nonnegative. Table 2.1 describes each parameter in the model.

TABLE 2.1

Model (2.1) Parameter Descriptions

Parameter	Description of Parameter
$u(x,t), v(x,t)$	population density at time t and location x
d	coefficient of diffusion
r	intrinsic rate of increase
k	maximum population size of the species that the environment can sustain (carrying capacity)
a	coefficient of competition
α	critical population density

Existence of Allee Effect

The growth function of the native species v in model (2.1) is given by

$$g(v) = r_2 v(v-\alpha)(1-v).$$

We note that the population has a negative growth rate when $0 < v < \alpha$, and a positive growth rate when $\alpha < v < 1$. It follows that the species v exhibits strong Allee effect with the critical population density α, where $0 < \alpha < 1$.

Equilibria of the Model

In order to achieve the equilibria of the model, we consider the following system of equations:

$$\begin{aligned} &r_1 u(1 - \tfrac{u}{k} - a_1 v) = 0, \\ &r_2 v\left((v-\alpha)(1-v) - a_2 u\right) = 0. \end{aligned} \tag{2.2}$$

By solving the equations, we get the trivial equilibrium $E_0 = (0,0)$, the monoculture equilibrium $E_1 = (0,1)$, $E_2 = (0,\alpha)$, $E_3 = (k,0)$ and the coexistence equilibrium $E_1^* = (u_1^*, v_1^*)$, $E_2^* = (u_2^*, v_2^*)$ where

$$\begin{aligned} u_1^* &= k(1 - a_1 v_1^*), \\ v_1^* &= \tfrac{1+\alpha+a_1a_2k-\sqrt{(1+\alpha+a_1a_2k)^2-4(\alpha+a_2k)}}{2}, \\ u_2^* &= k(1 - a_1 v_2^*), \\ v_2^* &= \tfrac{1+\alpha+a_1a_2k+\sqrt{(1+\alpha+a_1a_2k)^2-4(\alpha+a_2k)}}{2}. \end{aligned} \tag{2.3}$$

Note that E_1^* and E_2^* both exist if the following condition is satisfied:

$$2\sqrt{\alpha + a_2k} < 1 + \alpha + a_1a_2k < \min\{1 + \alpha + a_2k, 2\}. \tag{2.4}$$

It is easy to see that $v_1^* < v_2^*$, which implies $u_1^* > u_2^*$. So E_1^* locates on the lower right side of E_2^* when they both exist.

2.2 Local Stability

In order to understand the possible spatial transitions among these euqilibria, we study the local stability of each equilibrium by analyzing the corresponding characteristic equations of the following vector-valued function at each point:

$$\mathbf{f}(u, v) = \begin{pmatrix} r_1 u(1 - \frac{u}{k} - a_1 v) \\ r_2 v\left((v - \alpha)(1 - v) - a_2 u\right) \end{pmatrix}. \tag{2.5}$$

At $E_0 = (0, 0)$, the Jacobian matrix of (2.5) is given by

$$J_{E_0} = \begin{pmatrix} r_1 & 0 \\ 0 & -r_2\alpha \end{pmatrix}.$$

The eigenvalues of the above matrix J_{E_0} are $\lambda_1 = r_1$ and $\lambda_2 = -r_2\alpha$. Note that $\lambda_1 > 0$ and $\lambda_2 < 0$ since all parameters in this model are positive including r_1, r_2 and α. So the equilibrium $E_0 = (0, 0)$ is a saddle.

At $E_1 = (0, 1)$, the Jacobian matrix of (2.5) is given by

$$J_{E_1} = \begin{pmatrix} r_1(1 - a_1) & 0 \\ -r_2a_2 & r_2(\alpha - 1) \end{pmatrix}.$$

The eigenvalues of the above matrix J_{E_1} are $\lambda_1 = r_1(1-a_1)$ and $\lambda_2 = r_2(\alpha-1)$. We note that $\lambda_1 < 0$ when $a_1 > 1$ and $\lambda_1 > 0$ when $0 < a_1 < 1$, and that $\lambda_2 < 0$ since $0 < \alpha < 1$. So the equilibrium $E_1 = (0,1)$ is a sink if $a_1 > 1$, and it is a saddle if $0 < a_1 < 1$.

At $E_2 = (0,\alpha)$, the Jacobian matrix of (2.5) is given by

$$J_{E_2} = \begin{pmatrix} r_1(1-a_1\alpha) & 0 \\ -r_2a_2\alpha & r_2\alpha(1-\alpha) \end{pmatrix}$$

The eigenvalues of the above matrix J_{E_2} are $\lambda_1 = r_1(1-a_1\alpha)$ and $\lambda_2 = r_2\alpha(1-\alpha)$. We observe that $\lambda_1 < 0$ when $a_1\alpha > 1$ and $\lambda_1 > 0$ when $a_1\alpha < 1$, and that $\lambda_2 > 0$ because $0 < \alpha < 1$. So the equilibrium $E_2 = (0,\alpha)$ is a source if $a_1\alpha < 1$, and it is a saddle if $a_1\alpha > 1$.

At $E_3 = (k,0)$, the Jacobian matrix of (2.5) is given by

$$J_{E_3} = \begin{pmatrix} -r_1 & -r_1a_1k \\ 0 & -r_2(\alpha+a_2k) \end{pmatrix}$$

The eigenvalues of the above matrix J_{E_3} are $\lambda_1 = -r_1$, $\lambda_2 = -r_2(\alpha+a_2k)$, which are both negative since all parameters are positive. So the equilibrium $E_3 = (k,0)$ is a sink.

At $E_1^* = (u_1^*, v_1^*)$, the Jacobian matrix of (2.5) is given by

$$J_{E_1^*} = \begin{pmatrix} \frac{-r_1u_1^*}{k} & -r_1a_1u_1^* \\ -r_2a_2v_1^* & -r_2v_1^*(1+\alpha-2v_1^*) \end{pmatrix}.$$

The corresponding characteristic equation is then given by

$$(\lambda + \frac{r_1u_1^*}{k})\,(\lambda + r_2v_1^*(1+\alpha-2v_1^*)) - (r_2a_2v_1^*)(r_1a_1u_1^*) = 0,$$

which can be rewritten as the standard form of the quadratic equation in the following sense:

$$\lambda^2 + \left(\frac{r_1u_1^*}{k} - r_2v_1^*(1+\alpha-2v_1^*)\right)\lambda - \left(\frac{r_1r_2u_1^*v_1^*(1+\alpha-2v_1^*)}{k} + a_1a_2r_1r_2u_1^*v_1^*\right) = 0.$$

By applying the quadratic formula, we get the solutions of the above equation as the following:

$$\lambda_1 = \frac{r_2v_1^*(1+\alpha-2v_1^*)-\frac{r_1u_1^*}{k}+\sqrt{\left(\frac{r_1u_1^*}{k}-r_2v_1^*(1+\alpha-2v_1^*)\right)^2+4\left(\frac{r_1r_2u_1^*v_1^*(1+\alpha-2v_1^*)}{k}+a_1a_2r_1r_2u_1^*v_1^*\right)}}{2},$$
$$\lambda_2 = \frac{r_2v_1^*(1+\alpha-2v_1^*)-\frac{r_1u_1^*}{k}-\sqrt{\left(\frac{r_1u_1^*}{k}-r_2v_1^*(1+\alpha-2v_1^*)\right)^2+4\left(\frac{r_1r_2u_1^*v_1^*(1+\alpha-2v_1^*)}{k}+a_1a_2r_1r_2u_1^*v_1^*\right)}}{2}.$$

In order to obtain the local stability of this equilibrium, we need to determine the signs of λ_1 and λ_2. For the sake of simplicity, we let

$$R_1 = r_2v_1^*(1+\alpha-2v_1^*) - \frac{r_1u_1^*}{k},$$
$$R_2 = 4\left(\frac{r_1r_2u_1^*v_1^*(1+\alpha-2v_1^*)}{k} + a_1a_2r_1r_2u_1^*v_1^*\right).$$

So the two eigenvalues can be rewritten as

$$\lambda_1 = \frac{R_1+\sqrt{{R_1}^2+R_2}}{2},$$
$$\lambda_2 = \frac{R_1-\sqrt{{R_1}^2+R_2}}{2}.$$

We observe that

$$\begin{aligned} R_2 &= 4r_1r_2u_1^*v_1^*\left(\frac{1+\alpha-2v_1^*}{k}+a_1a_2\right) \\ &= 4r_1r_2u_1^*v_1^*\left(\frac{1+\alpha-2\cdot\frac{1+\alpha+a_1a_2k-\sqrt{(1+\alpha+a_1a_2k)^2-4(\alpha+a_2k)}}{2}}{k}+a_1a_2\right) \\ &= 4r_1r_2u_1^*v_1^*\cdot\frac{\sqrt{(1+\alpha+a_1a_2k)^2-4(\alpha+a_2k)}}{k} \\ &> 0 \end{aligned}$$

if and only if

$$2\sqrt{\alpha+a_2k} < 1+\alpha+a_1a_2k. \tag{2.6}$$

Note that (2.6) is valid when the existence condition (2.4) for E_1^* is satisfied. Thus, as long as E_1^* exists, it is always true that

$$R_2 > 0. \tag{2.7}$$

(2.7) then implies that

$$R_1 + \sqrt{{R_1}^2 + R_2} > 0,$$
$$R_1 - \sqrt{{R_1}^2 + R_2} < 0.$$

Thus we have $\lambda_1 > 0$ and $\lambda_2 < 0$, which indicates that $E_1^* = (u_1^*, v_1^*)$ is a saddle.

At $E_2^* = (u_2^*, v_2^*)$, the Jacobian matrix of (2.5) is given by

$$J_{E_2^*} = \begin{pmatrix} \frac{-r_1 u_2^*}{k} & -r_1 a_1 u_2^* \\ -r_2 a_2 v_2^* & -r_2 v_2^*(1+\alpha-2v_2^*) \end{pmatrix}$$

The corresponding characteristic equation of the above matrix is then given by

$$\lambda^2 + \left(\frac{r_1 u_2^*}{k} - r_2 v_2^*(1+\alpha-2v_2^*)\right)\lambda - \left(\frac{r_1 r_2 u_2^* v_2^*(1+\alpha-2v_2^*)}{k} + a_1 a_2 r_1 r_2 u_2^* v_2^*\right) = 0$$

For the sake of simplicity, we denote

$$C = -\frac{r_1 u_2^*}{k} + r_2 v_2^*(1+\alpha-2v_2^*).$$

Recall that

$$v_2^* = \frac{1+\alpha+a_1 a_2 k + \sqrt{(1+\alpha+a_1 a_2 k)^2 - 4(\alpha + a_2 k)}}{2} > 0,$$

which implies that

$$1+\alpha < 2v_2^*,$$

thus we have

$$C < 0. \tag{2.8}$$

In addition, we let

$$\begin{aligned} S &= 4\left(\frac{r_1 r_2}{k} u_2^* v_2^* (1+\alpha-2v_2^*) + a_1 a_2 r_1 r_2 u_2^* v_2^*\right) \\ &= 4 r_1 r_2 u_2^* v_2^* \left(\frac{1+\alpha-2v_2^*}{k} + a_1 a_2\right). \end{aligned}$$

TABLE 2.2

Summary of Existence and Local Stability Criteria of Equilibria in Model (2.1)

Equilibrium	**Existence Condition**	**Stability Criteria**
E_0	always exists	always unstable
E_1	always exists	stable when $a_1 > 1$ unstable when $0 < a_1 < 1$
E_2	always exists	always unstable
E_3	always exists	always stable
E_1^*	if (2.4) holds	always unstable
E_2^*	if (2.4) holds	always stable

By substituting v_2^* in part of the above equation with the formula given by (2.3), we have

$$\begin{aligned} S &= 4r_1r_2u_2^*v_2^*\left(\tfrac{1+\alpha-2v_2^*}{k} + a_1a_2\right) \\ &= 4r_1r_2u_2^*v_2^*\left(\frac{1+\alpha-2\cdot\frac{1+\alpha+a_1a_2k+\sqrt{(1+\alpha+a_1a_2k)^2-4(\alpha+a_2k)}}{2}}{k} + a_1a_2\right) \\ &= -4r_1r_2u_2^*v_2^*\frac{\sqrt{(1+\alpha+a_1a_2k)^2-4(\alpha+a_2k)}}{k} \\ &< 0 \end{aligned}$$

if and only if (2.6) holds.

We observe that the eigenvalues of the matrix $J_{E_2^*}$ can be written as

$$\begin{aligned} \lambda_1 &= \tfrac{C+\sqrt{C^2+4S}}{2}, \\ \lambda_2 &= \tfrac{C-\sqrt{C^2+4S}}{2}. \end{aligned}$$

Considering $C < 0$ and $S < 0$, we have that

$$\lambda_1 < 0,\ \lambda_2 < 0.$$

So $E_2^* = (u_2^*, v_2^*)$ is a sink if and only if (2.6) holds.

Table 2.2 summarizes the existence condition and the local stability of each equilibrium of model (2.1).

2.3 Global Stability

In order to show the existence of traveling wave solutions in (2.1), we also want to understand the global stability of certain equilibrium in the model. Before proceeding, we need the following lemmas:

Lemma 2.1. *(Butler-McGehee Theorem) Suppose that P is a hyperbolic rest point which is in $\omega(x)$, the omega limit set of $\gamma^+(x)$, but is not the entire omega limit set. Then $\omega(x)$ has nontrivial (i.e., different from P) intersection with the stable and the unstable manifolds of P.*

Lemma 2.2. *In the model (2.1), we denote the rectangle with the vertices $E_2^* = (u_2^*, v_2^*)$, $E_1 = (0,1)$, $(0, v_2^*)$ and $(u_2^*, 1)$ as R_1, and the rectangle with the vertices $E_1 = (0,1)$, $E_3 = (k,0)$, $(k,1)$ and $(0,0)$ as R_2. Then the following statements are valid:*

i. If the two coexistence equilibria E_1^* and E_2^* both exist, then R_1 is an invariant set;

ii. If the coexistence equilibria E_1^* and E_2^* do not exist, then R_2 is an invariant set.

Proof. We consider the corresponding ordinary differential equations of the model (2.1) given by the following:

$$\begin{aligned} u_t &= r_1 u(1 - \tfrac{u}{k} - a_1 v), \\ v_t &= r_2 v\left((v-\alpha)(1-v) - a_2 u\right), \end{aligned} \tag{2.9}$$

We prove the first statement in the lemma, that is when the two coexistence equilibria E_1^* and E_2^* both exist.

When $v = 1$ and $0 < u \leq u_2^*$, we have that

$$v_t = -a_2 r_2 u,$$

which is negative since $0 < u \leq u_2^*$. It indicates that any point starting from the upper edge of R_1 will move towards the inside of R_1.

When $u = 0$ and $v_2^* \leq v < 1$, we have that

$$u_t = 0,$$

which implies that any point starting from the left edge of R_1 will stay on this edge.

When $v = v_2^*$ and $0 \leq u < u_2^*$, we have that

$$v_t = r_2 v_2^* \left((v_2^* - \alpha)(1 - v_2^*) - a_2 u \right),$$

which is positive because $\alpha < v_2^* < 1$. It then indicates that any point starting from the lower edge of R_1 will move towards the inside of R_1.

When $u = u_2^*$ and $v_2^* < v \leq 1$, we have that

$$u_t = r_1 u_2^* \left(1 - \frac{u_2^*}{k} - a_1 v \right),$$

which is negative since $v > v_2^*$. It indicates that any point starting from the right edge of R_1 will move towards the inside of R_1.

Thus we have shown that when the two coexistence equilibria E_1^* and E_2^* exist, the rectangle R_1 is an invariant set. Similarly, we can show that R_2 is an invariant set when E_1^* and E_2^* do not exist. □

THEOREM 2.1. *Assume* $0 < a_1 < 1$. *Let* E_3 *and* E_2^* *be defined as above in Section 2.1, then the following statements are valid:*

- *i. If the two coexistence equilibria* E_1^* *and* E_2^* *both exist, then* E_2^* *is globally asymptotically stable;*
- *ii. If the coexistence equilibria* E_1^* *and* E_2^* *do not exist, then the mono-culture equilibrium* E_3 *is globally asymptotically stable.*

Proof. We shall prove this theorem by considering the following two cases:

Case i. If the two coexistence equilibria E_1^* and E_2^* both exist, we want to prove that E_2^* is globally asymptotically stable. Lemma 2.2 tells us that the rectangle R_1 is an invariant set in this case, thus the monotone dynamical system theory in [38] indicates that there are no limit cycles in R_1. If we denote a solution of (2.9) in R_1 by $\hat{\mathbf{x}}$, and denote the limit set of this solution by $\omega(\hat{\mathbf{x}})$, then we want to show that

$$E_1 \notin \omega(\hat{\mathbf{x}}). \tag{2.10}$$

We validate (2.10) by using the method of contradiction. Note that the mono-culture equilibrium $E_1 = (0, 1)$ is a saddle when $0 < a_1 < 1$. The stable manifold of E_1 is given by the set $\Omega_1 = \{(0, x) \mid x \in R,\ \alpha < x < 1 \text{ or } x > 1\}$. Assume that $E_1 \in \omega(\hat{\mathbf{x}})$, then Lemma 2.1 indicates that the intersection $\Omega_1 \cap \omega(\hat{\mathbf{x}})$ is nonempty and E_1 is not in it. Thus in this intersection set, there exists a point $(0, x_1) \in \omega(\hat{\mathbf{x}})$ with either $x_1 > 1$ or $\alpha < x_1 < 1$. The invariant property of the limit set $\omega(\hat{\mathbf{x}})$ indicates that the solutions starting from the intersection point $(0, x_1)$ as $t \to \infty$ or $t \to -\infty$ are all in the limit set $\omega(\hat{\mathbf{x}})$. Accordingly, we consider the following two cases:

a. If $x_1 > 1$, then the invariant property of the limit set $\omega(\hat{\mathbf{x}})$ implies that the set $\{(0, x) \mid x \in R\ , x > 1\} \subseteq \omega(\hat{\mathbf{x}})$. This is a contradiction with that fact that R_1 is an invariant set.

b. If $\alpha < x_1 < 1$, then the invariant property of the limit set $\omega(\hat{\mathbf{x}})$ implies that $(0, \alpha) \in \omega(\hat{\mathbf{x}})$. On the other hand, since $\alpha < v_2^*$ and R_1 is invariant, we have that $(0, \alpha) \notin \omega(\hat{\mathbf{x}})$. So this is again a contradiction.

Thus we have shown that $E_1 \notin \omega(\hat{\mathbf{x}})$, which implies that the coexistence equilibrium E_2^* is globally asymptotically stable.

Case ii. If the coexistence equilibria E_1^* and E_2^* do not exist, we want to demonstrate that the mono-culture equilibrium $E_3 = (k, 0)$ is globally asymptotically stable. Lemma 2.2 tells us that the rectangle R_2 is an invariant set in this case, thus the monotone dynamical system theory in [38] indicates that there are no limit cycles in R_2. If we denote a solution of (2.9) in R_2 by $\hat{\mathbf{y}}$, and denote the limit set of this solution by $\omega(\hat{\mathbf{y}})$, then we only need to show that

$$\begin{aligned} &E_0 \notin \omega(\hat{\mathbf{y}}), \\ &E_1 \notin \omega(\hat{\mathbf{y}}), \\ &E_2 \notin \omega(\hat{\mathbf{y}}). \end{aligned} \tag{2.11}$$

Since the equilibrium $E_2 = (0, \alpha)$ is a source when $0 < a_1 < 1$, thus it suffices to show that $E_2 \notin \omega(\hat{\mathbf{y}})$.

Note that the equilibrium E_0 is a saddle. The stable manifold of E_0 is given by the set $\Omega_2 = \{(0, y) \mid y \in R,\ 0 < y < \alpha \text{ or } y < 0\}$. Assume that $E_0 \in \omega(\hat{\mathbf{y}})$, then Lemma 2.1 indicates that the intersection $\Omega_2 \cap \omega(\hat{\mathbf{y}})$ is nonempty and E_0 is not in it. Thus in this intersection set, there exists a point $(0, y_1) \in \omega(\hat{\mathbf{y}})$ with either $y_1 < 0$ or $0 < y_1 < \alpha$. The invariant property of the limit set $\omega(\hat{\mathbf{y}})$ indicates that the solutions starting from the intersection point $(0, y_1)$ as $t \to \infty$ or $t \to -\infty$ are all in the limit set $\omega(\hat{\mathbf{y}})$. Accordingly, we consider the following two cases:

a. If $y_1 < 0$, then the invariant property of the limit set $\omega(\hat{\mathbf{y}})$ implies that the set $\{(0, y) \mid y \in R\ , y < 0\} \subseteq \omega(\hat{\mathbf{y}})$. This is a contradiction with that fact that R_2 is an invariant set.

b. If $0 < y_1 < \alpha$, then the invariant property of the limit set $\omega(\hat{\mathbf{y}})$ indicates that $(0, \alpha) \in \omega(\hat{\mathbf{y}})$, which is again a contradiction with the fact that $E_2 \notin \omega(\hat{\mathbf{y}})$. Thus we have shown that $E_0 \notin \omega(\hat{\mathbf{y}})$.

We still need to show that $E_1 \notin \omega(\hat{\mathbf{y}})$. Recall that the equilibrium E_1 is a saddle and the stable manifold of E_1 is given by Ω_1 in Case i. We assume that $E_1 \in \omega(\hat{\mathbf{y}})$, then Lemma 2.1 indicates that the intersection $\Omega_1 \cap \omega(\hat{\mathbf{y}})$ is nonempty and E_1 is not in it. Thus in this intersection set, there exists a point $(0, y_2) \in \omega(\hat{\mathbf{y}})$ with either $y_2 > 1$ or $\alpha < y_2 < 1$. The invariant property of the limit set $\omega(\hat{\mathbf{y}})$ then indicates that the solutions starting from the intersection point $(0, y_2)$ as $t \to \infty$ or $t \to -\infty$ are all in the limit set $\omega(\hat{\mathbf{y}})$. Then we consider the following two cases:

a. If $y_2 > 1$, then the invariant property of the limit set $\omega(\hat{\mathbf{y}})$ implies that the set $\{(0, y) \mid y \in R\ , y > 1\} \subseteq \omega(\hat{\mathbf{y}})$. This is a contradiction with that fact that R_2 is an invariant set.

b. If $\alpha < y_2 < 1$, then the invariant property of $\omega(\hat{\mathbf{y}})$ indicates that $(0, \alpha) \in \omega(\hat{\mathbf{y}})$, which is again a contradiction with the fact that $E_2 \notin \omega(\hat{\mathbf{y}})$. So we conclude that $E_1 \notin \omega(\hat{\mathbf{y}})$.

Thus we have demonstated that (2.11) is valid, which indicates that the mono-culture equilibrium $E_3 = (k, 0)$ is globally asymptotically stable in this case.

□

2.4 Spreading Speed and Linear Determinacy

Weinberger et al. [2] have provided sufficient conditions for the linear determinacy of the two-species cooperative models with certain assumptions. It is well known that a simple change of variables can convert a two-species competition model into a cooperative model. Take the competition model (2.1) as an example, the change of variables

$$p = u,\ q = 1 - v \tag{2.12}$$

converts the model into

$$\begin{aligned} p_t &= d_1 p_{xx} + r_1 p(1 - \tfrac{p}{k} - a_1 + a_1 q), \\ q_t &= d_2 q_{xx} + r_2 (q - 1)(q - q^2 - \alpha q - a_2 p), \end{aligned} \tag{2.13}$$

which is a cooperative system in the biological realistic range $0 \le p \le 1, 0 \le q \le 1$. That is, increasing either p or q will lead to the increase of q and p respectively.

We use $\hat{E}_0$, $\hat{E}_1$, $\hat{E}_2$, $\hat{E}_3$, $\hat{E}_1^*$ and $\hat{E}_2^*$ to denote the equilibria of the coorperative system (2.13), then we have the following mapping of the equilibria from the competition model (2.1) to the cooperative system:

$$
\begin{aligned}
E_0 &= (0,0) \longrightarrow \hat{E}_0 = (0,1),\\
E_1 &= (0,1) \longrightarrow \hat{E}_1 = (0,0),\\
E_2 &= (0,\alpha) \longrightarrow \hat{E}_2 = (0,1-\alpha),\\
E_3 &= (k,0) \longrightarrow \hat{E}_3 = (k,1),\\
E_1^* &= (u_1^*, v_1^*) \longrightarrow \hat{E}_1^* = (u_1^*, 1-v_1^*),\\
E_2^* &= (u_2^*, v_2^*) \longrightarrow \hat{E}_2^* = (u_2^*, 1-v_2^*).
\end{aligned}
$$

We assume that

$$0 < a_1 < 1, \tag{2.14}$$

then $E_1 = (0,1)$ is a saddle. $E_2^* = (u_2^*, v_2^*)$ exists and is stable when (2.4) is satisfied. Note that $E_3 = (k,0)$ is always stable.

We consider the spatial transition from the unstable state $E_1 = (0,1)$ to the target stable state

$$E := (u,v) = \begin{cases} E_2^* = (u_2^*, v_2^*) & \text{if } E_1^*, E_2^* \text{ both exist,}\\ E_3 = (k,0) & \text{if } E_1^*, E_2^* \text{ do not exist.} \end{cases} \tag{2.15}$$

By changing the variables as shown in (2.12), the above transition is then turned into the transition from $\hat{E}_1 = (0,0)$ to the converted target state

$$\hat{E} := (\hat{p}, \hat{q}) = \begin{cases} (u_2^*, 1-v_2^*) & \text{if } \hat{E}_1^*, \hat{E}_2^* \text{ both exist,}\\ (k,1) & \text{if } \hat{E}_1^*, \hat{E}_2^* \text{ do not exist.} \end{cases}$$

Figure 2.1 displays the coordinates of each equilibrium and the spatial transitions before and after the change of variables.

Theorem 2.2. *Suppose that all parameters of the model (2.1) are positive, that $0 < a_1 < 1$ and that the conditions*

$$
\begin{aligned}
&\tfrac{d_2}{d_1} \le 2,\\
&\max\left\{\tfrac{1}{1-a_1}, \tfrac{a_1 a_2 k + \alpha - 1}{1-a_1}\right\} \le \tfrac{r_2}{r_1}\left(2 - \tfrac{d_2}{d_1}\right)
\end{aligned}
\tag{2.16}
$$

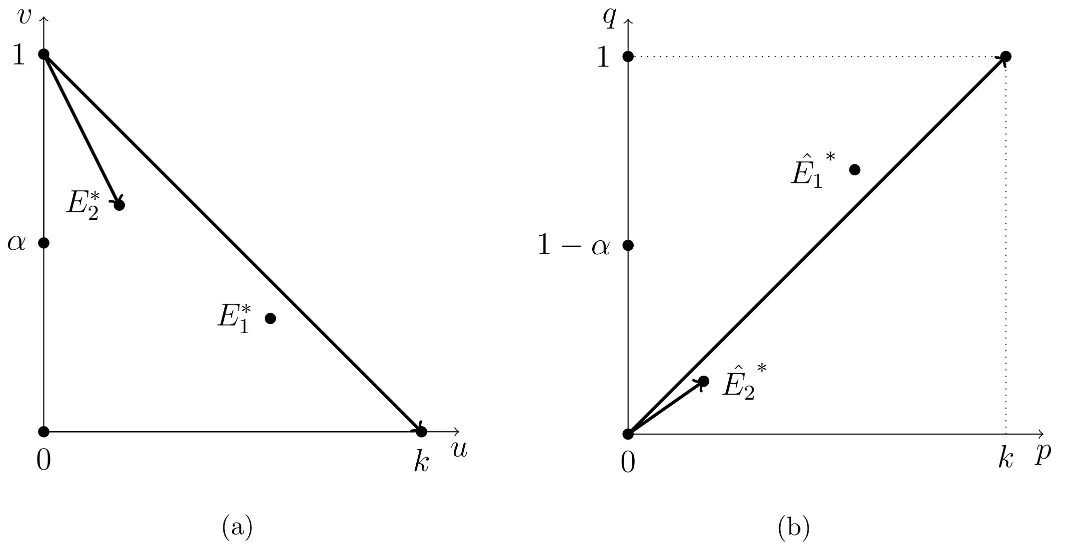


FIGURE 2.1 – Equilibria and spatial transitions in the reaction-diffusion system before and after the change of variables $p = u, q = 1 - v$: (a) Before the change of variables, when the two coexistence equilibria exist, the spatial transition is from $(0,1)$ to E_2^*; when the coexistence equilibria do not exist, the spatial transition is from $(0,1)$ to $(k,0)$. (b) After the change of variables, when the two coexistence equilibria exist, the spatial transition is from $(0,0)$ to $\hat{E}_2^*$; when the coexistence equilibria do not exist, the spatial tansition is from $(0,0)$ to $(k,1)$.

are satisfied. Then the spreading speed c^* *of the spatial transition from* E_1 *to* E *is equal to the spreading speed* $\bar{c} = 2\sqrt{d_1 r_1(1-a_1)}$ *of the linearization of model (2.1) at* $(0,1)$. *That is, the model (2.1) is linearly determinate.*

Proof. This theorem is an application of Weinberger's Theorem 4.2 in [2].

We aim to find an explicit formula for the spreading speed $\bar{c}$ based on the linear determinacy first. We consider the cooperative system (2.13) after changing the variables in the competition model (2.1), then the linearization of (2.13) at $(p,q) = (0,0)$ can be calculated as

$$\begin{aligned} p_t &= d_1 p_{xx} + r_1 p(1-a_1), \\ q_t &= d_2 q_{xx} - r_2(q - \alpha q - a_2 p). \end{aligned} \tag{2.17}$$

To apply Theorem 4.2 in [2], we need to find a matrix C_μ defined to be the coefficient matrix for the vector of the linear combinations of α_1 and α_2 obtained by substituting $p = \alpha_1 e^{-\mu x}, q = \alpha_2 e^{-\mu x}$ into the right-hand side of (2.17) and setting $x = 0$. So C_μ can be calculated as

$$C_\mu = \begin{pmatrix} d_1\mu^2 + r_1(1-a_1) & 0 \\ r_2 a_2 & d_2\mu^2 + r_2(\alpha - 1) \end{pmatrix}.$$

The principal eigenvalue of the first diagonal block of this upper triangular matrix C_μ is then given by

$$\gamma_1(\mu) = d_1\mu^2 + r_1(1-a_1). \tag{2.18}$$

An eigenvector corresponding to $\gamma_1(\mu)$ is given by the vector $(\zeta_1(\mu), \zeta_2(\mu))$, where

$$\begin{aligned} \zeta_1(\mu) &= \gamma_1(\mu) - \gamma_2(\mu), \\ \zeta_2(\mu) &= r_2 a_2. \end{aligned} \tag{2.19}$$

It is shown in [2] that

$$B_\mu = \exp\left(C_\mu\right),$$

so the principal eigenvalue λ_1 of the first diagonal block of B_μ has the following property:

$$\lambda_1(\mu) = e^{\gamma_1(\mu)}.$$

By applying the spreading speed formula (1.17) in Chapter 1, we get that the invasive species u spreads to infinity with the asymptotic speed of

$$\bar{c} = \inf_{\mu > 0}\left\{\frac{1}{\mu}\gamma_1(\mu)\right\}. \tag{2.20}$$

The infimum in (2.20) can be fullfilled when μ takes the value

$$\mu = \bar{\mu} = \sqrt{\frac{r_1(1-a_1)}{d_1}}. \tag{2.21}$$

By substituting (2.21) into (2.20), we have

$$\bar{c} = 2\sqrt{d_1 r_1(1-a_1)}. \tag{2.22}$$

If the spreading speed of the model (2.1) is equal to $\bar{c}$ in (2.22), i.e. $c^* = \bar{c} = 2\sqrt{d_1 r_1(1-a_1)}$, then the spreading speed of the model (2.1) is said to be linearly determined. In order to find the sufficient conditions for the linear determinacy, we shall make the following hypotheses which is a special case of Hypotheses 4.1 in [2].

Hypotheses 2.1.

i. *There exist equilibria* $(0,0)$ *and* (β_1, β_2) *with* β_1 *and* β_2 *positive, and there is no other constant all-species coexistence equilibrium* (α_1, α_2) *such that* $0 < \alpha_1 \leq \beta_1$ *and* $0 < \alpha_2 \leq \beta_2$*, i.e., there is no constant all-species coexistence equilibrium below* (β_1, β_2)*.*

ii. *The system (2.13) is cooperative in the sense that the growth term in the p-equation is nondecreasing in q, and the growth term in the q-equation is nondecreasing in p, i.e., an increase in any species is beneficial to all species.*

iii. *Neither equations in (2.13) has explicit dependence on space or time.*

iv. *The growth functions are continuous and piecewise continuously differentiable for* $0 \leq p \leq \beta_1$ *and* $0 \leq q \leq \beta_2$*.*

v. *The Jacobian matrix* C_μ *is in Frobenius form. The principal eigenvalue* $\gamma_1(0) = r_1(1-a_1)$ *of its upper left diagonal block is positive and is strictly larger than the principal eigenvalues* $\gamma_\sigma(0)$ *of its other diagonal blocks.*

vi. C_0 *has at least one nonzero entry to the left of each of its diagonal blocks other than the uppermost one, i.e., the element* c_{21} *in* C_0*, which is* $r_2 a_2$*, is positive.*

vii. *With* $\bar{\mu}$ *defined by (2.21),* $\gamma_1(\bar{\mu}) > \gamma_2(\bar{\mu})$*.*

viii. *For every positive number* ρ*, each of the right-hand sides of the system (2.13) evaluated at* $p = \rho\zeta_1(\bar{\mu}), q = \rho\zeta_2(\bar{\mu})$ *should be no larger than the corresponding* *right-hand sides of the linearization (2.17) evaluated at* $(\rho\zeta_1(\bar{\mu}), \rho\zeta_2(\bar{\mu}))$.

For hypothesis i, we showed at the beginning of this section that $\hat{E}_2^* = (u_2^*, 1 - v_2^*)$ and $\hat{E}_1 = (0,0)$ satisfy these conditions by letting $\beta_1 = u_1^*$ and $\beta_2 = 1 - v_2^*$. And it is easy to verify that the model (2.13) satisfies hypothesis ii to vi when $r_1(1-a_1) > 0$ and $r_2 a_2 > 0$.

For hypothesis vii, by (2.18) and (2.21) we have

$$\begin{aligned} \gamma_1(\bar{\mu}) &= 2r_1(1-a_1), \\ \gamma_2(\bar{\mu}) &= \tfrac{d_2 r_1 (1-a_1)}{d_1} + r_2(\alpha - 1). \end{aligned}$$

In order to make $\gamma_1(\bar{\mu}) > \gamma_2(\bar{\mu})$, the following inequality must be satisfied:

$$\frac{\alpha - 1}{1 - a_1} < \frac{r_1}{r_2}\left(2 - \frac{d_2}{d_1}\right). \tag{2.23}$$

Hypothesis $viii$ indicates that when $p = \rho\zeta_1(\bar{\mu})$ and $q = \rho\zeta_2(\bar{\mu})$, the following inequalities

$$r_1 p(1 - \frac{p}{k} - a_1 + a_1 q) \leq r_1 p(1 - a_1) \tag{2.24}$$

and

$$r_2(q-1)(q - q^2 - \alpha q - a_2 p) \leq -r_2(q - \alpha q - a_2 p) \tag{2.25}$$

must be satisfied. After simplification, (2.24) is equivalent to

$$a_1 k q \leq p. \tag{2.26}$$

Substitute $p = \rho\zeta_1(\bar{\mu})$ and $q = \rho\zeta_2(\bar{\mu})$ into (2.26), we have that

$$a_1 k \rho\zeta_2(\bar{\mu}) \leq \rho\zeta_1(\bar{\mu}). \tag{2.27}$$

We then substitute $\zeta_1(\bar{\mu}) = \gamma_1(\bar{\mu}) - \gamma_2(\bar{\mu})$ and $\zeta_2(\bar{\mu}) = r_2 a_2$ into (2.27) and have

$$a_1 k \rho r_2 a_2 \leq \rho\big(\gamma_1(\bar{\mu}) - \gamma_2(\bar{\mu})\big). \tag{2.28}$$

We have shown that $\gamma_1(\bar{\mu}) = d_1\bar{\mu}^2 + r_1(1-a_1)$ and $\gamma_2(\bar{\mu}) = d_2\bar{\mu}^2 + r_2(\alpha-1)$ earlier, so (2.28) can be written as

$$a_1 k\rho r_2 a_2 \leq \rho\big(d_1\bar{\mu}^2 + r_1(1-a_1) - d_2\bar{\mu}^2 - r_2(\alpha-1)\big). \tag{2.29}$$

Substitute $\bar{\mu} = \sqrt{\frac{r_1(1-a_1)}{d_1}}$ into (2.29), we get that

$$a_1 k\rho r_2 a_2 \leq \rho\left(d_1\frac{r_1(1-a_1)}{d_1} + r_1(1-a_1) - d_2\frac{r_1(1-a_1)}{d_1} - r_2(\alpha-1)\right),$$

which can be simplified and is equivalent to

$$\frac{a_1a_2k + \alpha - 1}{1-a_1} \leq \frac{r_1}{r_2}\left(2 - \frac{d_2}{d_1}\right). \tag{2.30}$$

On the other hand, (2.25) can be simplified and rewritten as

$$2q - q^2 - \alpha q - a_2 p \leq 0. \tag{2.31}$$

By substituting $p = \rho\zeta_1(\bar{\mu})$ and $q = \rho\zeta_2(\bar{\mu})$ into the above inequality, (2.31) becomes

$$2\rho\zeta_2(\bar{\mu}) - \big(\rho\zeta_2(\bar{\mu})\big)^2 - \alpha\rho\zeta_2(\bar{\mu}) - a_2\rho\zeta_1(\bar{\mu}) \leq 0. \tag{2.32}$$

By combining (2.18), (2.19) and (2.21), it follows that (2.32) is equivalent to

$$\frac{1 - r_2a_2\rho}{1-a_1} \leq \frac{r_1}{r_2}\left(2 - \frac{d_2}{d_1}\right). \tag{2.33}$$

The following inequality

$$\frac{1}{1-a_1} \leq \frac{r_1}{r_2}\left(2 - \frac{d_2}{d_1}\right) \tag{2.34}$$

can guarantee that (2.33) is satisfied for each positive ρ.

We note that the hypotheses *vii* and *viii* can be accepted when (2.30) and (2.34) hold concurrently, that is when

$$\begin{aligned} &\tfrac{d_2}{d_1} \leq 2, \\ &\max\left\{\tfrac{1}{1-a_1}, \tfrac{a_1a_2k+\alpha-1}{1-a_1}\right\} \leq \tfrac{r_2}{r_1}\left(2 - \tfrac{d_2}{d_1}\right). \end{aligned} \tag{2.35}$$

Thus Hypotheses 2.1 can be satisfied when all the parameters are positive, $0 < a_1 < 1$ and (2.35) all hold simultaneously. When all those conditions are satisfied, the cooperative system (2.13) is linearly determinate. Since the cooperative system (2.13) is equivalent to the original competition model (2.1), the above sufficient conditions for the linear determinacy of the cooperative system can be also applied to the competition model (2.1). $\square$

2.5 Existence of Traveling Waves

Li and Zhang [18] have established the existence of traveling wave solutions for the delayed cooperative recursions and reaction-diffusion models that are allowed to have more than two equilibria. In this section, we will apply Theorem 2.2 in [18] to the reaction-diffusion system (2.13) and show the existence of traveling wave solutions connnecting a mono-culture equilibrium and a coexistence equilibrium or a different mono-culture equilibrium in (2.1).

We have shown in Section 2.3 and 2.4 the global stability of $\hat{E}$ and that the invasion of the unstable state $\hat{E}_1 = (0,0)$ always produces a transition toward $\hat{E} = (\hat{p}, \hat{q})$. And we note that if $\hat{E}_2^*$ exists, then $v_2^* > \alpha$ since

$$\begin{aligned} v_2^* - \alpha =& \frac{1 + \alpha + a_1 a_2 k + \sqrt{(1 + \alpha + a_1 a_2 k)^2 - 4(\alpha + a_2 k)}}{2} - \alpha \\ =& \frac{1 - \alpha + a_1 a_2 k + \sqrt{(1 + \alpha + a_1 a_2 k)^2 - 4(\alpha + a_2 k)}}{2} \\ >& 0. \end{aligned}$$

This further implies

$$1 - v_2^* < 1 - \alpha.$$

Meanwhile, it is easy to see that $\hat{E}_2^*$ locates on the lower left side of $\hat{E}_1^*$, so $\hat{E}_2^* = (u_2^*, 1 - v_2^*)$ is vertically the lowest equlibrium besides $\hat{E}_1 = (0,0)$. With that being said, $\hat{E}_2^* = (u_2^*, 1 - v_2^*)$ is the equilibrium state which is the cloest to $(0,0)$ in the sense that there is no other constant equilibrium in the rectangle with vertices $(0,0)$, $(u_2^*, 1-v_2^*)$, $(0, 1-v_2^*)$ and $(u_2^*, 0)$ in (2.13).

Theorem 2.3. *Assume that* $0 < a_1 < 1$. *Let* c_+^* *be defined by (1.16) where* Q *is replaced by its time one solution map* Q_1. *Then for* $c \geq c_+^*$ *and* $c \neq \left(\alpha - \frac{1}{2}\right)\sqrt{2d_2r_2}$, *the model (2.1) has a monotone traveling wave solution* $W(x-ct)$ *connecting* E_1 *to* E *defined by (2.15), and such a traveling wave does not exist if* $c < c_+^*$. *In particular, when the spreading speed of system (2.1) is linearly determined, such a nonincreasing traveling wave solution exists if and only if* $c \geq c_+^*$.

Proof. We shall prove this theorem by considering the cooperative system (2.13) in the following two cases:

Case i: If (2.4) is satisfied, that is when the two coexistence equilibria both exist, then $\hat{E}_2^* = (u_2^*, 1-v_2^*)$ is the closest equilibrium to $(0,0)$ in the sense that there is no other constant equilibruim (ρ_1, ρ_2) which satisfies $0 < \rho_1 \leq u_2^*$ and $0 < \rho_2 \leq 1 - v_2^*$. According to Theorem 2.1 and 2.2 in [18], it suffices to show the cooperative system (2.13) has a nonincreasing traveling wave solution $W(x-ct)$ with $W(+\infty) = 0$ and $W(-\infty) = (u_2^*, 1-v_2^*)$ if and only if $c \geq c_+^*$. So we only need to show that for any $c \geq c_+^*$ and $c \neq \left(\alpha - \frac{1}{2}\right)\sqrt{2d_2r_2}$, there is no nonincreasing traveling wave solution of (2.13) which connects $(0,0)$ with either $(0,1)$ or $(0, 1-\alpha)$ when the two coexistence equilibria do not exist.

Case ii: When the two coexistence equilibria $\hat{E}_1^*$ and $\hat{E}_2^*$ do not exist, we assume there exists a nonincreasing traveling wave solution $(p(x-ct), q(x-ct))$ of (2.13) with $c \geq c_+^*$, which connects $(0,0)$ with either $(0,1)$ or $(0,1-\alpha)$, then $p = 0$ and $q(x-ct)$ is a nonincreasing traveling wave solution of

$$q_t = d_2 q_{xx} + r_2 q(1-q)(q-\nu), \tag{2.36}$$

given that $\nu = 1-\alpha$. Hadeler et al. [88] showed that there exists a unique traveling wave solution of (2.36) connecting $(0,0)$ and $(0,1)$ with a unique wave velocity of

c_1, where

$$c_1 = \left(\frac{1}{2} - \nu\right)\sqrt{2d_2r_2} = \left(\alpha - \frac{1}{2}\right)\sqrt{2d_2r_2}.$$

Thus if $c \geq c_+^*$ and $c \neq \left(\alpha - \frac{1}{2}\right)\sqrt{2d_2r_2}$, there is no traveling wave solution of (2.13) that connects $(0,0)$ and $(0,1)$.

Especially, when the linear determinacy conditions for system (2.1) hold, we have

$$c_+^* = \bar{c} = 2\sqrt{d_1r_1(1-a_1)}.$$

Thus, we only need to show that

$$c_+^* > c_1 = \left(\frac{1}{2} - \nu\right)\sqrt{2d_2r_2}, \tag{2.37}$$

which guarantees $c \neq c_1$ as long as $c \geq c_+^*$. We shall prove (2.37) by considering the following two cases:

Case i: When $\frac{1}{2} < \nu < 1$, (2.37) is simply true since $c_+^* > 0$.

Case ii: When $0 < \nu < \frac{1}{2}$, condition (2.16) implies that

$$r_1(1-a_1) \geq \frac{r_2}{2 - \frac{d_2}{d_1}},$$

so that

$$c_+^* = \bar{c} \geq 2\sqrt{\frac{d_2r_2}{2 - \frac{d_2}{d_1}}} = \sqrt{\frac{4d_1^2r_2}{2d_1 - d_2}}.$$

On the other hand, we have

$$c_1 = \left(\frac{1}{2} - \nu\right)\sqrt{2d_2r_2} < \sqrt{\frac{d_2r_2}{2}}.$$

Thus we have

$$\begin{aligned}\left(\frac{c_+^*}{c_1}\right)^2 &> \frac{4d_1^2 r_2}{2d_1 - d_2} \cdot \frac{2}{d_2 r_2} \\ &= \frac{8d_1^2}{(2d_1 - d_2)d_2} \\ &> \frac{8d_1^2}{2d_1(2d_1 - d_2)} \\ &= \frac{4d_1}{2d_1 - d_2} \\ &> \frac{4d_1}{2d_1} \\ &> 1,\end{aligned}$$

that is,

$$\left(\frac{1}{2} - \nu\right)\sqrt{2d_2 r_2} = c_1 < \bar{c} = c_+^*.$$

Thus we have proved that (2.37) is true.

Besides, we assume there exists a traveling wave solution connecting $(0,0)$ to the unstable source $(0,\nu)$, then it must spread at a unique wave speed which is negative. This is a contradiction with the fact that $c \geq c_+^* > 0$. Thus there is no such traveling wave solution which connects $(0,0)$ to $(0,\nu)$.

So we have completed the proof of Theorem 2.3 considering that the cooperative system (2.13) is equivalent to the competition model (2.1). □

CHAPTER 3
TWO-SPECIES DISCRETE-TIME SPATIO-TEMPORAL COMPETITION MODEL WITH ALLEE EFFECT

In this chapter we investigate the two-species discrete-time spatio-temporal competition model with Allee effect, which serves as an extension of the two-species discrete-time spatial spreading model (1.19). Similarly as in Chapter 2, we demonstrate the local stability of each equilibrium, and the global stability of a coexistence equilibrium and a mono-culture equilibrium. We will discuss the spatial transitions from a mono-culture equilibrium to an all-species coexistence equilibrium or a different mono-culture equilibrium. With certain assumptions, we provide the sufficient conditions for the linear determinacy of the model as well as a formula for the spreading speed of the spatial transitions based on the linear determinacy. We will also show the existence of traveling wave solutions based on these spatial transitions.

3.1 The Model

We introduce the two-species discrete-time spatio-temporal competition model based on the integro-difference equations:

$$\begin{aligned} p_{n+1}(x) &= \int_{R^1} \tfrac{(1+\rho_1)p_n(x-y)}{1+\rho_1(p_n(x-y)+\alpha_1 q_n(x-y))} k_1(y,dy), \\ q_{n+1}(x) &= \int_{R^1} \tfrac{(1+\rho_2)q_n^2(x-y)}{1+\rho_2(q_n(x-y)+\alpha_2 p_n(x-y))^2} k_2(y,dy) \end{aligned} \tag{3.1}$$

given that all parameters are positive and $\rho_2 > 1$. $p_n(x)$ and $q_n(x)$ describe the population densities of two species at time n and position x respectively, $k_1(y, dy)$ and $k_2(y, dy)$ are the dispersal kernals.

Note that this model assumes that the life cycle of the two species consists of a sedentary stage at which the two species are sedentary and compete locally by following the Beverton-Holt dynamics, and then the dispersal stage at which both species diffuse without growing or dying.

The dispersal kernals $k_1(y, dy)$ and $k_2(y, dy)$ are probability measures for the dispersals of the two species and satisfy

$$\int_{R^1} k_i(y, dy) = 1, \quad i = 1, 2. \tag{3.2}$$

We assume that the dispersal kernals k_i have the symmetry property:

$$k_i(-y, dy) = k_i(y, dy). \tag{3.3}$$

Property (3.3) and the convolution forms of (3.1) are reflections of the fact that the dispersal is isotropic and the space is homogeneous in the sense that the growth and dispersal properties are the same at each point.

Existence of Allee Effect

The growth function of the second species q in (3.1) is given by

$$g(q) = \frac{(1 + \rho_2)q^2}{1 + \rho_2 q^2}, \tag{3.4}$$

with $g(0) = 0$, $g(\frac{1}{\rho_2}) = \frac{1}{\rho_2}$, and $g(1) = 1$. It indicates that the population has a negative growth rate when $0 < q < \frac{1}{\rho_2}$, and a positive growth rate when $\frac{1}{\rho_2} < q < 1$. Thus, the population q exhibits strong Allee effect with the critical population density $\frac{1}{\rho_2}$, where $\rho_2 > 1$.

Equilibria of the Model

In order to achieve the equilibria of the model (3.1), we need to solve the following system of equations:

$$\begin{array}{l} \frac{(1+\rho_1)p}{1+\rho_1(p+\alpha_1 q)} = p, \\ \frac{(1+\rho_2)q^2}{1+\rho_2(q+\alpha_2 p)^2} = q. \end{array} \tag{3.5}$$

Then we obtain the trivial equilibrium $E_0 = (0, 0)$, the mono-culture equilibrium $E_1 = (0, 1)$, $E_2 = (1, 0)$, $E_3 = (0, \frac{1}{\rho_2})$ and the coexistence equilibrium $E_1^* = (p_1^*, q_1^*)$, $E_2^* = (p_2^*, q_2^*)$, where

$$\begin{aligned}
q_1^* &= \tfrac{1+\rho_2-2\alpha_2\rho_2(1-\alpha_1\alpha_2)+\left((1+\rho_2)^2-4\rho_2(1-\alpha_1\alpha_2)(\alpha_2(1+\rho_2)+1-\alpha_1\alpha_2)\right)^{1/2}}{2\rho_2(1-\alpha_1\alpha_2)^2},\\
q_2^* &= \tfrac{1+\rho_2-2\alpha_2\rho_2(1-\alpha_1\alpha_2)-\left((1+\rho_2)^2-4\rho_2(1-\alpha_1\alpha_2)(\alpha_2(1+\rho_2)+1-\alpha_1\alpha_2)\right)^{1/2}}{2\rho_2(1-\alpha_1\alpha_2)^2},\\
p_i^* &= 1-\alpha_1 q_i^*,\ i = 1, 2.
\end{aligned}$$

Note that the coexsistence equilibria both exist when the following condition is satisfied:

$$\begin{aligned}
&2\sqrt{\rho_2(1-\alpha_1\alpha_2)^2(1+\rho_2\alpha_2^2)} < 1+\rho_2-2\rho_2\alpha_2(1-\alpha_1\alpha_2)\\
&< \min\{1+\rho_2\alpha_2^2+\rho_2(1-\alpha_1\alpha_2)^2, 2\rho_2(1-\alpha_1\alpha_2)^2\}.
\end{aligned} \tag{3.6}$$

Besides, since $q_1^* > q_2^*$ and $p_1^* < p_2^*$, it follows that E_1^* locates on the lower right side of E_2^* when they both exist.

3.2 Local Stability

In order to discuss the possible spatial transitions among all these equilibria, we study the local stability of each equilibrium by analyzing the corresponding characteristic equations of the following vector-valued function at each point:

$$\mathbf{g}(p, q) = \begin{pmatrix} \frac{(1+\rho_1)p}{1+\rho_1(p+\alpha_1 q)} \\ \frac{(1+\rho_2)q^2}{1+\rho_2(q+\alpha_2 p)^2} \end{pmatrix}. \tag{3.7}$$

At $E_0 = (0, 0)$, the Jacobian matrix of (3.7) is given by

$$J_{E_0} = \begin{pmatrix} 1+\rho_1 & 0 \\ 0 & 0 \end{pmatrix}.$$

The eigenvalues of the above matrix J_{E_0} are $\lambda_1 = 1+\rho_1$, $\lambda_2 = 0$. Since $\rho_1 > 0$, we have $|\lambda_1| = |1+\rho_1| > 1$, thus the equilibrium $E_0 = (0, 0)$ is a saddle.

At $E_1 = (0, 1)$, the Jacobian matrix of (3.7) is given by

$$J_{E_1} = \begin{pmatrix} \frac{1+\rho_1}{1+\alpha_1\rho_1} & 0 \\ -\frac{2\alpha_2\rho_2}{1+\rho_2} & \frac{2}{1+\rho_2} \end{pmatrix}.$$

The eigenvalues of the above matrix J_{E_1} are $\lambda_1 = \frac{1+\rho_1}{1+\alpha_1\rho_1}$, $\lambda_2 = \frac{2}{1+\rho_2}$. Assume $0 < \alpha_1 < 1$, then $|\lambda_1| = |\frac{1+\rho_1}{1+\alpha_1\rho_1}| > 1$. Note that $|\lambda_2| < 1$ since $\rho_2 > 1$. Thus the equilibrium $E_1 = (0, 1)$ is a saddle if $0 < \alpha_1 < 1$.

At $E_2 = (1, 0)$, the Jacobian matrix of (3.7) is given by

$$J_{E_2} = \begin{pmatrix} \frac{1}{1+\rho_1} & -\frac{\alpha_1\rho_1}{1+\rho_1} \\ 0 & 0 \end{pmatrix}.$$

The eigenvalues of the above matrix J_{E_2} are $\lambda_1 = \frac{1}{1+\rho_1}$, $\lambda_2 = 0$. Since $\rho_1 > 0$, we will have $|\lambda_1| = |\frac{1}{1+\rho_1}| < 1$ and $|\lambda_2| = 0 < 1$. So the equilibrium $E_2 = (1, 0)$ is a sink.

At $E_3 = (0, \frac{1}{\rho_2})$, the Jacobian matrix of (3.7) is given by

$$J_{E_3} = \begin{pmatrix} \frac{1+\rho_1}{1+\rho_1\frac{\alpha_1}{\rho_2}} & 0 \\ -\frac{2\alpha_2}{1+\rho_2} & \frac{2}{1+\frac{1}{\rho_2}} \end{pmatrix}.$$

The eigenvalues of the above matrix J_{E_3} are $\lambda_1 = \frac{1+\rho_1}{1+\rho_1\frac{\alpha_1}{\rho_2}}$, $\lambda_2 = \frac{2}{1+\frac{1}{\rho_2}}$. Given $\rho_2 > 1$, it follows that $|\lambda_2| = |\frac{2}{1+\frac{1}{\rho_2}}| > 1$. So the equilibrium $E_3 = (0, \frac{1}{\rho_2})$ is unstable in the case that $\rho_2 > 1$. Addtionally, it is a saddle if $0 < \alpha_1 < 1$.

It is difficult to determine the local stability of the coexistence equilibrium E_1^* by analyzing its corresponding Jabobian matrix. A later discussion in Section 3.3 indicates that E_1^* is globally asymptotically stable, which indicates E_1^* is locally stable as well. The global stability of E_1^* also implies that $E_2^* = (p_2^*, q_2^*)$ is unstable.

Table 3.1 exhibits a summary of the existence condition and the local stability of each equilibrium.

TABLE 3.1

Summary of Existence and Local Stability Criteria of Equilibria in Model (3.1)

Equilibrium	**Existence Condition**	**Stability Criteria**
E_0	always exists	always unstable
E_1	always exists	Unstable if $0 < \alpha_1 < 1$ Stable if $\alpha_1 > 1$
E_2	always exists	always stable
E_3	always exists	Unstable if $\rho_2 > 1$
E_1^*	When (3.6) holds	always stable
E_2^*	When (3.6) holds	always unstable

3.3 Global Stability

For the purpose of showing the existence of traveling wave solutions, we shall study the global stability of the mono-culture equilibrium $E_2 = (1, 0)$ and the coexistence equilibrium $E_1^* = (p_1^*, q_1^*)$. Before proceeding, we need the following lemmas.

LEMMA 3.1. *(Monotone Convergence Lemma) If a sequence of real numbers is increasing and bounded above, then its supremum is the limit; If a sequence of real numbers is decreasing and bounded below, then its infimum is the limit.*

LEMMA 3.2. *(Squeeze Lemma) Let I be an interval having the point a as a limit point. Let f, g and h be functions defined on I, except possibly at a itself. Suppose that for every x in I not equal to a, we have:*

$$g(x) \leq f(x) \leq h(x)$$

and also suppose that:

$$\lim_{x \to a} g(x) = \lim_{x \to a} h(x) = L.$$

Then

$$\lim_{x \to a} f(x) = L.$$

Lemma 3.3. *In the model (3.1), we denote the rectangle with the vertices* ${E_1}^* = (p_1^*, q_1^*)$*,* $E_1 = (0,1)$*,* $(0, q_1^*)$ *and* $(p_1^*, 1)$ *as* R_1*, and the rectangle with the vertices* $E_0 = (0,0)$*,* $E_1 = (0,1)$*,* $E_2 = (1,0)$ *and* $(1,1)$ *as* R_2*, then the following statements are valid:*

i. *If the two coexistence equilibria* ${E_1}^*$ *and* ${E_2}^*$ *both exist, then* R_1 *is an invariant set;*

ii. *If the coexistence equilibria* ${E_1}^*$ *and* ${E_2}^*$ *do not exist, then* R_2 *is an invariant set.*

Proof. We consider the corresponding difference equations of (3.1) given by the following:

$$\begin{aligned} p_{n+1}(x) &= \tfrac{(1+\rho_1)p_n(x)}{1+\rho_1(p_n(x)+\alpha_1 q_n(x))}, \\ q_{n+1}(x) &= \tfrac{(1+\rho_2)q_n^2(x)}{1+\rho_2(q_n(x)+\alpha_2 p_n(x))^2}. \end{aligned} \tag{3.8}$$

We shall prove this lemma by considering the following four different cases:

Case i: When $q_n(x) = 1$ and $0 < p_n(x) \le p_1^*$, then we have

$$\begin{aligned} q_{n+1}(x) =& \frac{1+\rho_2}{1+\rho_2\left(1+\alpha_2 p_n(x-y)\right)^2} \\ <& 1 \end{aligned}$$

since $1 + \rho_2\left(1+\alpha_2 p_n(x-y)\right) > 1$. This implies that any point starting from the upper edge of R_1 will move towards the inside of R_1.

Case ii: When $q_n(x) = q_1^*$ and $0 \le p_n(x) < p_1^*$, we have that

$$\begin{aligned} q_{n+1}(x) =& \frac{(1+\rho_2){q_1^*}^2}{1+\rho_2\left(q_1^*+\alpha_2 p_n(x)\right)^2} \\ >& \frac{(1+\rho_2){q_1^*}^2}{1+\rho_2\left(q_1^*+\alpha_2 p_1^*\right)^2} \\ =& q_1^*. \end{aligned} \tag{3.9}$$

Thus any point starting from the lower edge of R_1 will move towards the inside of R_1.

Case iii: When $p_n(x) = 0$ and $q_1^* \leq q_n(x) < 1$, then we have

$$p_{n+1}(x) = 0.$$

Thus any point starting from the left edge of R_1 will stay on this edge.

Case iv: When $p_n(x) = p_1^*$ and $q_1^* < q_n(x) \leq 1$, then we have

$$\begin{aligned} p_{n+1}(x) =& \frac{(1+\rho_1)p_n(x)}{1+\rho_1\left(p_n(x)+\alpha_1 q_n(x)\right)} \\ =& \frac{(1+\rho_1)p_1^*}{1+\rho_1\left(p_1^*+\alpha_1 q_n(x)\right)} \\ <& \frac{(1+\rho_1)p_1^*}{1+\rho_1(p_1^*+\alpha_1 q_1^*)} \\ =& p_1^*. \end{aligned}$$

So any point starting from the right edge of R_1 will move towards the inside of R_1.

Thus it suffices to show that R_1 is an invariant set when the two coexistence equilibria exist. Similarly, we can prove that R_2 is an invariant set when the two coexistence equilibria do not exist. □

Lemma 3.4. *The change of variables*

$$u_n = p_n, v_n = 1 - q_n$$

converts the competition model (3.1) into the following system:

$$\begin{aligned} u_{n+1}(x) &= \int_{R^1} \tfrac{(1+\rho_1)u_n(x-y)}{1+\rho_1(\alpha_1+u_n(x-y)-\alpha_1 v_n(x-y))} k_1(y,dy), \\ v_{n+1}(x) &= \int_{R^1} \tfrac{\rho_2\alpha_2 u_n(x-y)(\alpha_2 u_n(x-y)+2-2v_n(x-y))+2v_n(x-y)-v_n^2(x-y)}{1+\rho_2(1-v_n(x-y)+\alpha_2 u_n(x-y))^2} k_2(y,dy). \end{aligned} \tag{3.10}$$

Then (3.10) is order-preserving in the biological range $0 \leq u_n \leq 1$, $0 \leq v_n \leq 1$.

Proof. To prove this lemma, we aim to show that increasing either u_n or v_n will lead to the increase of u_{n+1} and v_{n+1}.

Let

$$\begin{aligned} f(u_n,v_n) &= \tfrac{(1+\rho_1)u_n}{1+\rho_1(\alpha_1+u_n-\alpha_1 v_n)}, \\ g(u_n,v_n) &= \tfrac{\rho_2\alpha_2 u_n(\alpha_2 u_n+2-2v_n)+2v_n-{v_n}^2}{1+\rho_2(1-v_n+\alpha_2 {u_n}^2)}. \end{aligned} \tag{3.11}$$

Then we have

$$\begin{aligned}
f'_{u_n} =& \frac{(1+\rho_1)\,(1+\rho_1(\alpha_1+u_n-\alpha_1 v_n)) - \rho_1(1+\rho_1)u_n}{(1+\rho_1(\alpha_1+u_n-\alpha_1 v_n))^2} \\
=& \frac{(1+\rho_1)(1+\rho_1\alpha_1(1-v_n))}{(1+\rho_1(\alpha_1+u_n-\alpha_1 v_n))^2} \\
>& 0
\end{aligned}$$

since $0 \le v_n \le 1$. So $f(u_n, v_n)$ is increasing in u_n, and so is

$$u_{n+1}(x) = \int_{R^1} f(u_n, v_n)(x-y)k_1(y, dy).$$

Similarly, we have

$$\begin{aligned}
f'_{v_n} =& \frac{-(-\rho_1\alpha_1)}{(1+\rho_1(\alpha_1+u_n-\alpha_1 v_n)^2} \\
=& \frac{\rho_1\alpha_1}{(1+\rho_1(\alpha_1+u_n-\alpha_1 v_n)^2} \\
>& 0,
\end{aligned}$$

which implies that $f(u_n, v_n)$ is increasing in v_n, and so is

$$u_{n+1}(x) = \int_{R^1} f(u_n, v_n)(x-y)k_1(y, dy).$$

On the other hand, we have

$$\begin{aligned}
g'_{u_n} =& \frac{(2\rho_2{\alpha_2}^2 u_n + 2\rho_2\alpha_2 - 2\rho_2\alpha_2 v_n)(1+\rho_2(1-v_n+\alpha_2 u_n)^2)}{(1+\rho_2(1-v_n+\alpha_2 {u_n}^2))^2} \\
-& \frac{(\rho_2{\alpha_2}^2{u_n}^2 + 2\rho_2\alpha_2 u_n - 2\rho_2\alpha_2 u_n v_n + 2v_n - {v_n}^2)(2\rho_2\alpha_2(1-v_n+\alpha_2 u_n))}{(1+\rho_2(1-v_n+\alpha_2 {u_n}^2))^2} \\
=& \frac{2\rho_2\alpha_2(\alpha_2 u_n + 1 - v_n)(1+\rho_2 - 2v_n(1+\rho_2) + (1+\rho_2){v_n}^2)}{(1+\rho_2(1-v_n+\alpha_2 {u_n}^2))^2} \\
=& \frac{2\rho_2\alpha_2(\alpha_2 u_n + 1 - v_n)(1+\rho_2)(1-v_n)^2}{(1+\rho_2(1-v_n+\alpha_2 {u_n}^2))^2} \\
>& 0
\end{aligned}$$

since $0 \le v_n \le 1$ and all parameters are positive. Thus $g(u_n, v_n)$ is increasing in u_n, and so is

$$v_{n+1}(x) = \int_{R^1} g(u_n, v_n)(x-y)k_2(y, dy).$$

Similarly, we have

$$\begin{aligned}
g'_{v_n} =& \frac{(-2\rho_2\alpha_2 u_n + 2 - 2v_n)(1+\rho_2(1-v_n+\alpha_2 u_n)^2)}{(1+\rho_2(1-v_n+\alpha_2 {u_n}^2))^2} \\
&- \frac{(\rho_2{\alpha_2}^2{u_n}^2 - 2\rho_2\alpha_2 u_n - 2\rho_2\alpha_2 u_n v_n + 2v_n - {v_n}^2)(-2\rho_2(1-v_n+\alpha_2 u_n))}{(1+\rho_2(1-v_n+\alpha_2 {u_n}^2))^2} \\
=& \frac{-2\rho_2\alpha_2 u_n + 2 - 2v_n + 2\rho_2 - 2\rho_2 v_n + 2\rho_2\alpha_2 u_n}{(1+\rho_2(1-v_n+\alpha_2 {u_n}^2))^2} \\
=& \frac{2(1+\rho_2)(1-v_n)}{(1+\rho_2(1-v_n+\alpha_2 {u_n}^2))^2} \\
\geq& 0
\end{aligned}$$

when $0 \leq v_n \leq 1$. Note that

$$g'_{v_n} = 0$$

when $v_n = 1$. Hence $g(u_n, v_n)$ is increasing in v_n, and so is

$$v_{n+1}(x) = \int_{R^1} g(u_n, v_n)(x-y)k_2(y, dy).$$

Thus we have shown that increasing either u_n or v_n will lead to the increase of u_{n+1} and v_{n+1}, that is, (3.10) is order-preserving in the biological range $0 \leq u_n \leq 1$ and $0 \leq v_n \leq 1$. □

We use $\hat{E}_0$, $\hat{E}_1$, $\hat{E}_2$, $\hat{E}_3$, $\hat{E}_1^*$ and $\hat{E}_2^*$ to denote the equilibria of the coorperative system (3.10), and we have the following mapping of the equilibria from the competition model (3.1) to the cooperative system as shown below:

$$\begin{aligned}
&E_0 = (0,0) \longrightarrow \hat{E}_0 = (0,1), \\
&E_1 = (0,1) \longrightarrow \hat{E}_1 = (0,0), \\
&E_2 = (1,0) \longrightarrow \hat{E}_2 = (1,1), \\
&E_3 = (0, \tfrac{1}{\rho_2}) \longrightarrow \hat{E}_3 = (0, 1-\tfrac{1}{\rho_2}), \\
&E_1^* = (p_1^*, q_1^*) \longrightarrow \hat{E}_1^* = (p_1^*, 1-q_1^*), \\
&E_2^* = (p_2^*, q_2^*) \longrightarrow \hat{E}_2^* = (p_2^*, 1-q_2^*).
\end{aligned}$$

In the cooperative system (3.10), if we denote the rectangle with vertices $(0,0)$, $(0, 1-q_1^*)$, $(p_1^*, 1-q_1^*)$ and $(p_1^*, 0)$ by $\hat{R}_1$, and denote the rectangle with vertices $(0, 0)$, $(0, 1)$, $(1, 1)$ and $(1, 0)$ by $\hat{R}_2$, then it follows that $\hat{R}_1$ is an invariant set when the two coexistence equilibria exist, and $\hat{R}_2$ is an invariant set when the two coexistence equilibria do not exist. This is because the cooperative system (3.10) is equivalent to the original competition model (3.1).

THEOREM 3.1. *In the model (3.1), assume that* $0 < \alpha_1 < 1$. *Let* E_2 *and* E_1^* *be defined as in Section 3.1, then the following statements are valid:*

i. *If the two coexistence equilibria* E_1^* *and* E_2^* *both exist, then* E_1^* *is globally asymptotically stable;*

ii. *If the two coexistence equilibria* E_1^* *and* E_2^* *do not exist, then the mono-culture equilibrium* E_2 *is globally asymptotically stable.*

Proof. We consider the coorperative system (3.10) which is equivalent to the original competition model (3.1), then we want to first show that the equilibrium $\hat{E}_1^* = (p_1^*, 1 - q_1^*)$ is globally asymptotically stable when the two coexistence equilibria both exist.

Let λ_1 be the principal eigenvalue of the Jacobian matrix of (3.11) at $(0, 0)$, and denote the eigenvector corresponds to λ_1 by ζ_1, then $\lambda_1 > 1$ and ζ_1 has two elements which have the same signs. Inside the reactangle $\hat{R}_1$, let $\{\dot{E}_i\}_{i=0}^{\infty} = \{(\dot{p}_i, \dot{q}_i)\}_{i=0}^{\infty}$ be a sequence of solutions with $p_i > 0$ and $q_i > 0$ such that $(\dot{p}_0, \dot{q}_0)$ is on the direction of ζ_1 and that

$$\begin{pmatrix} \dot{p}_0 \\ \dot{q}_0 \end{pmatrix} - \begin{pmatrix} 0 \\ 0 \end{pmatrix} \leq \begin{pmatrix} \varepsilon \\ \epsilon \end{pmatrix}$$

for any sufficiently small $\varepsilon > 0$ and $\epsilon > 0$, i.e., $\dot{E}_0 = (\dot{p}_0, \dot{q}_0)$ is extremely close to the origin $\mathbf{0}$. Let Q be the operator of the system of equations (3.11), then the linear approximation theory indicates that

$$\dot{E}_1 := Q(\dot{E}_0) \approx Q(\mathbf{0}) + \lambda_1(\dot{E}_0 - \mathbf{0}) > \dot{E}_0,$$

that is,

$$\begin{pmatrix} \dot{p}_0 \\ \dot{q}_0 \end{pmatrix} \le \begin{pmatrix} \dot{p}_1 \\ \dot{q}_1 \end{pmatrix}.$$

By induction, we have

$$\begin{pmatrix} \dot{p}_0 \\ \dot{q}_0 \end{pmatrix} \le \begin{pmatrix} \dot{p}_1 \\ \dot{q}_1 \end{pmatrix} \le \begin{pmatrix} \dot{p}_2 \\ \dot{q}_2 \end{pmatrix} \le ...$$

Since $\hat{R}_1$ is an invariant set, according to Lemma 3.1, we have that

$$\lim_{i\to\infty} \begin{pmatrix} \dot{p}_i \\ \dot{q}_i \end{pmatrix} = \begin{pmatrix} p_1^* \\ 1-q_1^* \end{pmatrix}.$$

Let (p_i, q_i) be any solution in $\hat{R}_1$ such that

$$\begin{pmatrix} \dot{p}_0 \\ \dot{q}_0 \end{pmatrix} \le \begin{pmatrix} p_0 \\ q_0 \end{pmatrix} \le \begin{pmatrix} p_1^* \\ 1-q_1^* \end{pmatrix}.$$

The system (3.10) is order-preserving, thus we have

$$\begin{pmatrix} \dot{p}_1 \\ \dot{q}_1 \end{pmatrix} \le \begin{pmatrix} p_1 \\ q_1 \end{pmatrix} \le \begin{pmatrix} p_1^* \\ 1-q_1^* \end{pmatrix}.$$

Induction then tells us that

$$\begin{pmatrix} \dot{p}_i \\ \dot{q}_i \end{pmatrix} \le \begin{pmatrix} p_i \\ q_i \end{pmatrix} \le \begin{pmatrix} p_1^* \\ 1-q_1^* \end{pmatrix}.$$

for $i = 0, 1, 2, ...$

Lemma 3.2 indicates that

$$\lim_{i\to\infty} \begin{pmatrix} p_i \\ q_i \end{pmatrix} = \begin{pmatrix} p_1^* \\ 1-q_1^* \end{pmatrix}.$$

Thus any solution (p_i, q_i) starting from the inside of $\hat{R}_1$ will eventually approach the coexistence equilibrium $\hat{E}_1^* = (p_1^*, 1-q_1^*)$. That is, $\hat{E}_1^*$ is globally asymptotically stable in (3.10), i.e., E_1^* is globally asymptotically stable in the model (3.1).

Similarly, we are able to show that $E_2 = (1, 0)$ is globally asymptotically stable when the two coexistence equilibria do not exist in (3.1).

$\square$

3.4 Spreading Speed and Linear Determinacy

In this section, we aim to provide the sufficient conditions for the linear determinacy of the model (3.1) by applying Theorem 3.1 in [2].

Assume that $0 < \alpha_1 < 1$, then the mono-culture equilibrium $E_1 = (0, 1)$ is unstable. The coexistence equilibrium $E_1^* = (p_1^*, q_1^*)$ exists and it is stable when the inequality (3.6) is satisfied. Note that $E_2 = (1, 0)$ is always stable.

We shall consider the spatial transition from $E_1 = (0, 1)$ to the target state

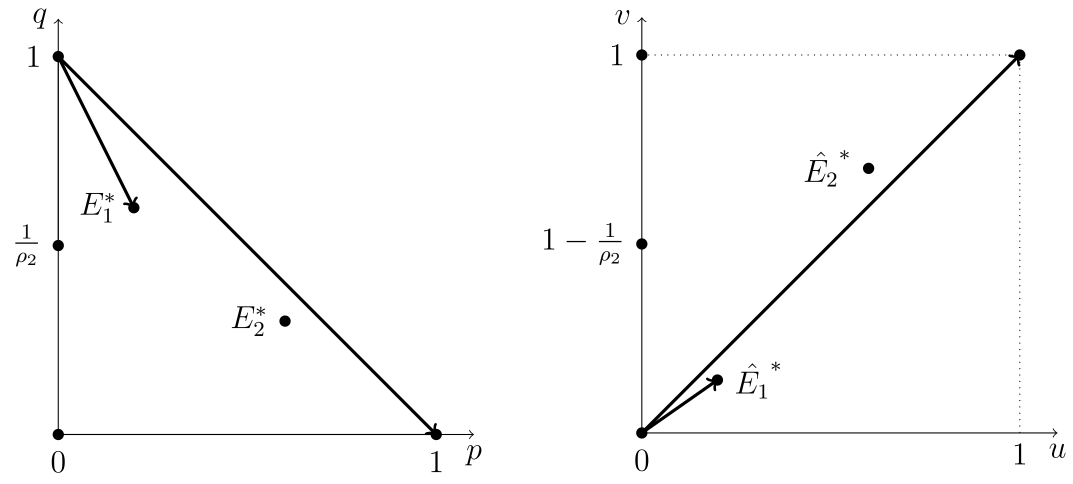
$$E := (p, q) = \begin{cases} E_1^* = (p_1^*, q_1^*) & \text{if } E_1^*,\ E_2^* \text{ both exist,} \\ \\ E_2 = (1, 0) & \text{if } E_1^*,\ E_2^* \text{ do not exist.} \end{cases} \tag{3.12}$$

In section 3.3 we have shown that the change of variables $u_n = p_n$ and $v_n = 1 - q_n$ converts the competiton model (3.1) into the cooperative system (3.10). Accordingly, we consider an equivalent transition in (3.10) from $\hat{E}_1 = (0, 0)$ to the target state

$$\hat{E} := (\hat{u}, \hat{v}) = \begin{cases} (p_1^*, 1 - q_1^*) & \text{if } \hat{E}_1^*,\ \hat{E}_2^* \text{ both exist,} \\ \\ (1, 1) & \text{if } \hat{E}_1^*,\ \hat{E}_2^* \text{ do not exist.} \end{cases} \tag{3.13}$$

Figure 3.1 displays the coordinates of each equilibrium and the spatial transitions before and after the change of variables.

Theorem 3.2. *Assume that* $0 < \alpha_1 < 1,\ \rho_2 > 1, \alpha_1\alpha_2 \leq 2$, *that the probability measures* k_1 *and* k_2 *in (3.1) are invariant under the reflection* $x \to -x$, *and that their moment generating functions* $\bar{k}_1(\mu)$ *and* $\bar{k}_2(\mu)$ *are finite for all* $\mu > 0$. *Let* $\bar{\mu}$



(a) (b)

FIGURE 3.1 – Equilibria and spatial transitions in the integro-difference system before and after the change of variables $u_n = p_n, v_n = 1 - q_n$: (a) Before the change of variables, when the two coexistence equilibria exist, the spatial transition is from $(0,1)$ to E_1^*; when the coexistence equilibria do not exist, the spatial transition is from $(0,1)$ to $(1,0)$. (b) After the change of variables, when the two coexistence equilibria exist, the spatial transition is from $(0,0)$ to $\hat{E}_1^*$; when the coexistence equilibria do not exist, the spatial tansition is from $(0,0)$ to $(1,1)$.

be the value of μ where the infimum in

$$\bar{c} = \inf_{\mu>0} \left\{ \mu^{-1} \ln \left(\frac{(1+\rho_1)\bar{k}_1(\mu)}{1+\alpha_1\rho_1} \right) \right\} \tag{3.14}$$

can be achieved. Assume that either

(a) $\bar{\mu}$ is finite, and

$$\frac{2+2\rho_2 max\{\alpha_1\alpha_2, 1\}}{1+\rho_2}\bar{k}_2(\bar{\mu}) \leq \frac{1+\rho_1}{1+\alpha_1\rho_1}\bar{k}_1(\bar{\mu}) \leq \frac{4\rho_2+2}{1+\rho_2}\bar{k}_2(\bar{\mu}), \tag{3.15}$$

or

(b) $\bar{\mu} = +\infty$, and there exists a sequence $\mu_\sigma \to \infty$ such that for each σ,

$$\frac{2+2\rho_2 max\{\alpha_1\alpha_2, 1\}}{1+\rho_2}\bar{k}_2(\mu_\sigma) \leq \frac{1+\rho_1}{1+\alpha_1\rho_1}\bar{k}_1(\mu_\sigma) \leq \frac{4\rho_2+2}{1+\rho_2}\bar{k}_2(\mu_\sigma). \tag{3.16}$$

Then the spreading speed c^* of the spatial transition from E_1 to E in the model (3.1) is equal to the spreading speed $\bar{c}$ defined by (3.14). That is, the model (3.1) is linearly determinate.

Proof. This theorem is a specialization of Weinberger and his coworkers' Theorem 3.1 in [2].

We aim to find a formula for the spreading speed $\bar{c}$ based on the linear determinacy first. We consider the cooperative system (3.10) after changing the variables in the original competition model (3.1), then the linearization of (3.10) at $(u, v) = (0, 0)$ is given by

$$\begin{aligned} u_{n+1}(x) &= \textstyle\int_{R^1} \frac{(1+\rho_1)u_n(x-y)}{1+\rho_1\alpha_1} k_1(y, dy), \\ v_{n+1}(x) &= \textstyle\int_{R^1} \frac{2\rho_2\alpha_2 u_n(x-y)+2v_n(x-y)}{1+\rho_2} k_2(y, dy). \end{aligned} \tag{3.17}$$

We need to find a matrix B_μ, which is defined to be the coefficient matrix for the vector of the linear combinations of α and β. We substitute $u = \alpha e^{-\mu x}$ and $v = \beta e^{-\mu x}$ into the right-hand side of (3.17), then multiply the result by $e^{\mu x}$ and write the vector as a matrix product $B_\mu \begin{pmatrix} \alpha \\ \beta \end{pmatrix}$, thus we have

$$B_\mu = \begin{pmatrix} \frac{1+\rho_1}{1+\alpha_1\rho_1}\bar{k}_1(\mu) & 0 \\ \frac{2\alpha_2\rho_2}{1+\rho_2}\bar{k}_2(\mu) & \frac{2}{1+\rho_2}\bar{k}_2(\mu) \end{pmatrix},$$

where $\bar{k}_i(\mu) = \int_{-\infty}^{+\infty} e^{\mu y} k_i(y, dy)$, $i = 1, 2$.

The principal eigenvalue of the first diagonal block of this upper triangular matrix B_μ is then given by

$$\lambda_1(\mu) = \frac{1+\rho_1}{1+\alpha_1\rho_1}\bar{k}_1(\mu). \tag{3.18}$$

An eigenvector of B_μ which corresponds to $\lambda_1(\mu)$ can be given by $\xi(\mu) = (\xi_1(\mu), \xi_2(\mu))$ where

$$\begin{aligned} \xi_1(\mu) &= \tfrac{1+\rho_1}{1+\alpha_1\rho_1}\bar{k}_1(\mu) - \tfrac{2}{1+\rho_2}\bar{k}_2(\mu), \\ \xi_2(\mu) &= \tfrac{2\alpha_2\rho_2}{1+\rho_2}\bar{k}_2(\mu). \end{aligned} \tag{3.19}$$

Lemma 2.3 in [2] indicates that the spreading speed of the linearized model (3.17) is given by

$$\bar{c} = \inf_{\mu>0} \left\{ \mu^{-1} \ln \lambda_1(\mu) \right\}. \tag{3.20}$$

By substituting (3.18) into (3.20), we have that

$$\bar{c} = \inf_{\mu>0} \left\{ \mu^{-1} \ln \left(\frac{1+\rho_1}{1+\alpha_1\rho_1} \bar{k}_1(\mu) \right) \right\}. \tag{3.21}$$

If the spreading speed of the model (3.1) is equal to the $\bar{c}$ in (3.21), i.e. $c^* = \bar{c}$, then the spreading speed of the model (3.1) is said to be linearly determined. In order to find the sufficient conditions for the linear determinacy, we shall make the following hypotheses which is a specialization of Hypotheses 2.1 in [2].

Hypotheses 3.1.

i. *There exist equilibria* $(0, 0)$ *and* (β_1, β_2) *with* β_1 *and* β_2 *both positive, and there is no other constant all-species coexistence equilibrium* (α_1, α_2) *such that* $0 < \alpha_1 \leq \beta_1$ *and* $0 < \alpha_2 \leq \beta_2$.

ii. *The model (3.10) is order-preserving.*

iii. *The equations in the model have no explicit dependence on either space or time.*

iv. $k_i(y, dy)$ *are nonnegative measures with* $k_i((-\infty, \infty)) = 1$, *and* $k_i(-y, dy) = k_i(y, dy)$ *for* $i = 1, 2$.

v. *The Jacobian matrix* B_μ *is in Frobenius form. The principal eigenvalue* $\lambda_1(0)$ *of its upper left diagonal block is greater than* 1, *and is strictly larger than the principal eigenvalues* $\lambda_\sigma(0)$ *of its other diagonal blocks.*

vi. B_0 *has at least one nonzero entry to the left of each of its diagonal blocks other than the uppermost one, i.e., the* $(2, 1)$ *element of* B_0 *is greater than* 0.

vii. *With* $\bar{\mu}$ *defined in the statement of Theorem 3.2, either*

   (a) $\bar{\mu}$ *is finite, then* $\lambda_1(\bar{\mu}) > \lambda_2(\bar{\mu})$, *and each of the right-hand sides of the system (3.10) evaluated at* $u = e^{-\bar{\mu}x}\xi_1(\bar{\mu})$, $v = e^{-\bar{\mu}x}\xi_2(\bar{\mu})$ *is no larger than* *the corresponding right-hand sides of the linearization (3.17) evaluated at the same values of* u *and* v*,*

or

(b) $\bar{\mu} = \infty$*, and there is a sequence* $\{\mu_\sigma\}$ *with* $\mu_\sigma \to \infty$ *as* $\sigma \to \infty$ *such that* $\lambda_1(\mu_\sigma) > \lambda_2(\mu_\sigma)$*, and each of the right-hand sides of the system (3.10) evaluated at* $u = e^{-\mu_\sigma x}\xi_1(\mu_\sigma)$*,* $v = e^{-\mu_\sigma x}\xi_2(\mu_\sigma)$ *is no larger than the corresponding right-hand sides of the linearization (3.17) evaluated at the same values of* u *and* v*.*

It is easy to verify that the cooperative system (3.10) satisfies hypothesis *i* to *iv*. Also note that we have shown that hypothesis *ii* is valid in Lemma 3.4.

For hypothesis *v* and *vi*, note that

$$B_0 = \begin{pmatrix} \frac{1+\rho_1}{1+\alpha_1\rho_1} & 0 \\ \frac{2\alpha_2\rho_2}{1+\rho_2} & \frac{2}{1+\rho_2} \end{pmatrix},$$

which implies that

$$\lambda_1(0) = \frac{1+\rho_1}{1+\alpha_1\rho_1}$$

and

$$\lambda_2(0) = \frac{2}{1+\rho_2}$$

are the principal eigenvalues of the first and second diagonal blocks of B_0.

It is easy to see that the $(2,1)$ element of B_0 is greater than 0 since all parameters are positive.

In order to make $\lambda_1(0) > 1$, α_1 must satisfy the following condition:

$$0 < \alpha_1 < 1. \tag{3.22}$$

Meanwhile, in order to make $\lambda_1(0) > \lambda_2(0)$, the following inequality must be satisfied:

$$\frac{1+\rho_1}{1+\alpha_1\rho_1} > \frac{2}{1+\rho_2}. \tag{3.23}$$

Since $\rho_2 > 1$, the right-hand side of (3.23) is less than 1. On the other hand, we have shown that the left-hand side of (3.23) is greater than 1, thus the inequality (3.23) is satisfied.

To validate hypothesis vii, we shall consider the following two cases:

Case i: When $\bar{\mu}$ is finite, we first want this inequality $\lambda_1(\bar{\mu}) > \lambda_2(\bar{\mu})$ to be satisfied. Note that $\xi_1(\bar{\mu}) = \lambda_1(\bar{\mu}) - \lambda_2(\bar{\mu})$, so a sufficient condition for the first part of this hypothesis actually takes the form of

$$\xi_1(\bar{\mu}) > 0.$$

On the other hand, a sufficient condition for the second part of this hypothesis takes the form of

$$\begin{aligned} &\xi_1(\bar{\mu}) \geq \alpha_1 \xi_2(\bar{\mu}), \\ &\xi_2(\bar{\mu}) \leq \alpha_2 \xi_1(\bar{\mu}) \leq 2\xi_2(\bar{\mu}), \end{aligned}$$

which is equivalent to

$$\begin{aligned} &\max\{\alpha_1, \tfrac{1}{\alpha_2}\}\xi_2(\bar{\mu}) \leq \xi_1(\bar{\mu}) \leq \tfrac{2}{\alpha_2}\xi_2(\bar{\mu}), \\ &\alpha_1\alpha_2 \leq 2. \end{aligned} \tag{3.24}$$

By substituting $\xi_1(\bar{\mu})$ and $\xi_2(\bar{\mu})$ from (3.19) into (3.24), we get the same conditions shown in (3.15). Besides, since $\xi_2(\bar{\mu}) > 0$, (3.24) also implies that $\xi_1(\bar{\mu}) > 0$. Thus the first part of hypothesis vii can be satisfied when (3.24) is true.

Case ii: When $\bar{\mu}$ is infinite, then there is a sequence $\{\mu_\sigma\}$ with $\mu_\sigma \to \infty$ such that similar sufficient conditions will be needed by replacing the $\bar{\mu}$ with μ_σ in each.

Since the cooperative system (3.10) is equivalent to the original competition model (3.1), the above sufficient conditions for the linear determinacy of the cooperative system can be also applied to the competition model (3.1). $\square$

3.5 Existence of Traveling Waves

In this section, we will apply Theorem 2.1 in [18] to the discrete-time model (3.10) and demonstrate the existence of traveling wave solutions connecting a mono-culture equilibrium and a coexistence equilibrium or a different mono-culture equilibrium in (3.1). Before proceeding, we need the following remark that has been proved in [28].

Remark 3.1. *By letting $u_n(x) = 0$, the cooperative system (3.10) will lead to the following second order integro-difference equation:*

$$v_{n+1}(x) = \int_{R^1} \frac{2v_n(x-y) - v_n^2(x-y)}{1 + \rho_2 \left(1 - v_n(x-y)\right)^2} k_2(y, dy). \tag{3.25}$$

Then there exists a unique traveling wave solution $W(x-nc)$ such that $W(-\infty) = 1$ and $W(+\infty) = 0$, with a unique wave speed c_1^*.

Theorem 3.3. *Assume that $0 < \alpha_1 < 1$ and $\rho_2 > 1$. Let c_+^* be defined by (1.16) and c_1^* be defined as the spreading speed of the spatial transition in (3.25). Then for $c \geq c_+^*$ and $c \neq c_1^*$, the model (3.1) has a monotone traveling wave $W(x-nc)$ connecting E_1 to E, and such a traveling wave does not exist if $c < c_+^*$.*

Proof. We shall prove this theorem by considering the cooperative system (3.10) in the following two cases:

Case i: When the two coexistence equilibria $\hat{E}_1^*$ and $\hat{E}_2^*$ both exist, Theorem 3.1 indicates that the equilibrium $\hat{E}_1^* = (p_1^*, 1 - q_1^*)$ is globally asymptotically attractive. If the unstable mono-culture equilibrium $\hat{E}_3 = (0, 1 - \frac{1}{\rho_2})$ locates vertically higher than the coexistence equilibrium $\hat{E}_1^*$, then $\hat{E}_1 = (0, 0)$ and $\hat{E}_1^*$ are the only equilibria in the rectangle $\hat{R}_1$. Thus it suffices to show that system (3.10) has a nonincreasing traveling wave solution $W(x - nc)$ with $W(+\infty) = 0$ and $W(-\infty) = (p_1^*, 1 - q_1^*)$ if and only if $c \geq c_+^*$. On the other hand, if the unstable mono-culture equilibrium $\hat{E}_3 = (0, 1 - \frac{1}{\rho_2})$ locates vertically lower than the coexistence equilibrium $\hat{E}_1^*$, then $\hat{E}_3$ is an extra equilibrium in the rectangle $\hat{R}_1$ besides $\hat{E}_1$ and $\hat{E}_1^*$. So we need to show that there is no nonincreasing traveling wave connecting $(0,0)$ to $\hat{E}_3$. We assume that for $c \geq c_+^*$ and $c \neq c_1^*$ there exists a nonincreasing traveling wave $w(x - nc)$ connecting $(0,0)$ to $\hat{E}_3$, then it follows that $c < 0$ since $\hat{E}_3$ is a source. Then this is a contradiction with that fact that $c \geq c_+^* > 0$. Thus there is no nonincreasing traveling wave connecting $(0,0)$ to $\hat{E}_3$ when $c \geq c_+^*$ and $c \neq c_1^*$.

Case ii: When the two coexistence equilibria $\hat{E}_1^*$ and $\hat{E}_2^*$ do not exist, we consider the rectangle $\hat{R}_2$. Note that there are two extra equilibria $\hat{E}_0 = (0,1)$ and $\hat{E}_3 = (0, 1 - \frac{1}{\rho_2})$ in $\hat{R}_2$ besides $(0,0)$ and $\hat{E}_1 = (1,1)$. Thus we need to show that there is no nonincreasing traveling wave connecting $(0,0)$ to either $\hat{E}_0 = (0,1)$ or $\hat{E}_3 = (0, 1 - \frac{1}{\rho_2})$ when $c \geq c_+^*$ and $c \neq c_1^*$.

Suppose that there exists a traveling wave solution $W(x - nc)$ connecting $(0,0)$ with $(0,1)$. According to Remark 3.1, the spreading speed of such a traveling wave is equal to c_1^*, and this spreading speed is unique. Hence as long as $c \neq c_1^*$, there is no such nonincreasing traveling wave solutions connecing $(0,0)$ with $(0,1)$.

On the other hand, if there exists a traveling wave solution $W(x - nc)$ connecting $(0,0)$ with $(0, 1 - \frac{1}{\rho_2})$, then its spreading speed must be negative, which is surely less than c_+^* since $c_+^* > 0$. Thus, there is no nonincreasing traveling wave solutions connecting $(0,0)$ with either $(0,1)$ or $(0, 1 - \frac{1}{\rho_2})$ when $c \geq c_+^*$ and $c \neq c_1^*$.

Note that the cooperative system (3.10) is equivalent to the competition model (3.1). Thus we have completed the proof of this theorem. $\square$

CHAPTER 4
TWO-SEX STAGE-STRUCTURED COMPETITION MODEL

In this chapter, we construct a two-sex stage-structured competition model with a birth pulse growth pattern, and carry out some initial analysis in the spreading speed of the model.

4.1 Model Formulation

Let M and F represent the number of adult males and females respectively. We assume that the contributions from the birth rates depend on the total population size $M + F$, that is, neither the males nor females are marriage dominant [35]. Barrying any demographic differences between the females and males, the sex ratio of the mating individuals, or the operational sex ratio, will reflect the sex ratio at birth. The birth sex ratio, in turn, is constrained to an evolutionally stable value, typically 0.5 due to the frequency-dependent advantage of producing the rarer sex [39]. With λ representing the instantaneous birth rate, this simple marriage function below will be applied into the model:

$$\Lambda(M, F) = \frac{1}{2}\lambda(M + F). \tag{4.1}$$

We consider a two-sex population with two development stages: a reproductive stage and a non-reproductive stage. At the reproductive stage, adult males and females disperse with the diffusion coefficients d_1 and d_2, they mate and give birth to the juveniles by following the marriage function given by (4.1). The juvenile males and females also diffuse at this stage, however, with relatively smaller diffusion coefficients d_3 and d_4 respectively. We assume that outside a reproduction season mortality takes its toll for adult male and female populations. As a result, only juveniles born from the reproductive stage survive and continue to disperse with the diffusion coefficients d_5 and d_6. Let $u_{n+1}(x)$ and $v_{n+1}(x)$ denote the density of the male and female populations at point x at the beginning of the reproductive stage in the $(n+1)$th year, then they are equal to the population density of the males and females at the end of last year's non-reproductive stage. In both stages, adults and juveniles die continuously due to the interaction of the population with the environment, as well as the competition between individuals which follows the mass action law with β and γ describing the effect of competition.

We assume that the reproductive stage is from time 0 to τ, and the non-reproductive stage is from time τ to 1, where $0 < \tau < 1$ with τ is closer to 0. So the reproductive stage is relatively shorter than the non-reproductive stage. Then the mathematical model that describes the spatial dynamics of the two-sex population in a unbounded space is given by

Reprodutive Stage:

$$\begin{aligned}
&u_t = d_1 u_{xx} - \alpha_1 u - \gamma_1 u^2 - \beta_1 uv,\\
&v_t = d_2 v_{xx} - \alpha_2 v - \gamma_2 v^2 - \beta_2 uv,\\
&m_t = d_3 m_{xx} + \tfrac{1}{2}\lambda(u+v) - \alpha_3 m - \gamma_3 m^2 - \beta_3 mf,\\
&f_t = d_4 f_{xx} + \tfrac{1}{2}\lambda(u+v) - \alpha_4 f - \gamma_4 f^2 - \beta_4 mf,\\
&u(x,0) = M_n(x),\\
&v(x,0) = F_n(x),\\
&m(x,0) = 0,\\
&f(x,0) = 0.
\end{aligned} \tag{4.2}$$

Non-Reproductive Stage:

$$\begin{aligned}
&M_t = d_5 M_{xx} - \alpha_5 M - \gamma_5 M^2 - \beta_5 MF,\\
&F_t = d_6 F_{xx} - \alpha_6 F - \gamma_6 F^2 - \beta_6 MF,\\
&M(x,\tau) = m(x,\tau),\\
&F(x,\tau) = f(x,\tau),\\
&u_{n+1}(x) = M(x,1),\\
&v_{n+1}(x) = F(x,1).
\end{aligned} \tag{4.3}$$

All parameters are assumed to be positive. Table 4.1 describes each parameter in the model.

In this model, the reproduction is assumed to occur only once a year, as we can see in many mannal species or the spawing season for many fish species. The model can be used to study the case that impulsive harvesting occurs periodically in a continuously growing and dispersing two-sex population. For example, it can be employed to describe the situation that outside the winter the population dynamics is governed by reaction-diffusion equations with certain mating pair formation, and during the winter the population stops reproducing but continues moving, and the population of the following season is recruited from the individuals that survive the winter.

4.2 The Linearization

In order to obtain the formula for the spreading speed in the two-sex model based on the linear determinacy, we consider the linearization of (4.2) and (4.3) at

TABLE 4.1

Two-Sex Model Parameter Descriptions

Parameter	Description of Parameter
$u(x,t), v(x,t)$	population density of adult males and females at reproductive stage at time t and location x
$m(x,t), f(x,t)$	population density of juvenile males and females at reproductive stage at time t and location x
$M(x,t), F(x,t)$	population density of young adult males and females at non-reproductive stage at time t and location x
d	diffusion coefficient
α	death rate
γ	coefficient of competition between individuals in the same group
β	coefficient of competition between genders
τ	time separation of reproductive stage and non-reproductive stage
λ	instantaneous birth rate

0 as shown below:

$$
\begin{aligned}
&u_t = d_1 u_{xx} - \alpha_1 u,\\
&v_t = d_2 v_{xx} - \alpha_2 v,\\
&m_t = d_3 m_{xx} + \tfrac{1}{2}\lambda(u+v) - \alpha_3 m,\\
&f_t = d_4 f_{xx} + \tfrac{1}{2}\lambda(u+v) - \alpha_4 f,\\
&M_t = d_5 M_{xx} - \alpha_5 M,\\
&F_t = d_6 F_{xx} - \alpha_6 F,\\
&u(x,0) = M_n(x),\\
&v(x,0) = F_n(x),\\
&m(x,0) = 0,\\
&f(x,0) = 0,\\
&M(\tau,x) = m(\tau,x),\\
&F(\tau,x) = f(\tau,x),\\
&u_{n+1}(x) = M(1,x),\\
&v_{n+1}(x) = F(1,x).
\end{aligned}
\tag{4.4}
$$

To get the spreading speed, we solve the linearized system (4.4) and then get the linearized moment generating matrix. We start by first solving the following equations in (4.4):

$$
\begin{aligned}
u_t &= d_1 u_{xx} - \alpha_1 u,\\
v_t &= d_2 v_{xx} - \alpha_2 v
\end{aligned}
\tag{4.5}
$$

with the initial conditions

$$
\begin{aligned}
u(x,0) &= M_n(x),\\
v(x,0) &= F_n(x).
\end{aligned}
$$

Before proceeding, we need the following remark.

Remark 4.1. *Let $\hat{u}(k,t)$ and $\hat{v}(k,t)$ denote the variable $v(x,t)$ and $v(x,t)$ respectively after the Fourier transformation, then*

$$
\begin{aligned}
\widehat{u_t}(k,t) &= \tfrac{\partial}{\partial t}\hat{u}(k,t),\\
\widehat{u_{xx}}(k,t) &= (ik)^2\hat{u}(k,t).
\end{aligned}
\tag{4.6}
$$

By Remark 4.1, after applying the Fourier transform, the u - equation in (4.5) turns into

$$\frac{\partial}{\partial t}\hat{u}(k,t) = d_1(ik)^2\hat{u}(k,t) - \alpha_1\hat{u}(k,t) \tag{4.7}$$

with the initial condition

$$\hat{u}(k,0) = \widehat{M_n}(k).$$

Equation (4.7) can be easily solved and we have

$$\hat{u}(k,t) = \widehat{M_n}(k)e^{-(d_1k^2+\alpha_1)t}. \tag{4.8}$$

By applying the inverse Fourier transform on $\hat{u}(k,t)$, we have that

$$\begin{aligned} u(x,t) &= \left(\widehat{M_n}(k)e^{-(d_1k^2+\alpha_1)t}\right)^{\vee} \\ &= \frac{1}{\sqrt{2\pi}}\int_{-\infty}^{\infty} M_n(\varepsilon)e^{-\frac{(x-\varepsilon)^2}{4d_1t}-\alpha_1 t}\cdot\frac{1}{\sqrt{2d_1t}}d\varepsilon \\ &= \frac{1}{2\sqrt{\pi d_1 t}}\int_{-\infty}^{\infty} M_n(\varepsilon)e^{-\frac{(x-\varepsilon)^2}{4d_1t}-\alpha_1 t}d\varepsilon. \end{aligned}$$

And $v(x,t)$ can be solved in a similar way. Thus the solutions of (4.5) are given by:

$$\begin{aligned} u(x,t) &= \tfrac{1}{2\sqrt{\pi d_1 t}}\textstyle\int_{-\infty}^{\infty} M_n(\varepsilon)e^{-\frac{(x-\varepsilon)^2}{4d_1t}-\alpha_1 t}d\varepsilon, \\ v(x,t) &= \tfrac{1}{2\sqrt{\pi d_2 t}}\textstyle\int_{-\infty}^{\infty} F_n(\varepsilon)e^{-\frac{(x-\varepsilon)^2}{4d_2t}-\alpha_2 t}d\varepsilon. \end{aligned} \tag{4.9}$$

Then we consider the following equations in (4.4):

$$\begin{aligned} m_t &= d_3m_{xx} + \tfrac{1}{2}\lambda(u+v) - \alpha_3 m, \\ f_t &= d_4m_{xx} + \tfrac{1}{2}\lambda(u+v) - \alpha_4 f \end{aligned} \tag{4.10}$$

with the initial conditions

$$m(x,0) = 0,$$

$$f(x,0) = 0.$$

By applying the Fourier transform with respect to x, the m - equation in (4.10) turns into

$$\frac{\partial}{\partial t}\hat{m}(k,t) = d_3(ik)^2\hat{m}(k,t) + \frac{1}{2}\lambda\left(\hat{u}(k,t)+\hat{v}(k,t)\right) - \alpha_3\hat{m}(k,t) \tag{4.11}$$

with this initial condition

$$\hat{m}(k,0) = 0.$$

Equation (4.11) can be solved as

$$\hat{m}(k,t) = \int_0^t \frac{1}{2}\lambda\left(\hat{u}(k,\tau_1) + \hat{v}(k,\tau_1)\right)e^{-(d_3k^2+\alpha_3)(t-\tau_1)}d\tau_1. \tag{4.12}$$

By applying the inverse Fourier transform to $\hat{m}(k,t)$, we have that

$$\begin{aligned} m(x,t) &= \int_0^t \left(\frac{1}{2}\lambda\left(\hat{u}(k,\tau_1) + \hat{v}(k,\tau_1)\right)e^{-(d_3k^2+\alpha_3)(t-\tau_1)}\right)^{\vee} d\tau_1 \\ &= \frac{1}{\sqrt{2\pi}}\int_0^t d\tau_1 \int_{-\infty}^{\infty} \frac{1}{2}\lambda\left(u(\xi,\tau_1) + v(\xi,\tau_1)\right)e^{-\frac{(x-\xi)^2}{4d_3(t-\tau_1)}-\alpha_3(t-\tau_1)}\frac{d\xi}{\sqrt{2d_3(t-\tau_1)}} \\ &= \frac{\lambda}{4\sqrt{\pi d_3(t-\tau_1)}}\int_0^t d\tau_1 \int_{-\infty}^{\infty} \left(u(\xi,\tau_1) + v(\xi,\tau_1)\right)e^{-\frac{(x-\xi)^2}{4d_3(t-\tau_1)}-\alpha_3(t-\tau_1)}d\xi. \end{aligned}$$

$f(x,t)$ can be solved in a similar way. And we have the solutions of (4.10) as the following:

$$\begin{aligned} m(x,t) &= \textstyle\int_0^t d\tau_1 \int_{-\infty}^{\infty} K_3(x-\xi,t-\tau_1)\left(u(\xi,\tau_1) + v(\xi,\tau_1)\right)d\xi, \\ f(x,t) &= \textstyle\int_0^t d\tau_1 \int_{-\infty}^{\infty} K_4(x-\xi,t-\tau_1)\left(u(\xi,\tau_1) + v(\xi,\tau_1)\right)d\xi \end{aligned} \tag{4.13}$$

where $K_i(x,t) = \frac{\lambda}{4\sqrt{\pi d_i t}}e^{-\frac{x^2}{4d_it}-\alpha_i t}, i = 3, 4.$

Then we solve the last two equations in system (4.4):

$$\begin{aligned} M_t &= d_5M_{xx} - \alpha_5 M, \\ F_t &= d_6M_{xx} - \alpha_6 F \end{aligned} \tag{4.14}$$

with the initial conditions

$$\begin{aligned} M(x,\tau) &= m(x,\tau), \\ F(x,\tau) &= f(x,\tau). \end{aligned}$$

After applying the Fourier transform with respect to x, the M - equation in (4.14) becomes

$$\frac{\partial}{\partial t}\hat{M}(k,t) = d_5(ik)^2\hat{M}(k,t) - \alpha_5\hat{M}(k,t) \tag{4.15}$$

with

$$\hat{M}(k,\tau) = \hat{m}(k,\tau).$$

The equation (4.15) can be solved as

$$\hat{M}(k,t) = \hat{m}(k,\tau)e^{-(d_5k^2+\alpha_5)(t-\tau)}. \tag{4.16}$$

To get $M(x,t)$, we need to apply the inverse Frourier transform to (4.16), and $F(x,t)$ can be solved in a similar way. Thus we have the solutions of system (4.14) as the following:

$$\begin{aligned}
M(x,t) &= \tfrac{1}{2\sqrt{\pi d_5(t-\tau)}} \int_{-\infty}^{\infty} m(\tau,\delta)e^{-\frac{(x-\delta)^2}{4d_5(t-\tau)}-\alpha_5(t-\tau)}d\delta,\\
F(x,t) &= \tfrac{1}{2\sqrt{\pi d_6(t-\tau)}} \int_{-\infty}^{\infty} f(\tau,\delta)e^{-\frac{(x-\delta)^2}{4d_6(t-\tau)}-\alpha_6(t-\tau)}d\delta.
\end{aligned}$$

In summary, the solutions of the linearization system (4.4) are given by

$$\begin{aligned}
u(x,t) &= \tfrac{1}{2\sqrt{\pi d_1 t}} \int_{-\infty}^{\infty} M_n(\varepsilon)e^{-\frac{(x-\varepsilon)^2}{4d_1t}-\alpha_1 t}d\varepsilon,\\
v(x,t) &= \tfrac{1}{2\sqrt{\pi d_2 t}} \int_{-\infty}^{\infty} F_n(\varepsilon)e^{-\frac{(x-\varepsilon)^2}{4d_2t}-\alpha_2 t}d\varepsilon,\\
m(x,t) &= \textstyle\int_0^t d\tau_1 \int_{-\infty}^{\infty} K_3(x-\xi,t-\tau_1)\left(u(\xi,\tau_1)+v(\xi,\tau_1)\right)d\xi,\\
f(x,t) &= \textstyle\int_0^t d\tau_1 \int_{-\infty}^{\infty} K_4(x-\xi,t-\tau_1)[(u(\xi,\tau_1)+v(\xi,\tau_1))\,d\xi,\\
M(x,t) &= \tfrac{1}{2\sqrt{\pi d_5(t-\tau)}} \int_{-\infty}^{\infty} m(\delta,\tau)e^{-\frac{(x-\delta)^2}{4d_5(t-\tau)}-\alpha_5(t-\tau)}d\delta,\\
F(x,t) &= \tfrac{1}{2\sqrt{\pi d_6(t-\tau)}} \int_{-\infty}^{\infty} f(\delta,\tau)e^{-\frac{(x-\delta)^2}{4d_6(t-\tau)}-\alpha_6(t-\tau)}d\delta,
\end{aligned} \tag{4.17}$$

where $K_i(x,t) = \frac{\lambda}{4\sqrt{\pi d_i t}}e^{-\frac{x^2}{4d_it}-\alpha_i t}, i = 3,4.$

In addition, based on the two conditions from (4.4):

$$\begin{aligned}
u_{n+1}(x) &= M(x,1),\\
v_{n+1}(x) &= F(x,1),
\end{aligned}$$

(4.17) can be turned into

$$
\begin{aligned}
u_{n+1}(x) =& M(x,1)\\
=& \frac{1}{2\sqrt{\pi d_5(1-\tau)}}\int_{-\infty}^{\infty} m(\tau,\delta)e^{-\frac{(x-\delta)^2}{4d_5(1-\tau)}-\alpha_5(1-\tau)}d\delta\\
=& \frac{1}{2\sqrt{\pi d_5(1-\tau)}}\int_{-\infty}^{\infty}\int_0^{\tau} d\tau_1 \int_{-\infty}^{\infty} K_3(\delta-\xi,\tau-\tau_1)((u(\xi,\tau_1)\\
&+ v(\xi,\tau_1))e^{-\frac{(x-\delta)^2}{4d_5(1-\tau)}-\alpha_5(1-\tau)}d\xi d\delta\\
=& \frac{1}{2\sqrt{\pi d_5(1-\tau)}}\int_{-\infty}^{\infty}\int_0^{\tau} d\tau_1 \int_{-\infty}^{\infty} K_3(\delta-\xi,\tau-\tau_1)\\
&\left(\frac{1}{2\sqrt{\pi d_1\tau_1}}\int_{-\infty}^{\infty} M_n(\varepsilon)e^{-\frac{(\xi-\varepsilon)^2}{4d_1\tau_1}-\alpha_1\tau_1}d\varepsilon\right.\\
&\left.+\frac{1}{2\sqrt{\pi d_2\tau_1}}\int_{-\infty}^{\infty} F_n(\varepsilon)e^{-\frac{(\xi-\varepsilon)^2}{4d_2\tau_1}-\alpha_2\tau_1}d\varepsilon\right)e^{-\frac{(x-\delta)^2}{4d_5(1-\tau)}-\alpha_5(1-\tau)}d\xi d\delta\\
=& \frac{1}{2\sqrt{\pi d_5(1-\tau)}}\int_{-\infty}^{\infty}\int_0^{\tau} d\tau_1 \int_{-\infty}^{\infty} K_3(\delta-\xi,\tau-\tau_1)\frac{1}{2\sqrt{\pi d_1\tau_1}}\\
&\int_{-\infty}^{\infty} M_n(\varepsilon)e^{-\frac{(\xi-\varepsilon)^2}{4d_1\tau_1}-\alpha_1\tau_1-\frac{(x-\delta)^2}{4d_5(1-\tau)}-\alpha_5(1-\tau)}d\varepsilon d\xi d\delta\\
&+\frac{1}{2\sqrt{\pi d_5(1-\tau)}}\int_{-\infty}^{\infty}\int_0^{\tau} d\tau_1 \int_{-\infty}^{\infty} K_3(\delta-\xi,\tau-\tau_1)\frac{1}{2\sqrt{\pi d_2\tau_1}}\\
&\int_{-\infty}^{\infty} F_n(\varepsilon)e^{-\frac{(\xi-\varepsilon)^2}{4d_2\tau_1}-\alpha_2\tau_1-\frac{(x-\delta)^2}{4d_5(1-\tau)}-\alpha_5(1-\tau)}d\varepsilon d\xi d\delta,
\end{aligned}
$$

and

$$
\begin{aligned}
v_{n+1}(x) =& F(x,1)\\
=& \frac{1}{2\sqrt{\pi d_6(1-\tau)}}\int_{-\infty}^{\infty}\int_0^{\tau} d\tau_1 \int_{-\infty}^{\infty} K_4(\delta-\xi,\tau-\tau_1)\frac{1}{2\sqrt{\pi d_1\tau_1}}\\
&\int_{-\infty}^{\infty} M_n(\varepsilon)e^{-\frac{(\xi-\varepsilon)^2}{4d_1\tau_1}-\alpha_1\tau_1-\frac{(x-\delta)^2}{4d_6(1-\tau)}-\alpha_6(1-\tau)}d\varepsilon d\xi d\delta\\
&+\frac{1}{2\sqrt{\pi d_6(1-\tau)}}\int_{-\infty}^{\infty}\int_0^{\tau} d\tau_1 \int_{-\infty}^{\infty} K_4(\delta-\xi,\tau-\tau_1)\frac{1}{2\sqrt{\pi d_2\tau_1}}\\
&\int_{-\infty}^{\infty} F_n(\varepsilon)e^{-\frac{(\xi-\varepsilon)^2}{4d_2\tau_1}-\alpha_2\tau_1-\frac{(x-\delta)^2}{4d_6(1-\tau)}-\alpha_6(1-\tau)}d\varepsilon d\xi d\delta.
\end{aligned}
$$

So to summarize, the linearization system (4.4) eventually leads to the system of equations as shown below:

$$
\begin{aligned}
u_{n+1}(x) =& \frac{1}{2\sqrt{\pi d_5(1-\tau)}} \int_{-\infty}^{\infty} \int_0^{\tau} d\tau_1 \int_{-\infty}^{\infty} K_3(\delta-\xi, \tau-\tau_1) \frac{1}{2\sqrt{\pi d_1 \tau_1}} \\
& \int_{-\infty}^{\infty} M_n(\varepsilon) e^{-\frac{(\xi-\varepsilon)^2}{4d_1\tau_1}-\alpha_1\tau_1-\frac{(x-\delta)^2}{4d_5(1-\tau)}-\alpha_5(1-\tau)} d\varepsilon d\xi d\delta \\
& + \frac{1}{2\sqrt{\pi d_5(1-\tau)}} \int_{-\infty}^{\infty} \int_0^{\tau} d\tau_1 \int_{-\infty}^{\infty} K_3(\delta-\xi, \tau-\tau_1) \frac{1}{2\sqrt{\pi d_2 \tau_1}} \\
& \int_{-\infty}^{\infty} F_n(\varepsilon) e^{-\frac{(\xi-\varepsilon)^2}{4d_2\tau_1}-\alpha_2\tau_1-\frac{(x-\delta)^2}{4d_5(1-\tau)}-\alpha_5(1-\tau)} d\varepsilon d\xi d\delta, \\
v_{n+1}(x) =& \frac{1}{2\sqrt{\pi d_6(1-\tau)}} \int_{-\infty}^{\infty} \int_0^{\tau} d\tau_1 \int_{-\infty}^{\infty} K_4(\delta-\xi, \tau-\tau_1) \frac{1}{2\sqrt{\pi d_1 \tau_1}} \\
& \int_{-\infty}^{\infty} M_n(\varepsilon) e^{-\frac{(\xi-\varepsilon)^2}{4d_1\tau_1}-\alpha_1\tau_1-\frac{(x-\delta)^2}{4d_6(1-\tau)}-\alpha_6(1-\tau)} d\varepsilon d\xi d\delta \\
& + \frac{1}{2\sqrt{\pi d_6(1-\tau)}} \int_{-\infty}^{\infty} \int_0^{\tau} d\tau_1 \int_{-\infty}^{\infty} K_4(\delta-\xi, \tau-\tau_1) \frac{1}{2\sqrt{\pi d_2 \tau_1}} \\
& \int_{-\infty}^{\infty} F_n(\varepsilon) e^{-\frac{(\xi-\varepsilon)^2}{4d_2\tau_1}-\alpha_2\tau_1-\frac{(x-\delta)^2}{4d_6(1-\tau)}-\alpha_6(1-\tau)} d\varepsilon d\xi d\delta.
\end{aligned}
\tag{4.18}
$$

(4.18) is in a form that will enable us to find the linearized moment generating matrix, and thus the spreading speed of the linearized system.

4.3 Spreading Speed of the Linearized System

In this section, we aim to find the formula for the spreading speed of the linearized system (4.4). Before proceeding, we need to find a matrix B_μ which is defined to be the coefficient matrix for the vector of the linear combinations of γ_1 and γ_2 obtained by substituting $M_n(x) = \gamma_1 e^{-\mu x}$ and $F_n(x) = \gamma_2 e^{-\mu x}$ into (4.18) and then multiplying both equations by $e^{\mu x}$ to offset the exponential terms. In order to get B_μ, we need to apply a set of variable substitutions in (4.18):

$$
\begin{aligned}
\delta' &= x - \delta, \\
\xi' &= x - \delta' - \xi, \\
\varepsilon' &= x - \delta' - \xi' - \varepsilon.
\end{aligned}
$$

After applying the variable substitutions and substituting $M_n(x) = \gamma_1 e^{-\mu x}$ and $F_n(x) = \gamma_2 e^{-\mu x}$ into (4.18), the integrations will finally offset the variables δ', ξ'

and ε'. Thus (4.18) turns into

$$\begin{aligned}
u_{n+1}(x) =& \frac{\gamma_1 e^{-\mu x} \cdot \lambda e^{-\alpha_3\tau+\mu^2 d_3\tau-\alpha_5(1-\tau)+\mu^2 d_5(1-\tau)} \left(e^{(\alpha_3-\alpha_1+\mu^2 d_1-\mu^2 d_3)\tau} - 1\right)}{2(\alpha_3-\alpha_1+\mu^2 d_1-\mu^2 d_3)} + \\
& \frac{\gamma_2 e^{-\mu x} \cdot \lambda e^{-\alpha_3\tau+\mu^2 d_3\tau-\alpha_5(1-\tau)\mu^2 d_5(1-\tau)} \left(e^{(\alpha_3-\alpha_2+\mu^2 d_2-\mu^2 d_3)\tau} - 1\right)}{2(\alpha_3-\alpha_2+\mu^2 d_2-\mu^2 d_3)}, \\
v_{n+1}(x) =& \frac{\gamma_1 e^{-\mu x} \cdot \lambda e^{-\alpha_4\tau+\mu^2 d_4\tau-\alpha_6(1-\tau)+\mu^2 d_6(1-\tau)} \left(e^{(\alpha_4-\alpha_1+\mu^2 d_1-\mu^2 d_4)\tau} - 1\right)}{2(\alpha_4-\alpha_1+\mu^2 d_1-\mu^2 d_4)} + \\
& \frac{\gamma_2 e^{-\mu x} \cdot \lambda e^{-\alpha_4\tau+\mu^2 d_4\tau-\alpha_6(1-\tau)+\mu^2 d_6(1-\tau)} \left(e^{(\alpha_4-\alpha_2+\mu^2 d_2-\mu^2 d_4)\tau} - 1\right)}{2(\alpha_4-\alpha_2+\mu^2 d_2-\mu^2 d_4)}.
\end{aligned}$$

The definition of B_μ implies that

$$\begin{pmatrix} u_{n+1}(x) \\ v_{n+1}(x) \end{pmatrix} = B_\mu \begin{pmatrix} \gamma_1 \\ \gamma_2 \end{pmatrix} e^{-\mu x},$$

so we have

$$B_\mu = \begin{pmatrix} c_{11} & c_{12} \\ c_{21} & c_{22} \end{pmatrix},$$

where

$$\begin{aligned}
c_{11} &= \frac{\lambda e^{-\alpha_3\tau+\mu^2 d_3\tau-\alpha_5(1-\tau)+\mu^2 d_5(1-\tau)} \left(e^{(\alpha_3-\alpha_1+\mu^2 d_1-\mu^2 d_3)\tau}-1\right)}{2(\alpha_3-\alpha_1+\mu^2 d_1-\mu^2 d_3)}, \\
c_{12} &= \frac{\lambda e^{-\alpha_3\tau+\mu^2 d_3\tau-\alpha_5(1-\tau)+\mu^2 d_5(1-\tau)} \left(e^{(\alpha_3-\alpha_2+\mu^2 d_2-\mu^2 d_3)\tau}-1\right)}{2(\alpha_3-\alpha_2+\mu^2 d_2-\mu^2 d_3)}, \\
c_{21} &= \frac{\lambda e^{-\alpha_4\tau+\mu^2 d_4\tau-\alpha_6(1-\tau)+\mu^2 d_6(1-\tau)} \left(e^{(\alpha_4-\alpha_1+\mu^2 d_1-\mu^2 d_4)\tau}-1\right)}{2(\alpha_4-\alpha_1+\mu^2 d_1-\mu^2 d_4)}, \\
c_{22} &= \frac{\lambda e^{-\alpha_4\tau+\mu^2 d_4\tau-\alpha_6(1-\tau)+\mu^2 d_6(1-\tau)} \left(e^{(\alpha_4-\alpha_2+\mu^2 d_2-\mu^2 d_4)\tau}-1\right)}{2(\alpha_4-\alpha_2+\mu^2 d_2-\mu^2 d_4)}.
\end{aligned}$$

The spreading speed in (4.4) is given by

$$\bar{c} = \inf_{\mu>0} \left(\mu^{-1} \ln(\lambda_1(\mu))\right), \tag{4.19}$$

where $\lambda_1(\mu)$ is the principal eigenvalue of B_μ.

The spreading speed formula in (4.19) is based on the linear determinacy of the two-sex model. However, we are unable to obtain the sufficient conditions for the linear determinacy of the model at this point. So in the next chapter, we will conduct numerical simulations on the traveling waves and spreading speeds of the model, and discuss the parameter values that can make the two-sex model given by (4.2) and (4.3) linearly determinate.

CHAPTER 5
NUMERICAL SIMULATION

We realize the difficulty in explicitly providing the linear determinacy conditions for the spreading speed in the two-sex stage-structured model given by (4.2) and (4.3). However, we believe it is still meaningful to understand if there is an opportunity for the model to be linearly determinate. In order to achieve that goal, we assign reasonable values to the parameters in the model, and conduct numerical simulations on the traveling wave solutions. By analyzing the traveling waves at different time, we get an approximation for the spreading speeds in the model. On the other hand, we calculate the spreading speed of the linearized system by applying the same set of values into the formula given by (4.19) in Chapter 4, then compare it with the simulated spreading speed of the two-sex model. In this chapter, we aim to find the the set of parameter values such that the two spreading speeds are equal, i.e., the two-sex model is linearly determinate.

Before proceeding, we choose the commonly used sine functions as the initial population densities for the adult male and female populations u and v, so we have

$$\begin{aligned} u(x,0) &= 0.5\sin(x), \\ v(x,0) &= 0.5\sin(x). \end{aligned} \tag{5.1}$$

Then the original two-sex model (4.2) and (4.3) turns into

$$\begin{aligned}
u_t &= d_1 u_{xx} - \alpha_1 u - \gamma_1 u^2 - \beta_1 uv,\\
v_t &= d_2 v_{xx} - \alpha_2 v - \gamma_2 v^2 - \beta_2 uv,\\
m_t &= d_3 m_{xx} + \tfrac{1}{2}\lambda(u+v) - \alpha_3 m - \gamma_3 m^2 - \beta_3 mf,\\
f_t &= d_4 f_{xx} + \tfrac{1}{2}\lambda(u+v) - \alpha_4 f - \gamma_4 f^2 - \beta_4 mf,\\
M_t &= d_5 M_{xx} - \alpha_5 M - \gamma_5 M^2 - \beta_5 MF,\\
F_t &= d_6 F_{xx} - \alpha_6 F - \gamma_6 F^2 - \beta_6 MF
\end{aligned} \tag{5.2}$$

with the initial and boundary conditions

$$\begin{aligned}
u(x,0) &= 0.5\sin(x),\\
v(x,0) &= 0.5\sin(x),\\
m(x,0) &= 0,\\
f(x,0) &= 0,\\
M(x,\tau) &= m(x,\tau),\\
F(x,\tau) &= f(x,\tau),\\
u_{n+1}(x) &= M(x,1),\\
v_{n+1}(x) &= F(x,1).
\end{aligned}$$

As we program in Matlab, we need to assign values to the two step variables Δx and Δt, which define how the space and time intervals will be divided. Experiments with various values of Δx and Δt have shown that $\Delta x = 0.2$ and $\Delta t = 0.005$ would be the optimal combination for a comprehensive consideration of reasonable run time and less error.

In the model, we have assumed the reprouduction occurs only once a year, and the populations exhibit a birth pulse growth pattern, i.e. the reproduction period is relatively shorter than the non-reproductive stage. For the sake of simplicity, we let $T = 1$ represent one year and assume that the length of reproduction period is $\tau = 0.3$.

TABLE 5.1

Two-Sex Model Parameter Values

i	d_i	α_i	β_i	γ_i
1	1.000	0.190	0.200	0.200
2	1.000	0.201	0.200	0.200
3	0.800	2.000	0.200	0.200
4	0.800	2.010	0.200	0.200
5	1.000	0.195	0.200	0.200
6	1.000	0.190	0.200	0.200

Table 5.1 gives the set of values we have assigned to all parameters in the model.

The Matlab figure 5.1a and 5.1b show the traveling wave solutions of female and male populations at the end of year $1, 5, 10, 15, 20, 25, 30, 35, 40$. As time proceeds, the speed of the traveling waves asymptotically approaches a constant value. This value can be obtained by measuring the distance between any two traveling waves after a certain period of time. We notice that the distance between any two adjacent traveling waves are very nearly the same starting from year 6. In order to improve the accuracy, we measured the distance between the traveling waves at the end of year $35, 36, 37, 38, 38$ and 40, then take the average.

Let ${c_f}^*$ and ${c_m}^*$ represent the spreading speeds of the female and male populations at the non-reproductive stage respectively, then Table 5.2 exhibits a comparison of these two with different values of the instantaneous birth rate λ. It is no surprise that the male and female populations actually spread at the same speed since they have the same life cycle.

At the end of Chapter 4, we provided the spreading speed formula in (4.19) based on the linear determinacy of the model. In this section, we apply the same set of parameter values given in Table 5.1 into the formula (4.19), and calculate $\bar{c}$ with the specific values of τ and λ, then compare it with the corresponding

TABLE 5.2

Comparison of ${c_m}^*$ and ${c_f}^*$ when $\tau = 0.3$

λ	c_m^*	c_f^*	Difference	Difference %
6	0.61	0.61	0.00	0%
8	1.22	1.22	0.00	0%
10	1.54	1.54	0.00	0%
12	1.76	1.75	0.00	0%
14	1.92	1.91	0.01	0%
20	2.25	2.25	0.00	0%

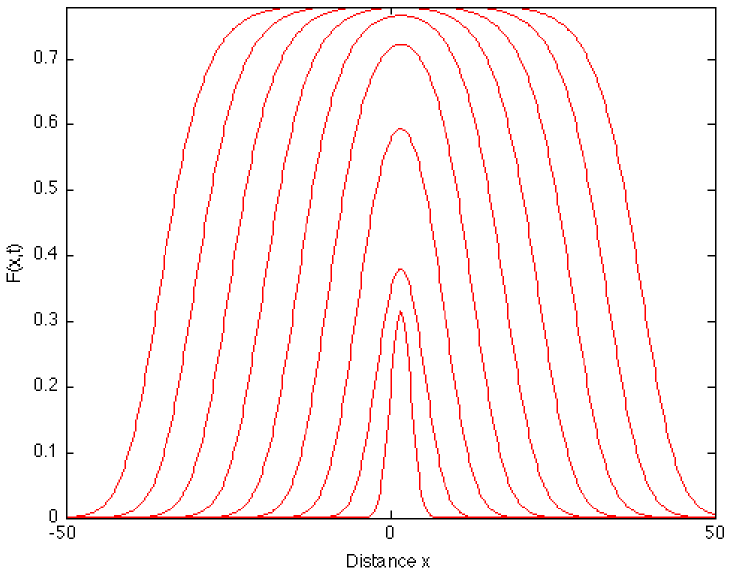
simulation of the female population's spreading speed ${c_f}^*$ in the original nonlinear model. Table 5.3 displays a complete comparison of $\bar{c}$ and c_f^* with different values of the instantaneous birth rate λ.

We note that given the parameter values we have assigned into the model, the two spreading speeds c_f^* and $\bar{c}$ have a better match when the instantaneous birth rate λ turns larger. The relative difference turns to be relatively stable when $\lambda \geq 75$, which is less than 1%. Thus we conclude that with the parameter values given in Table 5.1, $\tau = 0.3$ and $\lambda \geq 75$, the two-sex model given by (4.2) and (4.3) is linearly determinate.

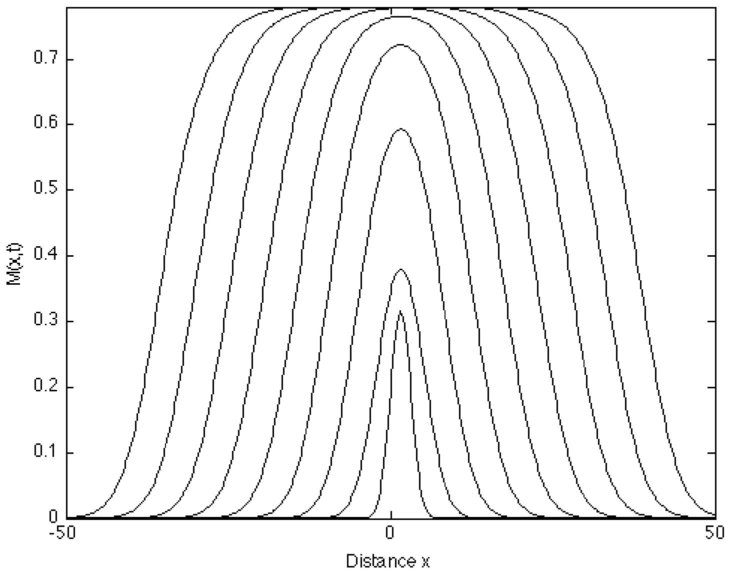
TABLE 5.3

Comparison of ${c_f}^*$ and $\bar{c}$ when $\tau = 0.3$

λ	$\bar{c}$	c_f^*	Absolute Difference	Relative Difference
8	1.2828	1.2222	0.0606	4.72%
10	1.5855	1.5376	0.0479	3.02%
12	1.7954	1.7527	0.0427	2.38%
14	1.9554	1.9140	0.0414	2.12%
20	2.2829	2.2473	0.0356	1.56%
30	2.6058	2.5753	0.0305	1.17%
50	2.9629	2.9319	0.0310	1.05%
75	3.2183	3.1944	0.0239	0.74%
100	3.3879	3.3602	0.0277	0.82%
125	3.5138	3.4857	0.0281	0.80%
150	3.6134	3.5887	0.0247	0.68%
500	4.2127	4.1871	0.0256	0.61%



(a) Traveling wave solutions of the female population at the end of year $1, 5, 10, 15, ..., 40$.



(b) Traveling wave solutions of the male population at the end of year $1, 5, 10, 15, ..., 40$.

FIGURE 5.1 – Traveling wave solutions of female and male populations at the end of year $1, 5, 10, 15, 20, 25, 30, 35, 40$, given $\lambda = 15$ and $\tau = 0.3$, with the initial condition $u(0, x) = v(0, x) = \frac{1}{2}\sin(x)$.

CHAPTER 6
CONCLUSION AND FUTURE DIRECTIONS

6.1 Conclusion

There have been extensive studies about the spreading speeds and traveling waves in two-species competition models without Allee effect. Allee effect occurs in many populations due to the difficulties in finding mates when population density is low, social dysfunction at small population sizes as well as many other factors. In this dissertation we proposed two two-species competition models with Allee effect, one is in the form of reaction-diffusion equations and the other is in the form of integro-difference equations which modeled the growth, spread and competition of the two species. These two models are extensions of the Lotka-Volterra competition model (1.18) and the discrete-time spatial spreading model (1.19) given in [14]. However, there is no Allee effect exhibited in those models.

In Chapter 2 and 3 we analyzed the reaction-diffusion system (2.1) and the integro-difference system (3.1). We showed how Allee effect resides in these models as well as how it affects the profiliation rate of the native species when the population density is low. We then obtained the existence and local stability criteria of the equilibria in the models. For the reaction-diffusion system (2.1), we applied Butler-McGehee Lemma to show that the global stability of one of the coexistence equilibria and one of the mono-culture equilibria can be completely determined. And for the integro-difference model (3.1), we applied the famous monotone convergence theorem, the squeeze theorem and the method of induction to show that the global stability of one of the coexistence equilibria and one of the mono-culture equilibria can be completely determined as well. We then discussed the spatial transitions from a mono-culture equilibrium to a coexistence equilibrium or a different mono-culture equilibrium. By applying Weinberger and his coworkers' Theorems 3.1 and 4.1 in [2], we obtained the sufficient conditions for the linear determinacy of the spreading speeds in both models. We also provided the formulas for the spreading speeds based on the linear determinacy conditions. We then established the existence of the traveling wave solutions connecting a mono-culture equilibrium with a coexistene equilibrium or a different mono-culture equilibrium by applying Li and Zhang' Theorems 2.1 and 3.1 in [18].

In Chapter 4 we proposed a two-sex stage-structured competition model with birth pulse growth pattern consisting of a reproductive stage model (4.2) and a non-reproductive stage model (4.3). We analyzed its linearization given by (4.4) and obtained the formula for the spreading speed $\bar{c}$ based on the linear determinacy of the original nonlinear model. However, we were unable to get the parameters range for the linear determinacy due to the complexity of the model. Hence in Chapter 5 we carried out numerical simulations on the traveling wave solutions and spreading speeds in the two-sex model. By adjusting the parameters in the model, we achieved a good match between the linear determinacy based spreading speed $\bar{c}$ and the spreading speed c_f^* of female population in the original nonlinear model. By observing the simulation results we conclude that there exists a set of values for the parameters in the model such that the two-sex model is linearly determinate.

6.2 Future Directions

For the two two-species competition models (2.1) and (3.1), we may consider future research in the following directions:

1. **Traveling wave connecting the origin and a coexistence equilibrium.** We have shown the existence of traveling wave solutions connecting a mono-culture equlibrium to a coexistence equilibrium or a different mono-culture equilibrium under certain conditions. However, we may be also interested in showing the existence of traveling wave connecting the origin with a co-existence equilibrium. This can be approached by constructing the lower and upper traveling wave solutions of the model. This work has been done before for the two-species competition modes without Allee effect. For the two-species models (2.1) and (3.1) with Allee effect, the proof could be much more complicated.

2. **Larger parameter range for the linear determinacy of the models.** We have obtained some sufficient conditions which assure the linear determinacy of the two two-species competition models in Theorem 2.2 and 3.2. In the reaction-diffusion competition model (2.1), the condition $d_2/d_1 \leq 2$ can be interpreted as requiring sufficiently large dispersal of the invader relative to the dispersal of the out-competed resident. And the condition that $\max\{1/(1-a_1), (a_1 a_2 k + \alpha - 1)/(1-a_1)\}$ is sufficiently small can be interpreted as requiring sufficiently weak interactions between the invader and resident. These theorems only give sufficient but not necessary conditions for the linear determinacy of the models. We may follow Hosono's analysis in the Lotka-Volterra model (1.18) in his paper [33] to seek a larger parameter range for the linear determincy of our models.

3. **Numerical simulations on the traveling waves and spreading speeds**

in the two models.

For the two-sex stage-structured competition model, we will consider the following extentions in the future:

1. **A more realistic mating formation.** For simplicity, we started our work with a linear mating function in the form of $\Lambda(M,F) = \frac{1}{2}\lambda(M+F)$ in the model. This format, however, has its drawbacks. For example, when either the male or female population density equals 0, this mating function still produces a positive birth rate, which is not realistic for dioecious species. Perhaps a more realistic mating format is that corresponding to the choice

   $$\Lambda(M,F) = 2\lambda \min(M,F),$$

   or

   $$\Lambda(M,F) = \frac{\lambda_f \lambda_m F M}{\lambda_f F + \lambda_m M}$$

   where λ_m and λ_f are positive constants. These forms apparently enhance the difficulty in seeking the spreading speed formula based on linear determinacy.

2. **Consider interactions from other species.** In the model, we investigated the spatial dynamics of the adult and juvenile populations with two sexes within a species. However, we ignored the potential interactions from other species. In the future, we may want to consider a two-species model which is more realistic for biological invasions.

3. **Consider Allee effect.** We may follow Eskola and Parvinen's work in [25] to add Allee effect in the model by adjusting the mate finding process.

4. **Consider different birth sex ratios for males and females in each generation.** We could assume a flexible sex ratio at birth in each generation, such that a fraction s is females and a fraction $1-s$ is males.

REFERENCES

[1] Global Invasive Species Database, http://www.issg.org/database.

[2] Weinberger H.F., Lewis M.A., Li B. (2002). Analysis of linear determinacy for spread in cooperative models. J. Math. Biol. 45, 183-218.

[3] Weinberger H.F. (1978). Asymptotic behavior of a model in population genetics. Lecture Notes in Mathematics 648, 47-96.

[4] Weinberger H.F. (1982). Long-time behavior of a class of biological models. SIAM J. Math. Anal. 13, 353-396.

[5] Lui R. (1983). Existence and stability of travelling wave solutions of a nonlinear integral operator. J. Math. Biol. 16, 199-220.

[6] Lui R. (1989). Biological growth and spread modeled by systems of recursions. I Mathematical theory. Mathematical Biosciences 93, 269-295.

[7] Lui R. (1989). Biological growth and spread modeled by systems of recursions. II Mathematical theory. Mathematical Biosciences 93, 297-312.

[8] Kot M. (1992). Discrete-time travelling waves: ecological examples. J. Math. Biol. 30, 413-436.

[9] Hart D.R., Gardner, R.H. (1997). A spatial model for the spread of invading organisms subject to competition. J. Math. Biol. 35, 935-948.

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

[11] Lewis, M.A. (1997). Variability, patchiness, and jump dispersal in the spread of an invading population. In: Tilman, D., Kareiva, P. (Eds.), Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions. Princeton University Press, Princeton, NJ, USA, pp. 46-69.

[12] Clark J.S. (1998). Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. Am. Natur. 152, 204-224.

[13] Meyer, Kimberly Ilene (2012). A spatial age-structured model of perennial plants with a seed bank. Electronic Theses and Dissertations. Paper 970.

[14] Mark A. Lewis, Bingtuan Li, Hans F. Weinberger (2002). Spreading speed and linear determinacy for two-species competition models. J. Math. Biol. 45, 219-233.

[15] Mark A. Lewis, Bingtuan Li (2012). Spreading speed, traveling waves, and minimal domain size in impulsive reaction-diffusion models. Bull. Math. Biol. 74, 2383-2402.

[16] M.A. Lewis, G. Schmitz, P. Kareiva, J.T. Trevors (1996). Models to examine containment and spread of genetically engineered microbes. Molecular Ecology 5, 165-175.

[17] Veit R., Lewis M. (1996). Dispersal, population growth and the Allee effect: dynamics of the house fish invasion of eastern North America. Am. Nat. 148, 255-274.

[18] Bingtuan Li, Liang Zhang (2011). Travelling wave solutions in delayed cooperative systems. Nonlinearity 24, 1759-1776.

[19] Bingtuan Li, Hans F. Weinberger, Mark A. Lewis (2005). Spreading speeds as slowest wave speeds for cooperative systems. Mathematical Biosciences 196, 82-98.

[20] Hans F. Weinberger and Bingtuan Li (2010). Spreading speeds and traveling waves for almost cooperative multispecies discrete-time recursions, pre-press.

[21] D.G. Kendall (1948). Stochatic process and population growth. J. Roy. Statist. Soc. B10, 183-212.

[22] M.A. Lewis, P. Kareiva (1993). Allee dynamics and the spread of invading organisms. Theoretical Population Biology 43, 141-158.

[23] Mark Kot, Jan Medlock, Timothy Reluga, D. Brian Walton (2004). Stochasticity, invasions, and branching random walks. Theoretical Population Biology 66, 175-184.

[24] Regina C. Almeida, Simone A. Delphim, Michel I. da S. Costa (2006). A numerical model to solve single-species invasion problems with Allee effects. Ecological Modelling 192, 601-617.

[25] Hanna T.M. Eskola, Kalle Parvinen (2010). The Allee effect in mechanistic models based on inter-individual interaction processes. Bulletin of Mathematical Biology 72, 184-207.

[26] Liang Zhang (2012). Traveling wave solutions in an integro-differential competition model. Discrete and Continuous Dynamical Systems Series B 17, 417-428.

[27] Wan-Tong Li, Guo Lin, Shigui Ruan (2006). Existence of travelling wave solutions in delayed reaction-diffusion systems with applications to diffusion-competition systems. Nonlinearity 19, 1253-1273.

[28] Guo Lin, Wan-Tong Li (2010). Spreading speeds and traveling wavefronts for second order integrodifference equations. J. Math. Anal. Appl. 361, 520-532.

[29] Jianhong Wu, Xingfu Zou (2001). Traveling wave fronts of reaction-diffusion systems with delay. Journal of Dynamics and Differential Equations 13, 651-687.

[30] A. Reardon, A. Novikov (n.d.). Front propagation in reaction-diffusion equations. Department of Mathematics, Pennsylvania State University.

[31] Juan Venegas-Ortiz, Rosalind J. Allen, Martin R. Evans (2014). Speed of invasion of an expanding population by a horizontally-transmitted trait. Genetics 196(2), 497-507.

[32] Allee W. C. (1938). The social life of animals. W. W. Norton and Co., New York.

[33] Hosono Y. (1998). The minimal speed of traveling fronts for a diffusive Lotka-Volterra competition model. Bull. Math. Biol. 60, 435-448.

[34] Zhang Tianran, Wendi Wang (2005). Mathematical models of two-sex population dynamics. Kôkyûroku 1432, 96-104.

[35] L. Goodman (1953). Population growth of the sexes. Biometrics 9, 212-225.

[36] A.G. Fredrickson (1971). A mathematical theory of age structure in sexual population: random mating and monogamous marriage models. Mathematical Biosciences 10, 117-143.

[37] J.H. Pollard (1997). Modelling the interaction between the sexes. Mathl. Comput. Modelling 26, 11-24.

[38] Hal L. Smith (1995). Monotone dynamical systems: an introduction to the theory of competitive and cooperative systems. American Mathematical Society.

[39] Tom E. X. Miller, Allison K. Shaw, Brian D. Inouye, Michael G. Neubert (2011). Sex-biased dispersal and the speed of two-sex invasions. The American Naturalist Vol. 177, No. 5.

[40] Aaron C. Ashih, William G. Wilson (2001). Two-sex population dynamics in space: effects of gestation time on persistence. Theoretical Population Biology 60, 93-106.

[41] Davis H.G., Taylor C.M., Civille J.C., Strong D.R. (2004). An allee effect at the front of a plant invasion: Spartina in a Pacific estuary. J. Ecol. 92, 321-327.

[42] Baker R., Dunn P. (1990). New directions in biological control, Alan Liss, New York.

[43] Okubo A., Maini P.K., Williamson M.H., Murray J.D. (1989). On the spatial spread of the grey squirrel in Britain. Proc. R. Soc. Lond. B 238, 113-125.

[44] Williamson M. (1989). Mathematical models of invasion, in J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmánek, M. Williamson (eds) Biological invasions: a global perspective. Wileym Chichester, UK.

[45] Fisher R.A. (1937). The wave of advance of advantageous genes. Annals of Eugenics 7, 355-369.

[46] Kolmogorov A., I. Petrovsky, N. Piskunov (1937). Study of the diffusion equation with growth of the quantity of matter and its application to a biological problem. Bull Univ Moscow, Ser Int, Sec A 1, 1-25.

[47] Skellam J. G. (1951). Random dispersals in theoretical populations. Biometrika 38, 196-218.

[48] Shigesada, N., Kawasaki, K. (1997). Biological invasions: theory and practice. Oxford: Oxford University Press.

[49] Tilman D., Kareiva P. (1997). Spatial ecology. Princeton: Princeton University Press.

[50] Okubo A., Levin S. (2001). Diffusion and ecological problems. New York: Springer.

[51] Murray J. D. (2002). Mathematical biology I: an introduction. Berlin: Springer

[52] Murray J. D. (2002). Mathematical biology II: spatial models and biomedical applications. Berlin: Springer.

[53] Cantrell R. S., Cosner C. (2003). Spatial ecology via reaction-diffusion equations. New York: Wiley.

[54] Andow D.A., Kareiva P.M., Levin S.A., Okubo A. (1990). Spread of invading organisms. Ecology 4, 177-188.

[55] Ammerman A. J., L. L. Cavalli-Sforza (1971). Measuring the rate of spread of early farming in europe. Man 6, 674-688.

[56] van den Bosch F., R. Hengeveld, J. A. J. Metz (1992). Analyzing the velocity of animal range expansion. Journal of Biogeography 19, 135-150.

[57] Mollinson D. (1991). Dependence of epidemic and population velocities on basic parameters. Mathematical Biosciences 107, 255-287.

[58] Young D. A., R. L. Bettinger (1995). Simulating the global human expansion in the late pleistocene. J. Archeological Sci. 22, 89-92.

[59] Hethcote H. W. (2000). The mathematics of infectious diseases. SIAM Review 42: 599-653.

[60] Murray J. D. (2004). Mathematical Biology, Volume I. Springer, New York.

[61] Ackland G. J., M. Signitzer, K. Stratford, M. H. Cohen (2007). Cultural hitchhiking on the wave of advance of beneficial technologies. Proc. Natl. Acad. Sci. USA. 104, 8714-8719.

[62] Rouzine I. M., E. Brunet, C. O. Wilke (2008). The traveling-wave approach to asexual evolution: Mullers ratchet and speed of adaptation. Theoretical population biology 73, 24-46.

[63] Barrett-Freeman C., M. R. Evans, D. Marenduzzo, W. C. K. Poon (2008). Nonequilibrium phase transition in the sedimentation of reproducing particles. Phys Rev Lett 101, 100602.

[64] Greulich P., B. Waclaw, R. J. Allen (2012). Mutational pathway determines whether drug gradients accelerate evolution of drug-resistant cells. Phys. Rev. Lett. 109, 088101.

[65] McKean H. P. (1975). Application of brownian motion to the equation of kolmogorov-petrovskii-piskunov. Comm. Pure. Appl. Math. 28, 323-331.

[66] Merkin J. H., D. J. Needham (1989). Propagating reaction-diffusion waves in a simple isothermal quadratic autocatalytic chemical system. J. Eng. Math. 23, 343-356.

[67] Merkin, J. H., D. J. Needham, S. K. Scott (1993). Coupled reaction-diffusion waves in an isothermal autocatalytic. chemical system. IMA J. Appl. Math. 50, 43-76.

[68] van Saarloos, W. (2003). Front propagation into unstable states. Phys. Rep. 386, 29-222.

[69] Derrida B., H. Spohn (1988). Polymers on disordered trees, spin glasses and traveling waves. J. Stat. Phys. 51, 817-840.

[70] Brunet E., B. Derrida (1997). Shift in the velocity of a front due to a cutoff. Phys. Rev. E. 56, 2597-2604.

[71] Majumdar S. N., P. L. Krapivsky (2002). Extreme value statistics and traveling fronts: application to computer science. Phys. Rev. E 65, 036127.

[72] Majumdar S. N., P. L. Krapivsky (2003). Extreme value statistics and traveling fronts: various applications. Physica A 318, 161-170.

[73] J. Crank (1980). The Mathematics of Diffusion, Oxford University Press.

[74] Wang Chunwei (2013). A stage-structured delayed reaction-diffusion model for competition between two species. Electronic Theses and Dissertations. Paper 1521.

[75] Caughley G. (1977). Analysis of vertebrate population. John & Wiley Sons, New York.

[76] Singh A., Nisbet R.M. (2007). Semi-discrete host-parasitoid models. J. Theor. Biol. 247, 733-742.

[77] Pachepsky E., Nisbet R.M., Murdoch W.W. (2008). Between discrete and continuous: consumer resource dynamics with synchronized reproduction. Ecology 89, 280-288.

[78] Kot Mark, William M Schaffer (1986). Discrete-time growth dispersal models. Mathematical Biosciences 80, 109-136.

[79] D.G. Aronson and H.F. Weinberger (1977). The asymptotic speed of propagation of a simple epidemic. Nonlinear diffusion (NSF-CBMS Regional Conf. Nonlinear Diffusion Equations, Univ. Houston, Houston, Tex., 1976), 1-23. Research Notes in Mathematics, 14. Pitman, London.

[80] D.G. Aronson and H.F. Weinberger (1975). Nonlinear diffusion in population genetics, conbustion, and nerve pulse propagation. Partial differential equations and related topics (Program, Tulane Univ., New Orleans, La., 1974), 5-94. Lecture Notes in Mathematics, 446. Springer, Berlin.

[81] D.G. Aronson and H.F. Weinberger (1978). Multidimensional nonlinear diffusion arising in population genetics. Adv. in Math. 30, no. 1, 33-76.

[82] Keyfitz N. (1972). The mathematics of sex and marriage, in "6th Berkeley Symposium on Mathematical Statistics and Probability" Vol. 4, 89-108.

[83] Pollard J. H. (1977). The continuing attempt to incorporate both sexes into marriage analysis, in "International Population Conference, Mexico", pp. 291-309, International Union for the Scientific Study of Population.

[84] Schoen R. (1988). Modeling multigroup populations. Plenum Press, New York.

[85] Keyfitz N. (1968). Introduction to the mathematics of population. Addison-Wesley, Reading, MA.

[86] Pollard J. H. (1973). Mathematical models for the growth of human populations. Cambridge University Press, Cambridge, MA.

[87] Hadeler K. P., Waldstätter R., and Wörz-Busekros A. (1988). Models for pair-formation in bisexual population. J. Math. Biol. 26, 635-649.

[88] Hadeler K.P., Rothe F. (1975). Traveling fronts in nonlinear diffusion equations. J. Math. Biol. 2, 251-263.

CURRICULUM VITAE

QUANCHENG MENG

EDUCATION

University of Louisville, Louisville, KY	
Ph.D., Applied and Industrial Mathematics	December 2015
M.A., Applied and Industrial Mathematics	December 2011
University of Science and Technology Beijing, Beijing, China	
B.S., Mathematics and Applied Mathematics	June 2009

PROFESSIONAL EXPERIENCE

Graduate Teaching Assistant, University of Louisville, Louisville, KY

Math 111: College Algebra	January 2010 - December 2014
Math 107: Finite Mathematics	
Math 109: Elementary Statistics	
Math 180: Elements of Calculus	

Instructor, University of Louisville, Louisville, KY

Math 111: College Algebra	Summer 2010 - Summer 2014
Math 180: Elements of Calculus	
Math 205: Calculus I	

Research Experience

University of Louisville, Louisville, KY	August 2011 - December 2014

Math Lab Tutor

University of Louisville, Louisville, KY	August 2009 - December 2014

PROFESSIONAL QUALIFICATIONS

SAS Certified Base Programmer for SAS 9	April 2014
SOA/CAS Exam MFE/3F	July 2013
SOA/CAS Exam P/1	November 2012
SOA/CAS Exam FM/2	June 2012

PROFESSIONAL MEMBERSHIPS

Tri-State Actuarial Club	Since 2012
University of Louisville Actuarial Student Organization	Since 2012
American Mathematical Society	Since 2009