ABSTRACT

BOSTIC, KATHRYN JORDAN WEST. Dynamical Behavior of a Discrete, One-island, Selection-migration Model with General Dominance. (Under the direction of James F. Selgrade.)

Selection and migration influence the demographic and genetic compositions of a population. A one-island model is studied, in which the island population receives immigrants from a continent population. Density-dependent selection takes place within the island population and then periodic migration occurs. The research conducted here studies a two-dimensional system of nonlinear difference equations that describe the change in allele frequency and population density over generations. For general dominance in fitness, biologically reasonable conditions ensure the existence of polymorphic equilibria. Conditions on the degree of dominance and the frequency of the allele migrating into the island population are necessary to prove uniqueness and stability of the equilibrium. The movement of the equilibrium due to a change in the degree of dominance is described. Increased prevalence of an allele associated with lower fitness in the island population due to the migration of that allele is shown. Conditions are found for the location and existence of attractors for this model. Approach rates to the attractor are approximated. The homeomorphic pieces of an attractor because of periodic migration as well as the effect of the amplitude of the oscillatory migration are discussed. A measure of allelic diversity is defined and used to study the effect of a change in the degree of dominance on changes in attractor properties. As genetically engineered crops become more prevalent, the one-island model may be useful for understanding the effects of transgenic escape on transgene frequency in natural populations.

Dynamical Behavior of a Discrete, One-island, Selection-migration Model with
General Dominance

by
Kathryn Jordan West Bostic

A dissertation submitted to the Graduate Faculty of
North Carolina State University
in partial fulfillment of the
requirements for the Degree of
Doctor of Philosophy

Applied Mathematics

Raleigh, North Carolina

2010

APPROVED BY:

_____   _____
Dr. James Selgrade   Dr. Alun Lloyd
Chair of Advisory Committee

_____   _____
Dr. Jesús Rodríguez   Dr. Ernest Stitzinger

BIOGRAPHY

Kathryn Jordan West, daughter of Sharyn and Harold West, was born on April 9, 1980, in Raleigh, North Carolina. She has one older sister, Jennifer. Jordan received a Bachelor of Science degree in mathematics and minors in Spanish and Computer Science from Meredith College in May 2002. She then began her graduate studies at North Carolina State University. Jordan married Christopher Bostic on June 21, 2003. She received a Master of Science in applied mathematics in 2005. In November 2008, Jordan and Chris welcomed Spencer and Mackenzie into their family. Jordan completed her doctorate in applied mathematics in 2010.

ACKNOWLEDGEMENTS

I would like to thank my advisor, Dr. Jim Selgrade, for his countless hours of help. He was patient when I had a hard time grasping a concept or when I had a stressful week. I am grateful for the direction he gave me on my research and the constructive comments he gave me to improve this dissertation. I appreciate his understanding of my wanting to balance both work and family.

I also appreciate the efforts of Dr. Jim Roberds. I am grateful for all the time he has spent discussing the genetic components of this thesis with me as well as the time he has spent providing constructive criticism for the paper. It has been a pleasure getting to talk not only about research but also about our lives and families.

I would like to thank Dr. Alun Lloyd, Dr. Jesús Rodríguez, and Dr. Ernest Stitzinger for the time they have taken to be on my committee.

I am grateful to Dr. John Griggs, Miriam Ansley, Seyma Bennett-Shabbir, Di Bucklad, Brenda Currin, Carolyn Gunton, Denise Seabrooks, and Charlene Wallace who have helped me through this journey. They have provided help and leadership to me both as a graduate student and as a teaching assistant. I also am grateful for the times I have gotten to visit with them and get to know them.

I would not have made it through the graduate experience if not for a great group of friends in the program. From homework problems to studying for qualifiers to answering random questions here or there, I am grateful for the friendship and support of fellow graduate students. I am glad to have shared this experience with April Alston, Rebecca Wills, Rebecca Kalhorn, Laurie Zack, Drew Pasteur, Benz Suanmali, Prakash Chanchana, and Ryan Siskind.

I also would like to thank my family. Most of all, I appreciate my husband Chris. He has been a great support throughout my years in school. He encouraged me when I was too tired or frustrated to keep working. He has let me follow through with completing my degree and has been a constant support. Also, Spencer and Mackenzie will not remember me going through this journey, but they have helped

me out. It is always nice after a long day of school to see their smiling faces and get a hug.

I am very fortunate to have a wonderful family, many of whom are nearby. My parents have been a great help through this entire journey. They have given me many rides in to the office, blessed me with homemade food, and watched my kids so that I could work. I am also blessed to have support from my extended family, my in-laws, and my close friends.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter 1

Introduction

Natural selection and migration are two primary processes in nature known to be involved in shaping the genetic composition of populations. The two phenomena perform different functions, whereas selection acts to remove poorly adapted individuals and the genes they carry from populations, migration infuses individuals and genetic variants into populations. Thus, selection works to move populations toward a higher level of adaptability and, in the process, tends to reduce genetic variability. Migration, in some circumstances, can enhance genetic variation within populations through gene transfer between populations. Numerous models have been proposed to study the ways these two evolutionary forces interact to alter and control the genetic constitution of populations. The simplest of these models is the continent-island, or one-island, model.

The continent-island model is a two population model that features unidirectional gene flow from a source population, or collection of populations, into a single population where natural selection may take place [15]. This model can be used to investigate the combined effects of migration and selection in a single population or island. In the research described here, the continent-island model is used to study previously unexplored effects of the joint action of a specific type of selection and migration on gene frequency and population size.

Because of its inherent properties, the continent-island model provides a suitable framework for the study of the undesirable spread of genetically engineered genes (transgenes) in plant populations. The movement of these genes and their potential persistence in non-targeted populations is of widespread interest to plant population biologists. We consider that the continent population serves as the source population for transgenes and use the one-island model to study how they become incorporated in natural, or non-targeted, populations. Investigations of the dynamical behavior for a continent-island system have the potential to provide basic information about the entrance and persistence of these artificially introduced genes in populations for which they are not intended.

Genetically engineered plant varieties first entered production agriculture in 1996. When methods developed in biotechnology are employed to insert new genetic material into the genome of an organism, a genetically engineered organism results [7]. Within ten years of the introduction of this technology, land area in the United States devoted to genetically engineered varieties exceeded that for traditionally bred varieties in commodity crops, such as corn, soybean, cotton, and canola. In fact, in 2007, more than half of the acreage planted to soybeans and corn in the United States was sown to genetically modified varieties [4, 35], indicating that growers of these crops have quickly adopted and expanded the use of this new technology. Nevertheless, the risks and rewards associated with growing these products of biotechnology are still under debate [4, 6, 7, 36].

Several likely causes have been suggested to explain the rapid adoption of this new system of crop production. These include the realization that genetically modified crops require reduced usage of agricultural chemicals, reduced labor to work the fields, and enhanced conservation of soil and water because tillage is reduced. In addition, this production system leads to more effective management of pests and weeds, and benefits then follow because less energy is required to produce high yields. Nonetheless, the impressive ecological and economic gains do not dampen concerns about possible negative effects that might result from transgenic crop culture. The full

range of consequences that follow conversion to genetically modified based systems of agriculture are not yet completely known. As a case in point, the issue of whether genetically modified crops are safe for human consumption is yet to be resolved [4]. Other anxieties relate to effects resulting from gene flow into non-targeted populations of wild or weedy relatives and also of pests. Ecological effects resulting from this type of gene flow are currently unpredictable because of the present lack of knowledge of the way transgenes behave in natural, feral, and other non-targeted populations and for the environments in which these populations are found [36, 38].

Genetically modified forests present some of the same concerns as transgenic crops but also introduce additional issues. Current forest tree improvement programs are based on traditional breeding techniques, but there is considerable interest in applying genetic engineering technology to develop genetically modified trees. Tree breeders presently are considering whether to employ transgenic technology to modify various wood traits [28], to produce faster growing trees, to enhance insect resistance in tree populations, as well as to develop trees that do not produce pollen [17]. Concerns exist about the consequences that engineered genes will have in natural tree populations, as well as unknown ecological risks that could be involved [38]. Transgenes might invade natural populations, and as a result, populations of locally adapted trees could be displaced, possibly endangering natural populations of some tree species. Because pollen and seeds of trees can travel large distances, genetically engineered genes have the potential to invade non-targeted populations that are long distances away from the original source populations [39]. Furthermore, trees have repeated and bountiful seed and pollen production years before harvest, and forest landscapes are typically made up of adjacent ownerships that have differing management production objectives [39]. Tree life spans are longer than those for crop species, so the negative effects of transgenic forestry will not be apparent as quickly as those that have surfaced for transgenic agronomic crop systems. Models, however, can be studied to obtain insight into how transgenes can affect forest populations.

We use a system of difference equations to study the behavior of gene frequencies

and population sizes in island populations that are subject to migration and natural selection. We begin by discussing the biological background for our model in Chapter 2. Characteristics of the model are described in Chapter 3. Then, in Chapter 4, we establish the existence of polymorphic equilibria and present conditions for uniqueness and stability of an equilibrium. More equilibrium results are given in Chapter 5, including a description of a transcritical bifurcation, as well as a discussion of the effects of varying the degrees of dominance in gene expression. The location, existence, and approach rates of attractors are addressed in Chapter 6. Finally, an allelic diversity measure is defined and discussed in Chapter 7.

Chapter 2

Background

In this chapter we describe the biological background for the mathematical model that provides the framework for the dynamics we investigate. First, we present some basic concepts that provide a foundation for our model. We then enumerate some of the effects caused by natural selection and migration, the two evolutionary phenomena that interact in our model, to determine the genetic and demographic properties of populations. Finally, we introduce the notion of dominance as a property related to genetic control of organism performance.

2.1 General Genetics

Before proceeding to a discussion of the effects resulting from natural selection and gene migration, we review some basic genetic terminology. For purposes of our analysis, we consider the gene to be the fundamental unit of heredity that codes for production of protein within a cell. We also consider the gene to be the agent by which this code is transferred from parent to offspring. Alternate forms that genes can take are referred to as alleles. The organized structures within cells on which genes occur are called chromosomes, and the position that a gene occupies on a chromosome is known as a locus. Most higher order organisms possess two copies of

the entire complement of chromosomes characteristic of their species (excluding sex chromosomes) and are said to have the property of diploidy. Genes on the autosomes - all chromosomes except the sex chromosomes - in these organisms are the focus of the behavior we study. A gamete is a mature reproductive cell produced by sexually mature individuals; for diploid individuals, they have a single copy of each autosomal gene. Following mating, the gametes contributed by each parent combine to form a zygote which develops into a multicellular individual. In general usage, an organism's genotype is considered to be its entire assemblage of genes. However, for our model and our discussion, we use this term to indicate the pair of alleles occurring at a single locus. The observable form that results from the interaction of the genotype with its environment is known as its phenotype. When the two alleles at a locus are identical in an organism, the individual is said to be homozygous at that locus, and when the two alleles are of different types, the individual is said to be heterozygous [13, 19].

In population genetics, a primary area of focus in research has been to study the effects that evolutionary forces have on genetic variability within and among populations. An effective method to evaluate the impact of these processes on genetic variability is to investigate their effect on the change in allele frequencies over generations. Allele frequency is a measure that indicates the proportion of the copies of all alleles at a locus occurring in a population's gene pool that are of a given type. When an allele at a locus occurs at a frequency between zero and one, a genetic polymorphism is said to exist. The appearance of a genetic polymorphism within a population indicates that the potential for genetic variability exists in the population.

2.2 Natural Selection

Natural selection is one of the major driving forces that causes evolution to take place. It can lead to rapid transformation of properties of individuals in a few generations or to gradual modification of traits over an extended number of generations. This process occurs when there is differential adaptation of phenotypes to the envi-

ronmental conditions of their habitat. Alleles involved in expression of characteristics associated with well-adapted phenotypes will be more prevalent in succeeding generations because the more maladapted phenotypes are removed from populations, either due to poor survival capabilities or inability to reproduce adequately. Although certain forms of natural selection can act to preserve genetic variability, commonly this process reduces genetic diversity as alleles that lead to high viability and fecundity reach high frequencies [8, 13].

Natural selection in which the size of the population is the ecological factor that influences the viability and fecundity of individuals is known as density-dependent selection. Initial investigations of effects that can result from this type of selection are reported in Roughgarden [26] and Anderson [1]. With density-dependent selection, population size is allowed to vary and is considered to be the environmental component that alters survival capabilities and reproductive success. Thus, population size is viewed both as a result of selection and as a factor that determines which genes are passed on to the subsequent generation. The influence of this type of selection on the genetic constitution of populations is studied by assuming that genotypes produce phenotypes that vary in fitness, a concept discussed in detail in the next section. For the majority of density-dependent selection models, fitnesses are assumed to decrease as population sizes increase [31].

2.3   Fitness

Evolutionary biologists have found it necessary to introduce the concept of fitness to effectively model the way natural selection causes change. Fitness is the single measure of the capacity of organisms to survive and contribute offspring to the next generation [19, 27]. As such, fitness may be viewed as a property of individuals, although it occasionally reflects properties of populations and even species [23]. As a result of this survival and reproduction process, some individuals have a higher fitness, because they are more successful in passing on genes to the subsequent gen-

eration than other individuals. For change to occur as a result of natural selection, it is essential that individuals within a population vary in fitness and that the differences are at least partially caused by differences in genetic composition. Therefore, a prerequisite for natural selection to be an effective evolutionary force is that fitness must have a heritable component [23].

In the density-dependent selection model we study, fitness values are assigned to each genotype. These values represent the total fitness of individuals having the same genotype and include the ability to survive and to produce offspring successfully. Consequently, they reflect the per capita contribution of individuals of the genotype to the population of individuals in the next generation. In evolutionary biology, these measures are often referred to as absolute fitnesses [13, 15, 23].

2.4   Migration

Regardless of whether populations occur naturally or in a controlled system, they rarely are isolated from others of the same species. Organisms, or their gametes, often migrate from one population to another, introducing their genes into different populations - a process evolutionary geneticists refer to as gene flow. Without the presence of opposing forces, this behavior causes populations to move towards identical genetic compositions. When other factors result in reduced genetic variability within populations, gene flow can lead to increased genetic diversity. As might be expected, the flow of transgenes into natural populations can be investigated using the models developed to study the effects of gene migration [7].

Migration models have been developed to study the interactions between two populations as well as more complex relationships that involve multiple populations. In these models, the flow of genes and individuals between populations can be either uni-directional or multi-directional. As already noted, the most basic of these paradigms is the continent-island model, where migration in each generation occurs from a continent population to an insular population [14, 15]. This model provides the framework

for the research reported here, where we consider that either transgenes or conventional genes are transmitted to an island population from a source population. We investigate allele frequency and population size changes that occur in the recipient population.

Allele frequency behavior in an island population undergoing constant migration has been studied previously for the basic two-allele genetics model in which population size is not included as a factor [14, 15]. Under these conditions, the allele frequency for the island populations approaches an equilibrium value that is equal to the allele frequency of the migrants. The rate of this approach depends upon the proportion of individuals in the island population that is contributed by the migrating population. These results can be interpreted to represent behavior of transgenes that repeatedly enter a population, provided the introduced genes do not affect fitness.

Most mathematical models in population dynamics and population genetics are autonomous [2], i.e. functional relationships in the models do not explicitly depend on time. However, in the research reported here, we assume that migration is periodic in time. The life cycles of insects, natural life cycle of various species, food availability, or seasonal weather could result in periodic migration [3, 9, 18]. The effects of environmental periodicity have been observed in a laboratory setting. For example, Jillson [18] experimented with a periodic food supply for the flour beetle, *Tribolium castaneum*, and noted fluctuations in population size. Henson and Cushing [16] studied Jillson's experiment and proved the existence and stability of periodic solutions. Costantino et al. [2] validated their results in laboratory experiments.

Franke and Selgrade [9] investigated mathematical issues associated with periodic immigration and devised an approach to study nonautonomous (time-dependent) dynamical systems by examining corresponding autonomous ones. Concepts they introduced will be used in our analysis of a periodic migration model.

2.5   Selection and Migration

Natural selection and migration frequently occur in the same population, making it important to study their combined effects on its genetic and demographic properties. Both processes are likely to be involved in determining the fate of transgenes that have entered natural populations. Our research focuses on dynamics for an island population considered in the context of the continent-island model that is undergoing natural selection and migration.

Natural selection and migration can have differing effects on populations with, for example, selection acting to reduce genetic variability and migration working to increase it up to a point. When the effects of both selection and migration are included in the basic, single locus two-allele genetics model, the dynamics that result differ from those generated by models that treat either of these forces as single factors. For example, in a model that includes selection as the sole active evolutionary force, a stable feasible allele frequency equilibrium is found only when the heterozygote phenotypic fitness is greater than the fitness value for each of the homozygotes. When migration is included in this model, stable equilibria exist for other fitness relationships among genotypes [15, 27, 32]. Similar results have been found for density-dependent selection models [24, 29, 30].

Allele frequency dynamics resulting from the interaction of selection and migration in an island population model were reported first in Haldane [11] and Wright [40]. Equilibrium results were described and determined to be influenced by the strength of selection compared to the strength of migration and the degree of dominance in phenotypic expression [11, 22, 40]. These analyses demonstrated that under certain circumstances, a deleterious allele, i.e. one that acts to reduce fitness, can remain in a population because of immigration [14]. Furthermore, with a high migration rate, an allele that promotes high fitness can disappear from an island population even though it is favored by selection. The possibility of such an elimination was first noticed and reported by Haldane [12]. Our Example 5.2 illustrates this phenomenon when the

degree of dominance of the deleterious allele is large enough.

2.6 Dominance in the Expression of Phenotypes

In the field of genetics, the concept of dominance refers to the influence that an allele has on phenotypic expressions for genotypes at a single locus. More specifically, it indicates the effect of an allele in the heterozygous state as compared to the effect of an allele occurring in the homozygous condition. An allele is said to be completely dominant when it has the same phenotypic effect in the heterozygous state as it does in the homozygous state. In contrast, an allele is said to be recessive when its effect in the heterozygous state is masked by the effect of a dominant allele. No dominance is the condition that occurs when the heterozygote phenotype is exactly intermediate between those two homozygotes. Overdominance, or heterozygote superiority, occurs when the heterozygote phenotype is greater than the phenotypes of the homozygotes. A range of other phenotypic dominance relationships also can occur for alleles. The degree of dominance is a quantitative measure that indicates the magnitude of allelic effects observed for the heterozygous state relative to those observed for homozygotes [8, 10].

For the model we analyze, the phenotypic expressions of interest are values for fitness, and we consider the effect of the degree of dominance on fitness relationships among genotypes. We introduce equations that define the degree of dominance for fitness functions in Chapter 3. As already noted, the degree of dominance for fitness has been shown to influence allele frequency equilibrium behavior arising in the basic genetic version of the continent-island model where population size effects are not included. Selgrade and Roberds [33, 34] have studied a density-dependent selection continent-island model and shown how complete dominance and no dominance can affect allele frequency and population size dynamics. We extend their analyses to include a wider range of dominance relationships and to study additional dynamics for that model.

Chapter 3

The Model

In this chapter, we introduce notation for the terminology discussed in the previous chapter. Then we incorporate the concepts to develop a system of difference equations for a postselection, density-dependent migration model. This system was proposed and previously studied by Roberds and Selgrade [24, 33]. We describe the phase space for the system of difference equations and present formulas that define the degree of dominance. We also compute partial derivatives of fitnesses with respect to the state variables.

3.1 Notation

We consider a diploid population with two alleles, A and a, at a single locus. In the transgene case, the A allele represents the transgene, and the a allele refers to the null allele. The population is composed of individuals with genotypes AA, Aa, and aa. We use a continent-island model in which density-dependent selection occurs in the island population. We denote the island population size by x and the frequency of the A allele in the island population by p, where $0 \leq p \leq 1$. The frequency of the a allele is $1 - p$.

Genotypic fitnesses, denoted by f_{AA}, f_{Aa}, and f_{aa}, are nonnegative functions of

population size. Allelic fitnesses are defined as linear combinations of genotypic fitnesses and are given by

$$f_A(p, x) \equiv p f_{AA}(x) + (1 - p) f_{Aa}(x) \text{ and}$$
$$f_a(p, x) \equiv p f_{Aa}(x) + (1 - p) f_{aa}(x).$$

The population mean fitness is defined by

$$f(p, x) \equiv p f_A(p, x) + (1 - p) f_a(p, x) = p^2 f_{AA}(x) + 2p(1 - p) f_{Aa}(x) + (1 - p)^2 f_{aa}(x).$$

3.2   Model Development

The model we study tracks the frequency p of allele A in the population and the population size x from one generation to the next, as described by Roughgarden [27]. Other models consider the numbers of each genotype present in the population. For instance, Li [20, 21] has studied the effect of mixing of transgenic mosquitoes that resist malaria with non-resistant mosquitoes in models without migration terms. He studied a two dimensional system that keeps track of the number of transgenic alleles as well as the number of null alleles [20]. Another model investigated by Li is a three dimensional system that depicts the number of wild genotypes, the number of homozygous transgenes as well as the number of heterozygous transgenes [21]. He reported stability and equilibrium results for these systems.

The model we use was first developed by Roberds and Selgrade [24]. Following selection in each generation, we assume g gametes immigrate to the island population from the continent population. The immigration process is illustrated in Figure 3.1. The frequency of the A allele in the migrant gametes is represented by q, a constant where $0 \leq q \leq 1$. After migration, random mating occurs. The number of gametes that unite to produce zygotes in the next generation is

$$2p^2 f_{AA}(x)x + 4p(1 - p) f_{Aa}(x)x + 2(1 - p)^2 f_{aa}(x)x + g,$$

and, hence, the population size in the next generation is

$$xf(p, x) + \frac{g}{2}.$$

The number of the gametes in the next generation that possess the A allele is

$$2p^2 f_{AA}(x)x + 2p(1-p)f_{Aa}(x)x + qg.$$

Hence, the frequency of the A allele in the next generation is

$$\frac{p^2 f_{AA}(x)x + p(1-p)f_{Aa}(x)x + q\frac{g}{2}}{p^2 f_{AA}(x)x + 2p(1-p)f_{Aa}(x)x + (1-p)^2 f_{aa}(x)x + \frac{g}{2}}.$$

The number of additional zygotes in the next generation due to immigration is denoted by $y = \frac{g}{2}$. Making this substitution, we have the following system of difference equations that describe the change in allele frequency and population size from generation n to generation $n+1$

$$p_{n+1} = \frac{p_n x_n f_A(p_n, x_n) + qy}{x_n f(p_n, x_n) + y}$$

$$x_{n+1} = x_n f(p_n, x_n) + y. \tag{3.1}$$

Selgrade and Roberds [33] described how periodic migration can be introduced into this system of equations. To follow how this can be accomplished, assume periodic migration into the island population from a continent population with period k, where k is a nonnegative integer. For $\alpha \in \mathbb{R}$, such that $0 \le \alpha < 1$, we multiply the constant immigration y by the factor $1 + \alpha g_k(n)$ where $-1 \le g_k(n) \le 1$ and $g_k(n+k) = g_k(n)$ for $n = 0, 1, 2, \ldots$, for example, $g_k(n) = \cos\left(\frac{2\pi n}{k}\right)$. This produces immigration of period k that varies between $y(1-\alpha)$ and $y(1+\alpha)$ and αy is the maximum variation in migration from y. To restrict the amount of migrants in the population, we assume that $y(1+\alpha) \le x$. Thus, in any generation, the migrating population is less than what is already present in the population. Including the immigration of period k,
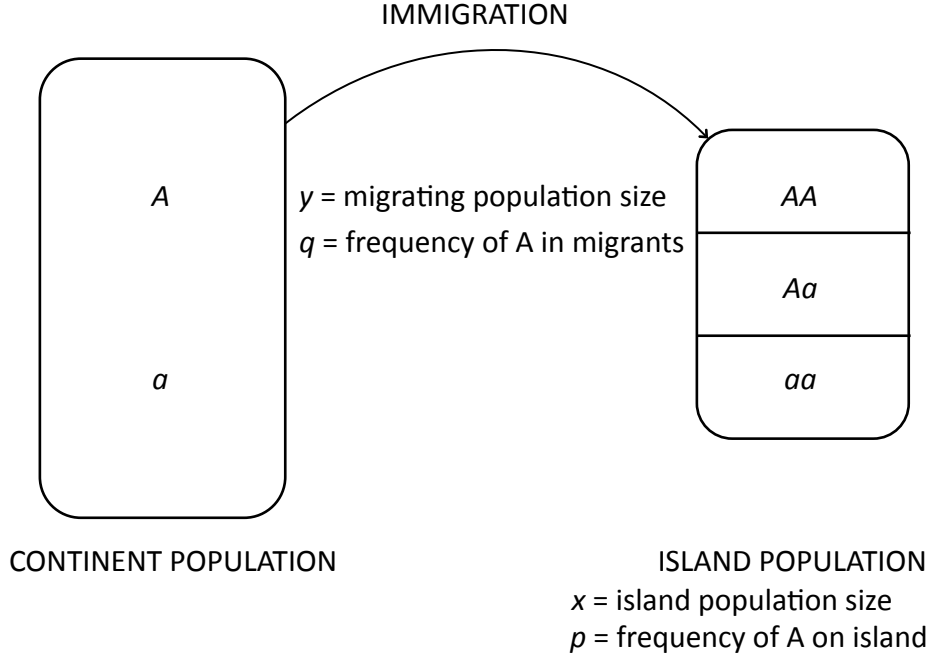
Figure 3.1: Schematic illustration of migration in the continent-island model

system (3.1) becomes

$$p_{n+1} = \frac{p_n x_n f_A(p_n, x_n) + qy(1 + \alpha g_k(n))}{x_n f(p_n, x_n) + y(1 + \alpha g_k(n))}$$

$$x_{n+1} = x_n f(p_n, x_n) + y(1 + \alpha g_k(n)). \tag{3.2}$$

We introduce a per capita migration rate per generation relative to the island population size $x > 0$ given by $h(x) = \dfrac{y}{x}$. The migration rate is a decreasing function of population size since $h'(x) = -\dfrac{y}{x^2} < 0$. Replacing y by $xh(x)$ in (3.2), the system

becomes

$$p_{n+1} = \frac{p_n f_A(p_n, x_n) + qh(x_n)(1 + \alpha g_k(n))}{f(p_n, x_n) + h(x_n)(1 + \alpha g_k(n))}$$

$$x_{n+1} = x_n(f(p_n, x_n) + h(x_n)(1 + \alpha g_k(n))),$$

(3.3)

which is the two-dimensional time-dependent dynamical system that we study.

3.3   Phase Space

When $\alpha = 0$, the transition equations become

$$p_{n+1} = \frac{p_n f_A(p_n, x_n) + qh(x_n)}{f(p_n, x_n) + h(x_n)}$$

$$x_{n+1} = x_n(f(p_n, x_n) + h(x_n)).$$

(3.4)

The phase space for the system (3.4) is the slot in the (p, x)-plane defined by

$$\mathcal{S} \equiv \{(p, x) : 0 \leq p \leq 1, 0 < x\}.$$

When $y = 0$ (i.e. $h = 0$), the vertical boundary lines of $\mathcal{S}$ are invariant and the alleles are fixed. If $y > 0$ and $0 < q < 1$, then points on $\{p = 0\}$ and $\{p = 1\}$ are mapped into the interior of $\mathcal{S}$. An orbit $\{(p_n, x_n) : n = 0, 1, 2, \ldots\}$ is obtained after repeated iteration of (3.4). The line $\{p = q\}$ divides the region $\mathcal{S}$ into two subregions

$$\mathcal{S}^+ \equiv \{(p, x) : q \leq p \leq 1, 0 < x\} \text{ and}$$

$$\mathcal{S}^- \equiv \{(p, x) : 0 \leq p \leq q, 0 < x\}.$$

The system (3.3) has periodic migration and is time-dependent. When plotting orbits of (3.3) in $\mathcal{S}$, different orbits may intersect. Including time as a phase variable will remedy this problem. Franke and Selgrade [9] studied a time-periodic system by looking at a corresponding time-independent dynamical system defined on the cylinder space $\mathcal{H}$ which is the Cartesian product of $\mathcal{S}$ and the discrete space $\{0, 1, \ldots k-1\}$,

i.e.

$$\mathcal{H} \equiv \{0, 1, \ldots, k-1\} \times \mathcal{S}.$$

The plane $\{p = q\}$ divides the region $\mathcal{H}$ into two subregions

$$\mathcal{H}^+ \equiv \{(n, p, x) : 0 \le n \le k-1, q \le p \le 1, 0 < x\} \text{ and}$$

$$\mathcal{H}^- \equiv \{(n, p, x) : 0 \le n \le k-1, 0 \le p \le q, 0 < x\}.$$

3.4 Degree of Dominance for Fitness

As discussed in the previous chapter, we are interested in the effects of varying the degree of dominance on the dynamical behavior produced by our model. The fitness for the heterozygote genotype can be expressed as a linear combination of the two homozygotic fitnesses, i.e. general dominance. For a real parameter δ, we have

$$f_{Aa}(x) = \delta f_{AA}(x) + (1 - \delta) f_{aa}(x) = f_{aa}(x) + \delta(f_{AA}(x) - f_{aa}(x)) \tag{3.5}$$

for all $x > 0$.

Complete dominance in fitness occurs when the heterozygote fitness is the same as one of the homozygote fitnesses. Clearly then, when $\delta = 1$, the A allele has the property of complete dominance, but when $\delta = 0$, it is the a allele that possesses this property. No dominance in fitness occurs when $\delta = \frac{1}{2}$, so $f_{Aa}(x) = \frac{1}{2}(f_{AA}(x) + f_{aa}(x))$. Selgrade and Roberds [33] studied the two-dimensional time-dependent dynamical system for the case of complete dominance and no dominance. For the case when $f_{AA}(x) > f_{aa}(x)$ and when $\delta > 1$, the phenomenon of overdominance occurs. Overdominance is thought to be irrelevant for investigations that treat transgenes. Partial dominance occurs when $0 < \delta < 1$. General dominance occurs when $0 \le \delta \le 1$ and is the major focus of our studies.

After substitution of expression (3.5) for $f_{Aa}(x)$ and rearranging terms, the allele

and mean fitnesses become

$$f_A(p, x) = f_{aa}(x) + (p + \delta - \delta p)(f_{AA}(x) - f_{aa}(x))$$
$$f_a(p, x) = f_{aa}(x) + \delta p(f_{AA}(x) - f_{aa}(x)) \tag{3.6}$$
$$f(p, x) = f_{aa}(x) + p(p + 2\delta - 2\delta p)(f_{AA}(x) - f_{aa}(x)).$$

And the partial derivatives of the allele and mean fitnesses are found to be:

$$\frac{\partial f_A}{\partial p} = (1 - \delta)(f_{AA}(x) - f_{aa}(x))$$

$$\frac{\partial f_A}{\partial x} = f'_{aa}(x) + (p + \delta - \delta p)(f'_{AA}(x) - f'_{aa}(x))$$

$$\frac{\partial f_a}{\partial p} = \delta(f_{AA}(x) - f_{aa}(x))$$

$$\frac{\partial f_a}{\partial x} = f'_{aa}(x) + \delta p(f'_{AA}(x) - f'_{aa}(x)) \tag{3.7}$$

$$\frac{\partial f}{\partial p} = 2(p + \delta - 2\delta p)(f_{AA}(x) - f_{aa}(x)) = 2(f_A(p, x) - f_a(p, x))$$

$$\frac{\partial f}{\partial x} = f'_{aa}(x) + p(p + 2\delta - 2\delta p)(f'_{AA}(x) - f'_{aa}(x)).$$

Chapter 4

Equilibria

In this chapter, we discuss properties of equilibria. We first define what an equilibrium is, in particular, a polymorphic equilibrium. We demonstrate that polymorphic equilibria exist for our model. Then, we give conditions that ensure an equilibrium is unique. Finally, we state conditions needed to ensure that the equilibrium is stable.

4.1 Definition

An equilibrium $E = (\bar{p}, \bar{x})$ occurs when both allele frequency $\bar{p}$, $0 \leq \bar{p} \leq 1$, and population density $\bar{x}$, $\bar{x} > 0$, are constant across generations, i.e. $p_n = \bar{p}$ and $x_n = \bar{x}$. Furthermore, an equilibrium E is said to be polymorphic if $0 < \bar{p} < 1$, i.e. both alleles persist in the population [8, 27]. From (3.3), an equilibrium $E = (\bar{p}, \bar{x})$ must satisfy the following system for all n:

$$
\begin{aligned}
\bar{p} &= \bar{p} f_A(\bar{p}, \bar{x}) + q h(\bar{x})(1 + \alpha g_k(n)) \\
1 &= f(\bar{p}, \bar{x}) + h(\bar{x})(1 + \alpha g_k(n)).
\end{aligned}
\tag{4.1}
$$

Since (4.1) has to hold for all n, the system in (3.3) has equilibria only if $g_k(n)$ is constant, i.e. the immigration is constant. Without loss of generality, we assume $\alpha = 0$ and examine the system of difference equations given in (3.4). Thus, at

equilibria,

$$\bar{p} = \bar{p}f_A(\bar{p}, \bar{x}) + qh(\bar{x})$$
$$1 = f(\bar{p}, \bar{x}) + h(\bar{x}).$$

(4.2)

Moreover, at an equilibrium, the frequency of allele a is constant, i.e., $1 - p_n = 1 - \bar{p}$, and

$$1 - \bar{p} = (1 - \bar{p})f_a(\bar{p}, \bar{x}) + (1 - q)h(\bar{x})$$

(4.3)

must be satisfied. A polymorphic equilibrium is a point of intersection of the three isocline curves:

$$\mathcal{C} \equiv \{(p, x) : f(p, x) + h(x) = 1\}$$
$$\mathcal{C}_A \equiv \{(p, x) : p[f_A(p, x) - 1] + qh(x) = 0\}$$
$$\mathcal{C}_a \equiv \{(p, x) : (1 - p)[f_a(p, x) - 1] + (1 - q)h(x) = 0\}.$$

(4.4)

The intersection of any pair of equations in (4.4) will determine E.

We assume fertility and survival rates are high when the population size is small, i.e. $f_{ij}(0) > 1$ for $i, j = A, a$. Due to crowding, genotypic fitnesses approach zero as the population size increases, so the genotypic fitnesses are decreasing functions of the population density. Accordingly, for $i, j = A, a$ we make the following assumption:

$$f'_{ij}(x) < 0 \text{ for all } x > 0, \ f_{ij}(0) > 1 \text{ and } f_{ij}(x) \to 0 \text{ as } x \to \infty.$$

(4.5)

From (4.5), it follows that $\frac{\partial f_A}{\partial x} < 0$, $\frac{\partial f_a}{\partial x} < 0$, and $\frac{\partial f}{\partial x} < 0$. The implicit function theorem says that the curves defined in (4.4) may be considered as the graphs of x as functions of p. We denote these by $\tilde{x}(p)$, $\tilde{x}_A(p)$, and $\tilde{x}_a(p)$, respectively. In fact,

we compute

$$\frac{d\tilde{x}}{dp} = \frac{-\frac{\partial f}{\partial p}}{\frac{\partial f}{\partial x} + h'},$$

$$\frac{d\tilde{x}_A}{dp} = \frac{1 - f_A - p\frac{\partial f_A}{\partial p}}{p\frac{\partial f_A}{\partial x} + qh'}, \text{ and} \qquad (4.6)$$

$$\frac{d\tilde{x}_a}{dp} = \frac{f_a - 1 - (1-p)\frac{\partial f_a}{\partial p}}{(1-p)\frac{\partial f_a}{\partial x} + (1-q)h'}.$$

4.2 Existence

From (4.5) and the fact that $h(x) \to 0$ as $x \to \infty$, Roberds and Selgrade [24] showed that $\tilde{x}(p)$ exists for each p, $0 \le p \le 1$, and $\mathcal{C}$ separates $\mathcal{S}$ into two subsets. For each p, $0 < p < 1$, $\tilde{x}_A(p)$ exists and there is a vertical asymptote at $p = 0$. Also, $\tilde{x}(1) > \tilde{x}_A(1)$. Thus, near $p = 0$, $\mathcal{C}_A$ is above $\mathcal{C}$ and at $p = 1$, $\mathcal{C}_A$ is below $\mathcal{C}$. Roberds and Selgrade concluded that the isoclines must intersect at least once and there is at least one polymorphic equilibrium. The only assumption they made about the fitnesses was (4.5), so their proof holds for the case of general dominance as well.

Theorem 4.1. *Fix $0 < q < 1$. Assume that genotype fitnesses satisfy (4.5), (3.5), $0 \le \delta \le 1$, and that $h(x) = \frac{y}{x}$ where $y > 0$ is constant. Then (3.4) has at least one polymorphic equilibrium, $E = (\bar{p}, \bar{x})$, $0 < \bar{p} < 1$ and $\bar{x} > 0$.*

We can make conclusions concerning the position of the allele frequency of the polymorphic equilibrium with respect to allele frequency of the migrants by looking at the equations in (4.2) satisfied at equilibrium. Multiplying the second equation in (4.2) by $\bar{p}$ and subtracting from the first equation gives

$$0 = \bar{p}[f_A(\bar{p}, \bar{x}) - f(\bar{p}, \bar{x})] + (q - \bar{p})h(\bar{x}).$$

Thus, using (3.6) yields,

$$(\bar{p} - q)h(\bar{x}) = \bar{p}[f_{AA}(\bar{x}) - f_{aa}(\bar{x})](1 - \bar{p})[\bar{p}(1 - \delta) + \delta(1 - \bar{p})]. \qquad (4.7)$$

If $f_{AA}(\bar{x}) \geq f_{aa}(\bar{x})$, the right hand side of (4.7) is nonnegative and thus $\bar{p} \geq q$. If $f_{AA}(\bar{x}) \leq f_{aa}(\bar{x})$, the right hand side of (4.7) is not positive and hence $\bar{p} \leq q$.

Proposition 4.2. *Assume that each genotype fitness satisfies (4.5), (3.5) and $0 \leq \delta \leq 1$. Let $E = (\bar{p}, \bar{x})$ be a polymorphic equilibrium. If $f_{AA}(\bar{x}) \geq f_{aa}(\bar{x})$, then $q \leq \bar{p} < 1$. If $f_{AA}(\bar{x}) \leq f_{aa}(\bar{x})$, then $0 < \bar{p} \leq q$.*

4.3 Uniqueness

Selgrade and Roberds [34] found conditions for which the polymorphic equilibrium is unique for the cases of complete dominance and no dominance. In addition, they made conclusions about the size of $\bar{p}$ compared to q.

Selgrade, Bostic, and Roberds [29] extended the conditions to show uniqueness for general dominance where we assumed $f_{AA}(x) > f_{aa}(x)$. We discuss these results and then extend and improve these conditions to show the polymorphic equilibrium is unique for the case of general dominance when $f_{AA}(\bar{x}) < f_{aa}(\bar{x})$.

4.3.1 Assume $f_{AA}(\bar{x}) > f_{aa}(\bar{x})$ at each equilibrium

To show that the the polymorphic equilibrium is unique, we will show that the isoclines can cross at most once. For $f_{AA}(\bar{x}) > f_{aa}(\bar{x})$ at each equilibrium, we will show that where the isoclines C and C_A cross,

$$\frac{d\tilde{x}_A}{dp} < \frac{d\tilde{x}}{dp}. \tag{4.8}$$

Thus, for $0 < p < 1$, as p increases, $\mathcal{C}$ crosses $\mathcal{C}_A$ from below to above and this can happen at most once. There will be one intersection of the isoclines, i.e. the polymorphic equilibrium is unique.

Using (4.6), for $0 < p < 1$, (4.8) is equivalent to

$$\frac{p\left(1 - f_A - p\frac{\partial f_A}{\partial p}\right)}{p\frac{\partial f_A}{\partial x} + qh'} = p\frac{d\tilde{x}_A}{dp} < p\frac{d\tilde{x}}{dp} = \frac{-2p(f_A - f_a)}{\frac{\partial f}{\partial x} + h'}. \tag{4.9}$$

By cross multiplying the first and last terms in (4.9) and moving all the terms to one side, we get the inequality

$$\left\{p\left(1 - f_A - p\frac{\partial f_A}{\partial p}\right)\right\}\left\{\frac{\partial f}{\partial x} + h'\right\} - \{-2p(f_A - f_a)\}\left\{p\frac{\partial f_A}{\partial x} + qh'\right\} < 0. \tag{4.10}$$

We want to show (4.10) holds at each equilibrium $E = (\bar{p}, \bar{x})$. We will use the first equation in (4.2) and substitute $qh(\bar{x})$ for $\bar{p}(1 - f_A)$ in (4.10). Using (3.6) and (3.7) and rearranging the terms according to the factors $f'_{AA}(\bar{x})$, $f'_{aa}(\bar{x})$, and $h'(\bar{x})$ (see Appendix A.1 for details of the computation), we obtain the inequality

$$\begin{aligned}
&f'_{AA}(\bar{x})\{(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))\bar{p}^2[\bar{p}^2(1 - \delta) + 2\delta\bar{p}(1 - \bar{p})(1 - \delta) + 2\delta^2(1 - \bar{p})]\} \\
&+ f'_{AA}(\bar{x})\{q\bar{p}h(\bar{x})(\bar{p} + 2\delta(1 - \bar{p}))\} + f'_{aa}(\bar{x})\{qh(\bar{x})(1 - \bar{p})(1 - \delta\bar{p} + \bar{p}(1 - \delta))\} \\
&+ f'_{aa}(\bar{x})\{(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))\bar{p}^2(1 - \delta)(1 - \bar{p})^2(2\delta - 1)\} \\
&+ h'(\bar{x})\{qh(\bar{x}) + (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))\bar{p}[2\delta q(1 - \bar{p}) + \bar{p}(1 - \delta)(2q - 1)]\} < 0.
\end{aligned} \tag{4.11}$$

Since we are assuming (4.5), all the terms are negative or zero except possibly the term on the third line and the final term. The term in the third line is not positive if $\frac{1}{2} \leq \delta \leq 1$. The last term is not positive if $\frac{1}{2} \leq q \leq 1$. We have for $f_{AA}(\bar{x}) > f_{aa}(\bar{x})$ that (4.11) holds if $\frac{1}{2} \leq \delta \leq 1$ and $\frac{1}{2} \leq q \leq 1$ that the polymorphic equilibrium is unique.

4.3.2   Assume $f_{AA}(\bar{x}) < f_{aa}(\bar{x})$ at each equilibrium

For $f_{AA}(\bar{x}) < f_{aa}(\bar{x})$ at each equilibrium, to show that the polymorphic equilibrium is unique, we will show that where the isoclines C and C_a cross,

$$\frac{d\tilde{x}}{dp} < \frac{d\tilde{x}_a}{dp}. \tag{4.12}$$

Hence C will cross C_a from above to below as p increases for $0 < p < 1$ and this can happen at most once. Therefore, there will be one intersection of the isoclines and the equilibrium is unique.

For $0 < p < 1$, (4.12) is equivalent to showing

$$\frac{-2(1-p)(f_A - f_a)}{\frac{\partial f}{\partial x} + h'} = (1-p)\frac{d\tilde{x}}{dp} < (1-p)\frac{d\tilde{x}_a}{dp} = \frac{(1-p)\left(f_a - 1 - (1-p)\frac{\partial f_a}{\partial p}\right)}{(1-p)\frac{\partial f_a}{\partial x} + (1-q)h'}. \tag{4.13}$$

Cross multiplying the first and last terms in (4.13) and moving all the terms to one side, we obtain the inequality

$$\{-2(1-p)(f_A - f_a)\}\{(1-p)\frac{\partial f_a}{\partial x} + (1-q)h'\} - \{\frac{\partial f}{\partial x} + h'\}\{(1-p)(f_a - 1 - (1-p)\frac{\partial f_a}{\partial p})\} < 0. \tag{4.14}$$

We use (4.3) to substitute $(q-1)h(\bar{x})$ for $(1-\bar{p})(f_a - 1)$ in (4.14) to show that (4.14) holds at each equilibrium $E = (\bar{p}, \bar{x})$. We use the fitnesses and their derivatives given in (3.6) and (3.7) and rearrange terms by factors of $f'_{AA}(\bar{x})$, $f'_{aa}(\bar{x})$, and $h'(\bar{x})$ (see

details in Appendix A.2) to obtain the inequality

$$
\begin{aligned}
&f'_{AA}(\bar{x})\{((f_{AA}(\bar{x}) - f_{aa}(\bar{x}))\delta\bar{p}^2(1-\bar{p})^2(2\delta-1)\}\\
&+ f'_{AA}(\bar{x})\{\bar{p}(1-q)(\bar{p}+2\delta(1-\bar{p}))h(\bar{x})\}\\
&+ f'_{aa}(\bar{x})\{(1-\bar{p})(1-\delta\bar{p}+\bar{p}(1-\delta))(1-q)h(\bar{x})\}\\
&+ f'_{aa}(\bar{x})\{((f_{AA}(\bar{x}) - f_{aa}(\bar{x}))(1-\bar{p})^2[-\delta(1-\bar{p})^2 - 2\bar{p}(1-\delta)(1-\delta\bar{p})]\}\\
&+ h'(\bar{x})[(1-q)h(\bar{x}) + (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))(1-\bar{p})[2\bar{p}(\delta-1)(1-q) + \delta(\bar{p}-1)(1-2q)]]\\
&< 0.
\end{aligned}
$$

$$(4.15)$$

Assuming (4.5), all the terms in (4.15) are negative or zero except possibly the first term and the last term. The first term is negative if $0 \le \delta \le \dfrac{1}{2}$. The last term is negative if $0 \le q \le \dfrac{1}{2}$. For $f_{AA}(\bar{x}) < f_{aa}(\bar{x})$, we have that (4.15) holds and the polymorphic equilibrium is unique if $0 \le \delta \le \dfrac{1}{2}$ and $0 \le q \le \dfrac{1}{2}$.

We have the following result:

Theorem 4.3. *Assume that each genotype fitness satisfies (4.5) and (3.5). For $f_{AA}(\bar{x}) > f_{aa}(\bar{x})$, if $\dfrac{1}{2} \le \delta \le 1$ and $\dfrac{1}{2} \le q \le 1$ then the polymorphic equilibrium is unique and $q < \bar{p} < 1$. For $f_{AA}(\bar{x}) < f_{aa}(\bar{x})$ if $0 \le \delta \le \dfrac{1}{2}$ and $0 \le q \le \dfrac{1}{2}$ then the polymorphic equilibrium is unique and $0 < \bar{p} < q$.*

4.4 Stability

To determine whether a polymorphic equilibrium is locally stable, we examine the Jury conditions [5]. We evaluate Jacobian matrix of the right hand side of (3.4) at $E = (\bar{p}, \bar{x})$ to obtain $D(E)$. The polymorphic equilibrium is locally stable if both eigenvalues of $D(E)$, λ_1 and λ_2, are inside the unit circle. The Jury conditions state that the equilibrium is locally stable if and only if $|\text{tr}[D(E)]| < 1 + \det[D(E)] < 2$. We consider this condition in pieces to arrive at results related to local stability.

The Jacobian at equilibrium is

$$D(E) = \begin{bmatrix} f_A + \bar{p}\left(\frac{\partial f_A}{\partial p} - \frac{\partial f}{\partial p}\right) & \bar{p}(1-\bar{p})\left(\frac{\partial f_A}{\partial x} - \frac{\partial f_a}{\partial x}\right) + h'(\bar{x})(q-\bar{p}) \\ \bar{x}\frac{\partial f}{\partial p} & 1 + \bar{x}\left(\frac{\partial f}{\partial x} + h'(\bar{x})\right) \end{bmatrix}. \quad (4.16)$$

4.4.1   Determinant

We first derive an expression for the determinant of the Jacobian. We propose that $\det[D(E)] < 1$. If the eigenvalues are complex and $\det[D(E)] < 1$ then the equilibrium is locally stable. Using (3.6) and (3.7), for $0 \le \delta \le 1$, we compute that the determinant of $D(E)$ in terms of the derivatives of the genotype fitnesses is (see Appendix A.3.1 for details of the computation)

$$\begin{aligned} \det[D(E)] = & f_{Aa}(\bar{x}) + 2\bar{p}(1-\bar{p})(1-2\delta)(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) \\ & + \bar{x}f'_{AA}(\bar{x})[f_{AA}(\bar{x})\delta\bar{p}^2 + f_{aa}(\bar{x})\bar{p}(\bar{p}(1-\delta) + 2\delta(1-\bar{p}))] \\ & + \bar{x}f'_{aa}(\bar{x})[f_{AA}(\bar{x})(1-\bar{p})(2\bar{p}(1-\delta) + \delta(1-\bar{p})) + f_{aa}(\bar{x})(1-\bar{p})^2(1-\delta)] \\ & + \bar{x}h'(\bar{x})[f_{aa}(\bar{x}) + (\bar{p} + \delta - 2\delta q - 2\bar{p}q - 2\delta\bar{p} + 4\delta\bar{p}q)(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))]. \end{aligned}$$
$$(4.17)$$

We define the term multiplied by $\bar{x}h'(\bar{x})$, as

$$H(q, \delta) = f_{aa}(\bar{x}) + (2\bar{p} + \delta - 2\delta q - 2\bar{p}q - 2\delta\bar{p} + 4\delta\bar{p}q)(f_{AA}(\bar{x}) - f_{aa}(\bar{x})). \quad (4.18)$$

4.4.1.1   Assume $f_{AA}(\bar{x}) > f_{aa}(\bar{x})$

For $f_{AA}(\bar{x}) > f_{aa}(\bar{x})$, assuming (4.5) and using $\bar{p} > q$, we rewrite $H(q, \delta)$ (4.18) as

$$\begin{aligned} H(q, \delta) &= f_{aa}(\bar{x}) + (\bar{p} - \delta q + \delta - \delta q + \bar{p} - 2\bar{p}q - 2\delta\bar{p} + 4\delta\bar{p}q)(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) \\ &> f_{aa}(\bar{x}) + [q - \delta q + \delta - \delta q + \bar{p}(1-2q)(1-2\delta)](f_{AA}(\bar{x}) - f_{aa}(\bar{x})) \\ &= f_{aa}(\bar{x}) + [q(1-\delta) + \delta(1-q) + \bar{p}(1-2\delta)(1-2q)](f_{AA}(\bar{x}) - f_{aa}(\bar{x})). \end{aligned}$$

Thus, we have that

$$
\begin{aligned}
\det[D(E)] <& f_{Aa}(\bar{x}) + 2\bar{p}(1-\bar{p})(1-2\delta)(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) \\
&+ \bar{x}f'_{AA}(\bar{x})\bar{p}[\delta\bar{p}f_{AA}(\bar{x}) + (\bar{p}(1-\delta) + 2\delta(1-\bar{p}))f_{aa}(\bar{x})] \\
&+ \bar{x}f'_{aa}(\bar{x})(1-\bar{p})[(2\bar{p}(1-\delta) + \delta(1-\bar{p}))f_{AA}(\bar{x}) + (1-\bar{p})(1-\delta)f_{aa}(\bar{x})] \\
&+ \bar{x}h'(\bar{x})[(q(1-\delta) + \delta(1-q))(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) + f_{aa}(\bar{x}) \\
&\qquad + \bar{p}(1-2\delta)(1-2q)(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))].
\end{aligned}
$$
(4.19)

Rewriting the first equation in (4.2), we have $\bar{p}(1 - f_A(\bar{p}, \bar{x})) = qh(\bar{x})$. The right hand side is positive and hence $f_A(\bar{p}, \bar{x}) < 1$. Also, using (3.6),

$$
1 > f_A(\bar{p}, \bar{x}) = \bar{p}f_{AA}(\bar{x}) + (1-\bar{p})f_{Aa}(\bar{x}) = \bar{p}(f_{AA}(\bar{x}) - f_{Aa}(\bar{x})) + f_{Aa}(\bar{x}).
$$

Using (3.5) and (4.2), the first term in (4.19) is less than one. The second term is not positive if $\frac{1}{2} \leq \delta \leq 1$. Since we are assuming (4.5), the last term is not positive if $\frac{1}{2} \leq \delta \leq 1$ and $\frac{1}{2} \leq q \leq 1$. The other terms in the determinant are negative. Thus, for $f_{AA}(\bar{x}) > f_{aa}(\bar{x})$, $\det[D(E)] < 1$ if $\frac{1}{2} \leq \delta \leq 1$ and $\frac{1}{2} \leq q \leq 1$.

4.4.1.2 Assume $f_{AA}(\bar{x}) < f_{aa}(\bar{x})$

For $f_{AA}(\bar{x}) < f_{aa}(\bar{x})$, we assume (4.5) and $\bar{p} < q$.

We want to determine conditions where $H(q, \delta)$ is positive. We use that at equi-

librium $\bar{p} < q$ to obtain

$$
\begin{aligned}
H(q, \delta) =& [2\bar{p} + \delta - 2\delta q - 2\bar{p}q - 2\delta\bar{p} + 4\delta\bar{p}q - 1](f_{AA}(\bar{x}) - f_{aa}(\bar{x})) + f_{AA}(\bar{x}) \\
>& [-1 + \delta - 2\delta q + 2\bar{p} - 2\bar{p}q - 2\delta\bar{p} + 4\delta\bar{p}q](f_{AA}(\bar{x}) - f_{aa}(\bar{x})) \\
=& [-1 + 2q + 2\delta - 4\delta q + \bar{p} - 2\bar{p}q - 2\delta\bar{p} + 4\delta\bar{p}q - 2q - \delta + \bar{p} + 2\delta q] \\
& * (f_{AA}(\bar{x}) - f_{aa}(\bar{x})) \\
=& [(2q - 1)(1 - 2\delta) + \bar{p}(1 - 2q)(1 - 2\delta) + 2q(\delta - 1) + \bar{p} - \delta](f_{AA}(\bar{x}) - f_{aa}(\bar{x})) \\
>& [(1 - 2q)(1 - 2\delta)(\bar{p} - 1) + 2\bar{p}(\delta - 1) + \bar{p} - \delta](f_{AA}(\bar{x}) - f_{aa}(\bar{x})) \\
=& [(1 - 2q)(1 - 2\delta)(\bar{p} - 1) + 2\delta\bar{p} - \bar{p} - \delta](f_{AA}(\bar{x}) - f_{aa}(\bar{x})) \\
=& [(1 - 2q)(1 - 2\delta)(\bar{p} - 1) + (\delta(\bar{p} - 1) + \bar{p}(\delta - 1)](f_{AA}(\bar{x}) - f_{aa}(\bar{x})).
\end{aligned}
$$

Hence,

$$
\begin{aligned}
\det[D(E)] <& f_{Aa}(\bar{x}) + 2\bar{p}(1 - \bar{p})(1 - 2\delta)(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) \\
& + \bar{x}f'_{AA}(\bar{x})\bar{p}[\delta\bar{p}f_{AA}(\bar{x}) + (\bar{p}(1 - \delta) + 2\delta(1 - \bar{p}))f_{aa}(\bar{x})] \\
& + \bar{x}f'_{aa}(\bar{x})(1 - \bar{p})[(2\bar{p}(1 - \delta) + \delta(1 - \bar{p}))f_{AA}(\bar{x}) + (1 - \bar{p})(1 - \delta)f_{aa}(\bar{x})] \\
& + \bar{x}h'(\bar{x})[(1 - 2q)(1 - 2\delta)(\bar{p} - 1) + (\delta(\bar{p} - 1) + \bar{p}(\delta - 1)](f_{AA}(\bar{x}) - f_{aa}(\bar{x})).
\end{aligned}
$$
(4.20)

Using (4.3), we have that $(1 - \bar{p})(1 - f_a(\bar{p}, \bar{x})) = (1 - q)h(\bar{x})$. The right hand side is positive, so $f_a(\bar{p}, \bar{x}) < 1$. Also, using (3.5), we know that $f_{aa}(\bar{x}) > f_{Aa}(\bar{x})$. We have $f_a(\bar{p}, \bar{x}) = \bar{p}f_{Aa}(\bar{x}) + (1 - \bar{p})f_{aa}(\bar{x}) = (1 - \bar{p})(f_{aa}(\bar{x}) - f_{Aa}(\bar{x})) + f_{Aa}(\bar{x}) < 1$. Hence, $f_{Aa}(\bar{x}) < 1$.

For $f_{AA}(\bar{x}) < f_{aa}(\bar{x})$, the second term is not positive if $0 \le \delta \le \dfrac{1}{2}$. The last term is not positive if both $0 \le \delta \le \dfrac{1}{2}$ and $0 \le q \le \dfrac{1}{2}$. The other terms in the determinant are negative.

We have established the following result:

Lemma 4.4. *For a polymorphic equilibrium $E = (\bar{p}, \bar{x})$ exhibiting (3.5) and (4.5)*

if $f_{AA}(\bar{x}) > f_{aa}(\bar{x})$ *and if* $\dfrac{1}{2} \leq q \leq 1$ *and* $\dfrac{1}{2} \leq \delta \leq 1$ *then* $\det(D(E)) < 1$. *If* $f_{AA}(\bar{x}) < f_{aa}(\bar{x})$ *and if* $0 \leq q \leq \dfrac{1}{2}$ *and* $0 \leq \delta \leq \dfrac{1}{2}$ *then* $\det(D(E)) < 1$.

If the respective conditions on q and δ are met, and if the eigenvalues of $D(E)$ are complex then they are both inside the unit circle and E is locally asymptotically stable.

4.4.2 $\quad 1 - \mathbf{tr}[D(E)] + \det[D(E)]$

Next, we want to find conditions so that $1 - \mathrm{tr}[D(E)] + \det[D(E)] > 0$. If we can prove this, then if $\det[D(E)] < 1$, we can guarantee an upper bound on the eigenvalues of $D(E)$ because

$$1 - \mathrm{tr}[D(E)] + \det[D(E)] = 1 - (\lambda_1 + \lambda_2) + \lambda_1\lambda_2 = (1 - \lambda_1)(1 - \lambda_2).$$

Thus, if eigenvalues are real, they both must be less than 1. However, we still need a lower bound on the eigenvalues to make a conclusion about stability.

We compute (see details of the computation in Appendix A.3.2, equation (A.14))

$$
\begin{aligned}
&1 - \mathrm{tr}[D(E)] + \det[D(E)] \\
&= \bar{x} f'_{AA}(\bar{x})[f_{AA}(\bar{x})\delta\bar{p}^2 + f_{aa}(\bar{x})(\bar{p}^2 + 2\delta\bar{p} - 3\delta\bar{p}^2) - \bar{p}^2 - 2\delta\bar{p} + 2\delta\bar{p}^2] \\
&\quad + \bar{x} f'_{aa}(\bar{x})[f_{AA}(\bar{x})(2\bar{p} + \delta - 4\delta\bar{p} - 2\bar{p}^2 + 3\delta\bar{p}^2) \\
&\qquad\qquad + f_{aa}(\bar{x})(-2\bar{p} - \delta + 2\delta\bar{p} + \bar{p}^2 - \delta\bar{p}^2 + 1) + \bar{p}^2 + 2\delta\bar{p} - 2\delta\bar{p}^2 - 1] \\
&\quad + \bar{x} h'(\bar{x})[f_{AA}(\bar{x})(2\bar{p} - 2\delta\bar{p} + \delta - 2\bar{p}q - 2\delta q + 4\delta\bar{p}q) \\
&\qquad\qquad + f_{aa}(\bar{x})(-2\bar{p} + 2\delta\bar{p} - \delta + 2\bar{p}q + 2\delta q - 4\delta\bar{p}q + 1) - 1].
\end{aligned}
$$

$$(4.21)$$

We examine terms that are multipliers for the various derivatives. The terms that are multiplied by $\bar{x} f'_{AA}(\bar{x})$ are denoted by $A(\delta)$ where

$$A(\delta) = f_{AA}(\bar{x})\delta\bar{p}^2 + f_{aa}(\bar{x})(\bar{p}^2 + 2\delta\bar{p} - 3\delta\bar{p}^2) - 2\delta\bar{p} - \bar{p}^2 + 2\delta\bar{p}^2.$$

The terms multiplied by $\bar{x}f'_{aa}(\bar{x})$ are denoted as $B(\delta)$ where

$$B(\delta) = f_{AA}(\bar{x})(2\bar{p} + \delta - 4\delta\bar{p} - 2\bar{p}^2 + 3\delta\bar{p}^2) + f_{aa}(\bar{x})(-2\bar{p} - \delta + 2\delta\bar{p} + \bar{p}^2 - \delta\bar{p}^2 + 1)$$
$$+ 2\delta\bar{p} - 2\delta\bar{p}^2 - 1 + \bar{p}^2.$$

And finally, the terms multiplied by $\bar{x}h'(\bar{x})$ are represented as $C(q, \delta)$, giving

$$C(q, \delta) = f_{AA}(\bar{x})(2\bar{p} - 2\delta\bar{p} + \delta - 2\bar{p}q - 2\delta q + 4\delta\bar{p}q)$$
$$+ f_{aa}(\bar{x})(-2\bar{p} + 2\delta\bar{p} - \delta + 2\bar{p}q + 2\delta q - 4\delta\bar{p}q + 1) - 1.$$

4.4.2.1 Assume $f_{AA}(\bar{x}) > f_{aa}(\bar{x})$

For $f_{AA}(\bar{x}) > f_{aa}(\bar{x})$, we rewrite the terms multiplied by $\bar{x}f'_{AA}(\bar{x})$ (see equation (A.15)) as

$$A(\delta) = \bar{p}[\bar{p}(f_{Aa}(\bar{x}) - 1) + 2\delta(1 - \bar{p})(f_{aa}(\bar{x}) - 1)].$$

Since $f_{Aa}(\bar{x}) < 1$ and $f_{aa}(\bar{x}) < 1$ when $f_{AA}(\bar{x}) > f_{aa}(\bar{x})$, then $A(\delta) < 0$ for all δ, $0 \le \delta \le 1$.

For the terms multiplied by $\bar{x}f'_{aa}(\bar{x})$, we consider the cases for $f_{AA}(\bar{x}) \le 1$ and $f_{AA}(\bar{x}) > 1$ separately. First, when $f_{AA}(\bar{x}) \le 1$, we compute (see equation (A.16))

$$B(\delta) = (1 - \bar{p})[(2\bar{p}(1 - \delta) + \delta(1 - \bar{p}))(f_{AA}(\bar{x}) - 1) + (1 - \bar{p})(1 - \delta)(f_{aa}(\bar{x}) - 1)].$$

Because we assume $f_{AA}(\bar{x}) \le 1$, $B(\delta) < 0$ for all δ, $0 \le \delta \le 1$. For the case $f_{AA}(\bar{x}) > 1$, we use that at equilibrium, $f_A(\bar{p}, \bar{x}) - f_{aa}(\bar{x}) = (\bar{p} + \delta - \delta\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))$ and $f_A(\bar{p}, \bar{x}) - 1 < 0$. As computed in (A.17),

$$B(\delta) < (1 - \bar{p})\bar{p}(1 - 2\delta)(f_{AA}(\bar{x}) - 1).$$

When $f_{AA}(\bar{x}) > 1$ and $\frac{1}{2} \le \delta \le 1$, $B(\delta) < 0$. Therefore, for $f_{AA}(\bar{x}) > 1$ or $f_{AA}(\bar{x}) < 1$, when $\frac{1}{2} \le \delta \le 1$ then $B(\delta) < 0$.

For the terms multiplied by $\bar{x}h'(\bar{x})$, (see (A.18) for details) we compute

$$C(q, \delta) < [\bar{p}(1 - \delta)(1 - 2q) - 2\delta q(1 - \bar{p})](f_{AA}(\bar{x}) - f_{aa}(\bar{x})).$$

And, $C(q, \delta) < 0$ when $\frac{1}{2} \leq q \leq 1$ for all δ, $0 \leq \delta \leq 1$.

Thus for $f_{AA}(\bar{x}) > f_{aa}(\bar{x})$ since we are assuming (4.5), when $\frac{1}{2} \leq \delta \leq 1$ and $\frac{1}{2} \leq q \leq 1$, then $1 - \text{tr}[D(E)] + \det[D(E)] > 0$.

4.4.2.2 Assume $f_{AA}(\bar{x}) < f_{aa}(\bar{x})$

When $f_{AA}(\bar{x}) < f_{aa}(\bar{x})$, for terms multiplied by $\bar{x}f'_{AA}(\bar{x})$, we examine the cases $f_{aa}(\bar{x}) \leq 1$ and $f_{aa}(\bar{x}) > 1$ individually. First, we consider the condition $f_{aa}(\bar{x}) \leq 1$, we compute (see (A.19)) that

$$A(\delta) = \bar{p}^2(f_{Aa}(\bar{x}) - 1) + 2\delta\bar{p}(1 - \bar{p})(f_{aa}(\bar{x}) - 1).$$

And $A(\delta) \leq 0$ if $f_{aa}(\bar{x}) < 1$ for all δ, $0 \leq \delta \leq 1$. When $f_{aa}(\bar{x}) > 1$, we compute (see (A.20))

$$A(\delta) < \bar{p}(1 - \bar{p})(2\delta - 1)(f_{aa}(\bar{x}) - 1).$$

If $f_{aa}(\bar{x}) > 1$, $A(\delta) < 0$ when $0 \leq \delta \leq \frac{1}{2}$. If $f_{aa}(\bar{x}) \leq 1$ or $f_{aa}(\bar{x}) > 1$ when $0 \leq \delta \leq \frac{1}{2}$, then $A(\delta) < 0$.

For the terms multiplied by $\bar{x}f'_{aa}(\bar{x})$, we showed (see (A.21)) that

$$B(\delta) < (1 - \bar{p})\bar{p}(1 - 2\delta)(f_{AA}(\bar{x}) - 1)$$

When $f_{AA}(\bar{x}) < f_{aa}(\bar{x})$, we have that $f_{AA}(\bar{x}) < 1$. Thus, $B(\delta) < 0$ when $0 \leq \delta \leq \frac{1}{2}$.

For the terms multiplied by $\bar{x}h'(\bar{x})$, we compute (see (A.22))

$$C(q, \delta) < [(\bar{p}(1 - \delta) + \delta(1 - \bar{p}))(1 - 2q) + \bar{p}(1 - \delta)](f_{AA}(\bar{x}) - f_{aa}(\bar{x})).$$

For $f_{AA}(x) < f_{aa}(x)$, when $0 \leq q \leq \dfrac{1}{2}$, $C(q, \delta) < 0$.

Thus, with Lemma 4.4, we have the following result:

Proposition 4.5. *Let $E = (\bar{p}, \bar{x})$ be a polymorphic equilibrium exhibiting (3.5) and (4.5). For $f_{AA}(\bar{x}) > f_{aa}(\bar{x})$, if $\dfrac{1}{2} \leq q \leq 1$ and $\dfrac{1}{2} \leq \delta \leq 1$ then the real eigenvalues of $D(E)$ are less than 1 and the complex eigenvalues are inside the unit circle. For $f_{AA}(\bar{x}) < f_{aa}(\bar{x})$, if $0 \leq q \leq \dfrac{1}{2}$ and $0 \leq \delta \leq \dfrac{1}{2}$ then the real eigenvalues of $D(E)$ are less than 1 and the complex eigenvalues are inside the unit circle. In both cases, $1 - tr[D(E)] + \det[D(E)] > 0$.*

In Roberds and Selgrade [24] where complete dominance was assumed, it was shown that the additional assumption

$$0 < 1 + \text{tr}[D(E)] + \det[D(E)]$$

guarantees real eigenvalues are inside the unit circle. Their argument applies equally well to the case of general dominance.

4.5   Summary

Roberds and Selgrade [24] proved that for $0 < q < 1$ polymorphic equilibria exist for our model. We found conditions for which the polymorphic equilibrium is unique. We have results about uniqueness and conditions for stability if the fitness for the genotype AA is superior to the fitness for the genotype aa at equilibrium. If the heterozygote fitness is midway between the fitnesses of the homozygotes or closer to the fitness of homozygote AA ($\dfrac{1}{2} \leq \delta \leq 1$) and if at least half of the migrants into the island population are the A allele ($\dfrac{1}{2} \leq q \leq 1$), then there is an unique equilibrium, which is stable under additional assumptions. Also, the frequency of allele A at equilibrium will be greater than the frequency of A in the migrant population (i.e. $\bar{p} > q$).

We proved similar results if the genotypic fitnesses have the reverse relationship, i.e. $f_{AA}(\bar{x}) < f_{aa}(\bar{x})$. If the heterozygote is halfway between the two homozygote fitnesses or closer to that fitness of homozygote aa $(0 \leq \delta \leq \frac{1}{2})$ and at most half of the migrants are the A allele $(0 \leq q \leq \frac{1}{2})$, then the polymorphic equilibrium is unique, and with additional assumptions is stable. Also, we proved that the allele frequency of A at equilibrium is less than the frequency of A in the migrant population (i.e. $\bar{p} < q$).

Chapter 5

Additional Equilibrium Results

Additional equilibrium results are presented in this chapter. First, we investigate the effects resulting from varying the degree of dominance. Then, we demonstrate that under particular conditions a transcritical bifurcation occurs.

5.1 Varying the Degree of Dominance

In this section, we study how both the allele frequency of the polymorphism and the island population size change as the degree of dominance varies, i.e. how $\bar{p}$ and $\bar{x}$ values are affected by shifts in δ.

We use the system satisfied at equilibrium, (4.2), to define functions F and G as follows:

$$F(p, x, \delta) = pf_A + qh - p$$

$$G(p, x, \delta) = f + h - 1.$$

The values of p, x, and δ at equilibrium are simultaneous solutions of $F = 0$ and $G = 0$. The Implicit Function Theorem permits us to express the p and x coordinates

of a solution in terms of the parameter δ in a neighborhood of a solution provided

$$\det \begin{bmatrix} \frac{\partial F}{\partial p} & \frac{\partial F}{\partial x} \\ \frac{\partial G}{\partial p} & \frac{\partial G}{\partial x} \end{bmatrix} \neq 0.$$

Hence, for an equilibrium $E = (\bar{p}, \bar{x})$, $\bar{p}$ and $\bar{x}$ may be considered functions of δ and the derivatives can be expressed in terms of the appropriate Jacobian determinants (see Taylor and Mann [37] for details on formulas). Therefore, the derivative of $\bar{p}$ with respect to δ is:

$$\frac{d\bar{p}}{d\delta} = -\det \begin{bmatrix} \frac{\partial F}{\partial \delta} & \frac{\partial F}{\partial x} \\ \frac{\partial G}{\partial \delta} & \frac{\partial G}{\partial x} \end{bmatrix} \Big/ \det \begin{bmatrix} \frac{\partial F}{\partial p} & \frac{\partial F}{\partial x} \\ \frac{\partial G}{\partial p} & \frac{\partial G}{\partial x} \end{bmatrix}. \tag{5.1}$$

And the derivative of $\bar{x}$ with respect to δ is

$$\frac{d\bar{x}}{d\delta} = -\det \begin{bmatrix} \frac{\partial F}{\partial p} & \frac{\partial F}{\partial \delta} \\ \frac{\partial G}{\partial p} & \frac{\partial G}{\partial \delta} \end{bmatrix} \Big/ \det \begin{bmatrix} \frac{\partial F}{\partial p} & \frac{\partial F}{\partial x} \\ \frac{\partial G}{\partial p} & \frac{\partial G}{\partial x} \end{bmatrix}. \tag{5.2}$$

The component partial derivatives for the determinants are

$$\begin{aligned}
\frac{\partial F}{\partial \delta} &= \bar{p}\frac{df_A}{d\delta} = \bar{p}(1-\delta)(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) \\
\frac{\partial F}{\partial x} &= \bar{p}\frac{df_A}{dx} + qh'(\bar{x}) \\
\frac{\partial F}{\partial p} &= f_A + \bar{p}\frac{\partial f_A}{\partial p} - 1 \\
\frac{\partial G}{\partial \delta} &= 2\bar{p}(1-\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) \\
\frac{\partial G}{\partial x} &= \frac{df}{dx} + h'(\bar{x}) \\
\frac{\partial G}{\partial p} &= \frac{\partial f}{\partial p}
\end{aligned} \tag{5.3}$$

(see Appendix B for details).

The numerator of (5.1) is computed (see equation (B.2) to be

$$-\frac{\partial F}{\partial \delta}\frac{\partial G}{\partial x}+\frac{\partial F}{\partial x}\frac{\partial G}{\partial \delta} = \bar{p}(1-\bar{p})(f_{AA}(\bar{x})-f_{aa}(\bar{x}))[\bar{p}^2 f'_{AA}(\bar{x})-(1-\bar{p})^2 f'_{aa}(\bar{x})+(2q-1)h'(\bar{x})].$$
(5.4)

For $f_{AA}(\bar{x}) > f_{aa}(\bar{x})$, the sign of (5.4) is determined the the term in brackets. For $f_{AA}(\bar{x}) < f_{aa}(\bar{x})$, the sign of (5.4) will be opposite the term in brackets as $f_{AA}(\bar{x}) - f_{aa}(\bar{x}) < 0$. Because we assume (4.5), for any $\bar{x}$, the sign of the first term is negative and the sign of the second term is positive. For $0 \leq q \leq \frac{1}{2}$, the third term is positive. For $\frac{1}{2} \leq q \leq 1$, the third term is negative. Without having more knowledge of the relationship of the derivatives of genotypic fitnesses, no general conclusion can be made about the sign of (5.4).

The numerator of (5.2) is computed (see equation B.5) to be

$$-\frac{\partial F}{\partial p}\frac{\partial G}{\partial \delta} + \frac{\partial F}{\partial \delta}\frac{\partial G}{\partial p} = 2\bar{p}(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))^2[2\bar{p}^2 - 2\delta\bar{p}^2 - \bar{p} - \delta^2 + 2\delta^2\bar{p}]$$
$$+ 2\bar{p}(1 - \bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))(1 - f_{aa}(\bar{x})).$$
(5.5)

For $f_{AA}(\bar{x}) > f_{aa}(\bar{x})$, if we can show the term in brackets in (5.5) is positive then we can conclude that (5.5) is positive. Without additional restrictions, no general conclusions can be made. Similarly, for $f_{AA}(\bar{x}) < f_{aa}(\bar{x})$, if we can show the term in brackets is negative, then we could conclude that (5.5) is negative. Without additional assumptions, no conclusion can be made on the sign of (5.5).

The denominator of both (5.1) and (5.2) is computed (see equation (B.3)) as

$$\frac{\partial F}{\partial p}\frac{\partial G}{\partial x} - \frac{\partial F}{\partial x}\frac{\partial G}{\partial p} = f'_{AA}(\bar{x})[\delta\bar{p}^2 f_{AA}(\bar{x}) + (\bar{p}^2 + 2\delta\bar{p} - 3\delta\bar{p}^2)f_{aa}(\bar{x}) - \bar{p}^2 - 2\delta\bar{p} + 2\delta\bar{p}^2]$$
$$+ f'_{aa}(\bar{x})[(2\bar{p} - 2\bar{p}^2 + \delta - 4\delta\bar{p} + 3\delta\bar{p}^2)f_{AA}(\bar{x})$$
$$+ (-2\bar{p} + \bar{p}^2 - \delta + 2\delta\bar{p} - \delta\bar{p}^2 + 1)f_{aa}(\bar{x})$$
$$+ (\bar{p}^2 + 2\delta\bar{p} - 2\delta\bar{p}^2 - 1)]$$
$$+ h'(\bar{x})[(2\bar{p} + \delta - 2\delta\bar{p} + 4\delta\bar{p}q - 2\bar{p}q - 2\delta q)f_{AA}(\bar{x})$$
$$+ (1 - 2\bar{p} - \delta + 2\delta\bar{p} - 4\delta\bar{p}q + 2\bar{p}q + 2\delta q)f_{aa}(\bar{x}) - 1]$$
$$(5.6)$$

We examine terms grouped according to the derivatives for f_{AA}, f_{aa}, and h. For terms multiplied by $f'_{AA}(\bar{x})$, we denote them by $A(\delta)$ where

$$A(\delta) = f_{AA}(\bar{x})\delta\bar{p}^2 + f_{aa}(\bar{x})(\bar{p}^2 + 2\delta\bar{p} - 3\delta\bar{p}^2) - 2\delta\bar{p} - \bar{p}^2 + 2\delta\bar{p}^2.$$

The terms multiplied by $f'_{aa}(\bar{x})$ are denoted as $B(\delta)$ where

$$B(\delta) = f_{AA}(\bar{x})(2\bar{p} + \delta - 4\delta\bar{p} - 2\bar{p}^2 + 3\delta\bar{p}^2) + f_{aa}(\bar{x})(-2\bar{p} - \delta + 2\delta\bar{p} + \bar{p}^2 - \delta\bar{p}^2 + 1)$$
$$+ 2\delta\bar{p} - 2\delta\bar{p}^2 - 1 + \bar{p}^2.$$

Denote the terms that are multiplied by $h'(\bar{x})$ as $C(q, \delta)$, with

$$C(q, \delta) = f_{AA}(\bar{x})(2\bar{p} - 2\delta\bar{p} + \delta - 2\bar{p}q - 2\delta q + 4\delta\bar{p}q)$$
$$+ f_{aa}(\bar{x})(-2\bar{p} + 2\delta\bar{p} - \delta + 2\bar{p}q + 2\delta q - 4\delta\bar{p}q + 1) - 1.$$

These are the same expressions we obtained for $1 - \text{tr}[D(E)] + \det[D(E)]$ (see Subsection 4.4.2). As proven in the stability computations (see Appendix A.3.2.1), we can show that for $f_{AA}(\bar{x}) > f_{aa}(\bar{x})$ when $x > 0$ and assuming (4.5), if $\frac{1}{2} \le q \le 1$ and $\frac{1}{2} \le \delta \le 1$, then (5.6) is greater than zero. Similarly, for $f_{AA}(\bar{x}) < f_{aa}(\bar{x})$, assuming (4.5) and if $0 \le q \le \frac{1}{2}$ and $0 \le \delta \le \frac{1}{2}$ then (5.6) is greater than zero (see Appendix

A.3.2.2 for details).

The following example illustrates how $\bar{p}$ and $\bar{x}$ change as δ increases from 0 to 1.

Example 5.1. Take $y = 1$ and genotype fitnesses

$$f_{AA}(x) = e^{1-x} \text{ and } f_{aa}(x) = e^{1-4x}.$$

Clearly $f_{AA}(x) > f_{aa}(x)$ for all $x > 0$. For $q = 0.8$, the first and last terms in brackets of (5.4) are both negative and the middle term is positive for any $\bar{x}$. When $\delta = 0$, then $E = (\bar{p}, \bar{x}) \approx (0.879, 1.664)$. We calculate that $\dfrac{d\bar{p}}{d\delta} \approx -0.0481 < 0$ and $\dfrac{d\bar{x}}{d\delta} \approx 0.599 > 0$. Hence, $\bar{p}$ decreases as δ increases and $\bar{x}$ increases as δ increases (see Figure 5.1(a)). At equilibrium, from Proposition 4.2, when $f_{AA}(\bar{x}) > f_{aa}(\bar{x})$ we have $\bar{p} > q$. Numerical simulations indicate that $\bar{p}$ decreases monotonically from 0.879 to 0.821 and $\bar{x}$ increases monotonically from 1.664 to 1.787 (see Table 5.1). In fact, as δ increases from 0 to 1, $\bar{p}$ approaches q.

Table 5.1: Equilibrium movement as δ varies when $q = 0.8$ in Example 5.1. For $f_{AA}(x) = e^{1-x}$, $f_{aa}(x) = e^{1-4x}$ and $y = 1$, $\bar{p}$ decreases and $\bar{x}$ increases as δ increases from 0 to 1.

δ	$(\bar{p}, \bar{x})$	$\dfrac{d\bar{p}}{d\delta}$	$\dfrac{d\bar{x}}{d\delta}$
0	(0.879, 1.664)	-0.0481	0.599
0.2	(0.869, 1.682)	-0.0528	0.430
0.4	(0.858, 1.704)	-0.0572	0.297
0.6	(0.846, 1.728)	-0.0608	0.205
0.8	(0.834, 1.756)	-0.0632	0.155
1	(0.821, 1.787)	-0.0642	0.141

When $0 < q < \dfrac{1}{2}$, the first term in (5.4) is negative and the second and third terms are positive for any $\bar{x}$. For $q = 0.4$ and $\delta = 0$, then $E = (\bar{p}, \bar{x}) \approx (0.524, 1.28)$. We compute $\dfrac{d\bar{p}}{d\delta} \approx -0.0239 < 0$ and $\dfrac{d\bar{x}}{d\delta} \approx 0.694 > 0$. Hence, $\bar{p}$ decreases and $\bar{x}$ increases as δ increases (see Figure 5.1(b)). Numerical simulations indicate that $\bar{p}$ decreases

monotonically from 0.524 to 0.506 and $\bar{x}$ increases monotonically from 1.280 to 1.652 (see Table 5.2). As δ increases from 0 to 1, $\bar{p}$ approaches 0.5.

Table 5.2: Equilibrium movement as δ varies when $q = 0.4$ in Example 5.1. For $f_{AA}(x) = e^{1-x}$, $f_{aa}(x) = e^{1-4x}$ and $y = 1$, $\bar{p}$ decreases and $\bar{x}$ increases as δ increases from 0 to 1.

δ	$(\bar{p}, \bar{x})$	$\dfrac{d\bar{p}}{d\delta}$	$\dfrac{d\bar{x}}{d\delta}$
0	(0.524, 1.280)	-0.0239	0.694
0.2	(0.519, 1.360)	-0.0215	0.540
0.4	(0.515, 1.438)	-0.0190	0.424
0.6	(0.511, 1.513)	-0.0166	0.336
0.8	(0.508, 1.584)	-0.0145	0.268
1	(0.506, 1.652)	-0.0126	0.215

For $q = 0.3$ and $\delta = 0$, then $E = (\bar{p}, \bar{x}) \approx (0.388, 1.174)$. We calculate that $\dfrac{d\bar{p}}{d\delta} \approx 0.0703 > 0$ and $\dfrac{d\bar{x}}{d\delta} \approx 0.602 > 0$. Hence, both $\bar{p}$ and $\bar{x}$ increase as δ increases (see Figure 5.1(c)). Numerical simulations indicate that $\bar{p}$ increases monotonically from 0.388 to 0.423 and $\bar{x}$ increases monotonically from 1.174 to 1.590 (see Table 5.3). As δ increases from 0 to 1, $\bar{p}$ approaches 0.5.

Table 5.3: Equilibrium movement as δ varies when $q = 0.3$ in Example 5.1. For $f_{AA}(x) = e^{1-x}$, $f_{aa}(x) = e^{1-4x}$ and $y = 1$, $\bar{p}$ increases and $\bar{x}$ increases as δ increases from 0 to 1.

δ	$(\bar{p}, \bar{x})$	$\dfrac{d\bar{p}}{d\delta}$	$\dfrac{d\bar{x}}{d\delta}$
0	(0.388, 1.174)	0.0703	0.602
0.2	(0.400, 1.265)	0.0500	0.522
0.4	(0.409, 1.353)	0.0359	0.432
0.6	(0.415, 1.437)	0.0264	0.348
0.8	(0.420, 1.516)	0.0199	0.274
1	(0.423, 1.590)	0.0154	0.210

When $\dfrac{1}{2} \leq q \leq 1$, numerical simulations show that as δ increases, $\bar{p}$ decreases. No conclusion can be made about how $\bar{p}$ moves with respect to δ when $0 \leq q < \dfrac{1}{2}$ as we
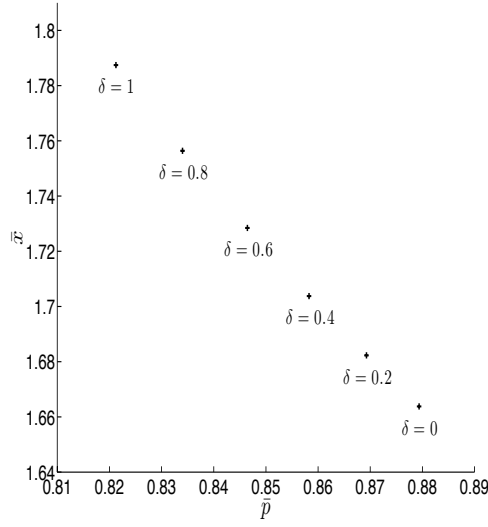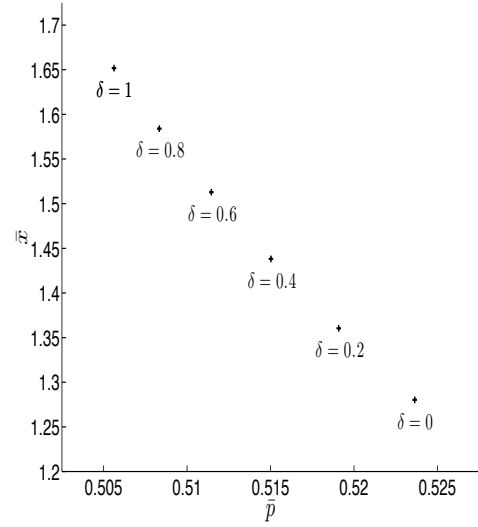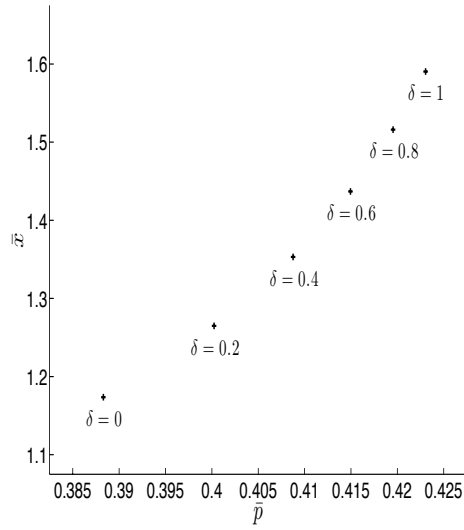
(a) $q = 0.8$

(b) $q = 0.4$

(c) $q = 0.3$

Figure 5.1: Equilibrium movement for various values of q as δ varies in Example 5.1. For $f_{AA}(x) = e^{1-x}$, $f_{aa}(x) = e^{1-4x}$, and $y = 1$, the movement of $(\bar{p}, \bar{x})$ as δ increases from from 0 to 1.

have an example where $\bar{x}$ increases as well as one where $\bar{x}$ decreases. Regardless the value of q, numerical simulations indicate that $\bar{x}$ increases as δ increases.

We offer a possible explanation for what was seen in the previous example when $f_{AA}(\bar{x}) > f_{aa}(\bar{x})$. When $\frac{1}{2} \leq q \leq 1$, the immigration rate of A into the island population is high. When $\delta = 0$, the heterozygote fitness is the same as the homozygote aa fitness, but the high migration rate means that there is a high frequency for the A allele in the population and thus the value of $\bar{p}$ is large. As δ increases to 1, the heterozygote fitness becomes larger as it is more similar to the homozygote AA fitness. This results in an increase in frequency for the heterozygote Aa genotype and thus an increase in the frequency of the a allele. Thus, there is a decrease in the frequency of the A allele which means a decrease in $\bar{p}$. In fact, as δ increases from 0 to 1, $\bar{p}$ decreases ($\frac{d\bar{p}}{d\delta} < 0$) and moves towards q.

We also note that for $f_{AA}(\bar{x}) > f_{aa}(\bar{x})$, when q is small, the immigration rate of the A allele into the island population is low. When $\delta = 0$, the heterozygote fitness is equal to the fitness of the homozygote aa. There is a small representation of the A allele in the population, so $\bar{p}$ is small. As δ increases to 1, the heterozygote fitness improves, so there is an increase in the heterozygote inventory within the population, resulting in an increase in the frequency of the A allele. Hence, $\bar{p}$ increases.

For $f_{AA}(\bar{x}) > f_{aa}(\bar{x})$, when $q < \frac{1}{2}$, but close to $\frac{1}{2}$, the movement of $\bar{p}$ with respect to δ can be determined depending on the value for $\bar{p}$. Migration contributes slightly greater numbers for the a allele than the A allele at these q values. When $\bar{p} > \frac{1}{2}$, as δ increases toward 1, heterozygote fitness increases leading to a greater heterozygote presence. Therefore, the a allele increases in the population and the value of $\bar{p}$ decreases. If, however, $\bar{p} < \frac{1}{2}$ when $\delta = 0$, as δ increases to 1, heterozygote fitness improves, leading to an increase in the number of heterozygotes. Thus, there is an increase in the A allele and $\bar{p}$ increases.

Regardless of the value for q, when $f_{AA}(\bar{x}) > f_{aa}(\bar{x})$, $\bar{x}$ seems to increase as δ increases. Mean fitness becomes larger as δ increases because $\frac{\partial f}{\partial \delta} = 2\bar{p}(1-\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) > 0$. Thus, because $\bar{x} = \bar{x}f(\bar{p}, \bar{x}) + y$, at equilibrium

$\bar{x}$ increases as δ increases.

5.2 Transcritical Bifurcation

We now consider a scenario in which a less fit allele migrates into an island population. In this case, only the less fit allele migrates into the population. If the degree of dominance is large enough, then we show that the island population has a stable equilibrium. Such an equilibrium occurs as a result of a transcritical bifurcation in which the degree of dominance is the parameter. In terms of a transgenic model, we assume that the transgene A is less fit than the a allele and is the only allele migrating into the population. If the degree of dominance is large enough, then a stable equilibrium exists at which the frequency of the A is 1.

To set the stage for this case, we assume that $f_{aa} > f_{AA}$, $q = 1$ and that the fitnesses are constant, i.e., do not vary with x. Using the equations satisfied at equilibrium, (4.2), we rewrite the second equation of (4.2) as $h(\bar{x}) = 1 - f(\bar{p})$. Using this equality to substitute for $h(x)$ in the first equation of (4.2) and moving the nonzero terms to the right hand side gives

$$
\begin{aligned}
0 &= \bar{p}(f_A(\bar{p}) - 1) + 1 - f(\bar{p}) \\
&= \bar{p}[f_{aa} + (\bar{p} + \delta - \delta\bar{p})(f_{AA} - f_{aa}) - 1] + 1 - f_{aa} - (\bar{p}^2 + 2\delta\bar{p} - 2\delta\bar{p}^2)(f_{AA} - f_{aa}) \\
&= 1 - \bar{p} - f_{aa} + \bar{p}f_{aa} + (\bar{p}^2 + \delta\bar{p} - \delta\bar{p}^2 - \bar{p}^2 - 2\delta\bar{p} + 2\delta\bar{p}^2)(f_{AA} - f_{aa}) \\
&= 1 - \bar{p} - f_{aa} + \bar{p}f_{aa} + (-\delta\bar{p} + \delta\bar{p}^2)(f_{AA} - f_{aa}) \\
&= (1 - \bar{p}) - f_{aa}(1 - \bar{p}) - \delta\bar{p}(1 - \bar{p})(f_{AA} - f_{aa}) \\
&= (1 - \bar{p})(1 - f_{aa} - \delta\bar{p}(f_{AA} - f_{aa})).
\end{aligned}
$$

$$(5.7)$$

Thus, there are two solutions for $\bar{p}$. The equilibrium frequency for the A allele is either $\bar{p} = 1$ or $\bar{p} = \dfrac{1 - f_{aa}}{\delta(f_{AA} - f_{aa})}$.

Substituting $\bar{p} = 1$ into the second equation of (4.2) yields $\bar{x} = \dfrac{y}{1 - f_{AA}}$. In order

to have a positive population size, we need $0 < f_{AA} < 1$. Considering the solution $\bar{p} = \dfrac{1 - f_{aa}}{\delta(f_{AA} - f_{aa})}$, we note that to have $\bar{p} > 0$, we require $f_{aa} > 1$. Also, it is clear that the two solutions for $\bar{p}$ are identical when $\delta = \delta_1 = \dfrac{1 - f_{aa}}{f_{AA} - f_{aa}}$.

To determine results about local stability for $E = (\bar{p}, \bar{x})$ when $\bar{p} = 1$, substitute $q = 1$ and $\bar{p} = 1$ into the Jacobian matrix (4.16), to obtain

$$
\begin{aligned}
D(E) &= \begin{bmatrix} f_A + \left(\frac{\partial f_A}{\partial p} - \frac{\partial f}{\partial p} \right) & 0 \\ \bar{x}\frac{\partial f}{\partial p} & 1 + \bar{x}h'(\bar{x}) \end{bmatrix} \\
&= \begin{bmatrix} f_{aa} + (f_{AA} - f_{aa}) + (1-\delta)(f_{AA} - f_{aa}) - 2(1-\delta)(f_{AA} - f_{aa}) & 0 \\ \bar{x}\frac{\partial f}{\partial p} & 1 - \bar{x}\frac{y}{\bar{x}^2} \end{bmatrix} \\
&= \begin{bmatrix} f_{AA} - (1-\delta)(f_{AA} - f_{aa}) & 0 \\ \bar{x}\frac{\partial f}{\partial p} & 1 - \frac{y}{\bar{x}} \end{bmatrix} \\
&= \begin{bmatrix} \delta f_{AA} + (1-\delta)f_{aa} & 0 \\ \bar{x}\frac{\partial f}{\partial p} & f \end{bmatrix} \\
&= \begin{bmatrix} f_{Aa} & 0 \\ \bar{x}\frac{\partial f}{\partial p} & f_{AA} \end{bmatrix}.
\end{aligned}
$$

$$(5.8)$$

Thus, when $\bar{p} = 1$, the eigenvalues are $\lambda_1(\delta) = f_{Aa}$ and $\lambda_2(\delta) = f_{AA}$. To have a positive population size at equilibrium, we have established that $0 < f_{AA} = \lambda_2(\delta) < 1$. Thus the stability of $E = (\bar{p}, \bar{x}) = (\bar{p}(\delta), \bar{x}(\delta))$ at $\bar{p} = 1$ will be determined by $\lambda_1(\delta)$.

When $\delta = \delta_1$, clearly $\lambda_1 = f_{Aa} = 1$. Because f_{Aa} decreases as a function of δ, $f_{Aa} > 1$ for $\delta < \delta_1$, and $f_{Aa} < 1$ for $\delta > \delta_1$. If we consider the stability of equilibrium $E = (1, \bar{x})$ as a function of the parameter δ, then $E(\delta) = (1, \bar{x}(\delta))$ is unstable when $\delta < \delta_1$ and stable when $\delta > \delta_1$.

To determine the stability of $E = (\bar{p}, \bar{x}) = (\bar{p}(\delta), \bar{x}(\delta))$ when $\bar{p} = \dfrac{1 - f_{aa}}{\delta(f_{AA} - f_{aa})}$, we apply the Jury conditions (see Section 4.4). For $\delta > \delta_1$, we break the Jury conditions into parts to prove that the equilibrium is unstable. Since we are considering the

fitnesses to be constant with respect to x, we can rewrite (4.21) as

$$
\begin{aligned}
&1 - \text{tr}[D(E)] + \det[D(E)] \\
&= \bar{x}h'(\bar{x})\left[f_{AA}(2\delta\bar{p} - \delta) + f_{aa}(\delta - 2\delta\bar{p} + 1) - 1\right] \\
&= \bar{x}h'(\bar{x})\left[f_{aa} - 1 + (2\delta\bar{p} - \delta)(f_{AA} - f_{aa})\right] \\
&= \bar{x}h'(\bar{x})[f_{aa} - 1 - \delta(f_{AA} - f_{aa}) + 2\delta\frac{1 - f_{aa}}{\delta(f_{AA} - f_{aa})}(f_{AA} - f_{aa})] \\
&= \bar{x}h'(\bar{x})\left[f_{aa} - 1 + 2 - 2f_{aa} - \delta f_{AA} + \delta f_{aa}\right] \\
&= \bar{x}h'(\bar{x})\left[1 - f_{Aa}\right].
\end{aligned}
\tag{5.9}
$$

When $\delta > \delta_1$, $1 - f_{Aa} > 0$ and

$$
1 - \text{tr}[D(E)] + \det[D(E)] = 1 - (\lambda_1(\delta) + \lambda_2(\delta)) + \lambda_1(\delta)\lambda_2(\delta) = (1 - \lambda_1(\delta))(1 - \lambda_2(\delta)) < 0.
\tag{5.10}
$$

This implies that one eigenvalue is larger than 1. Hence, for $\bar{p} = \dfrac{1 - f_{aa}}{\delta(f_{AA} - f_{aa})}$, the equilibrium $E(\delta)$ is unstable when $\delta > \delta_1$.

To prove that E is stable when $\bar{p} = \dfrac{1 - f_{aa}}{\delta(f_{AA} - f_{aa})}$ and $\delta < \delta_1$, we apply the Jury conditions to a sufficiently small neighborhood around $(\bar{p}, \bar{x}) = (1, \bar{x}(\delta_1))$. First, note that when $\delta = \delta_1$, $f_{Aa} = 1$ and the Jacobian (5.8) becomes

$$
D(E) = \begin{bmatrix} 1 & 0 \\ \bar{x}\frac{\partial f}{\partial p} & f_{AA} \end{bmatrix}.
$$

At $\delta = \delta_1$, $\lambda_1(\delta_1) = f_{Aa} = 1$ and $0 < \lambda_2(\delta_1) = f_{AA} < 1$. Because of the continuity of eigenvalues as functions of δ, for δ near δ_1, $\lambda_1(\delta) \approx 1$ and $0 < \lambda_2(\delta) < 1$. Thus, in a neighborhood of δ_1, $\text{tr}[D(E)] = \lambda_1(\delta) + \lambda_2(\delta) > 0$ and $|\text{tr}[D(E)]| = \text{tr}[D(E)]$. Also, the determinant is a continuous function of δ. At $\delta = \delta_1$, $\det[D(E)] = f_{AA} < 1$. Thus, in a neighborhood of δ_1, $\det[D(E)] < 1$ and hence

$$
1 + \det[D(E)] < 2.
\tag{5.11}
$$

When $\delta < \delta_1$, we have $f_{Aa} > 1$, and from (5.9),

$$1 - \text{tr}[D(E)] + \det[D(E)] = \bar{x}h'(\bar{x})(1 - f_{Aa}) > 0.$$

Thus, rearranging terms and using $|\text{tr}[D(E)]| = \text{tr}[D(E)]$, for $\delta < \delta_1$,

$$|\text{tr}[D(E)]| < 1 + \det[D(E)]. \tag{5.12}$$

For δ near δ_1, $\delta < \delta_1$, when $\bar{p} = \dfrac{1 - f_{aa}}{\delta(f_{AA} - f_{aa})}$ using (5.11) and (5.12)

$$|\text{tr}[D(E)]| < 1 + \det[D(E)] < 2 \tag{5.13}$$

and the Jury conditions hold. Thus, when $\bar{p} = \dfrac{1 - f_{aa}}{\delta(f_{AA} - f_{aa})}$ the equilibrium E is stable when δ is near δ_1 with $\delta < \delta_1$.

For $E = (\bar{p}(\delta), \bar{x}(\delta))$, when $\bar{p} = 1$, we have shown that as δ increases through δ_1, the equilibrium goes from an unstable to stable. When $\bar{p} = \dfrac{1 - f_{aa}}{\delta(f_{AA} - f_{aa})}$, E changes from a stable to an unstable equilibrium. For $f_{aa} > f_{AA}$, $q = 1$, and constant fitnesses, a transcritical bifurcation occurs at $(\delta, \bar{p}) = (\delta_1, 1) = \left(\dfrac{1 - f_{aa}}{f_{AA} - f_{aa}}, 1 \right)$.

Example 5.2. Take $y = 1$, $q = 1$, and genotype fitnesses

$$f_{AA} = 0.7 \text{ and } f_{aa} = 1.5.$$

Clearly, $f_{AA}(x) < f_{aa}(x)$ for all $x > 0$. As defined above,

$$\delta_1 = \frac{1 - f_{aa}}{(f_{AA} - f_{aa})} = \frac{1 - 1.5}{0.7 - 1.5} = \frac{-0.5}{-0.8} = \frac{5}{8} = 0.625.$$

There are two equilibrium values for $\bar{p}(\delta)$, $\bar{p}(\delta) = 1$ and $\bar{p}(\delta) = \dfrac{1 - f_{aa}}{\delta(f_{AA} - f_{aa})} = \dfrac{5}{8\delta}$.

When $\bar{p} = 1$, we have $\bar{x} = \dfrac{y}{1 - f_{AA}} = \dfrac{1}{1 - 0.7} \approx 3.333$. Clearly, $0 < \lambda_2(\delta) = f_{AA} = 0.7 < 1$. The stability of $E \approx (1, 3.333)$ will be determined by $\lambda_1(\delta) = f_{Aa} = f_{aa} + \delta(f_{AA} - f_{aa}) = 1.5 - 0.8\delta$. When $\delta = 0.4$, $\lambda_2(\delta) = 1.18$

and $E = (\bar{p}, \bar{x}) \approx (1, 3.333)$ is unstable. When $\delta = 0.8$, $\lambda_2(\delta) = 0.86 < 1$ and $E = (\bar{p}, \bar{x}) \approx (1, 3.333)$ is stable. For $\delta < \delta_1$, $E = (\bar{p}, \bar{x}) \approx (1, 3.333)$ is unstable. For $\delta > \delta_1$, $E = (\bar{p}, \bar{x}) \approx (1, 3.333)$ is stable.

The other equilibriums value for $\bar{p}$ is $\bar{p}(\delta) = \dfrac{1 - 1.5}{\delta(0.7 - 1.5)} = \dfrac{5}{8\delta}$. Using (4.2), we compute

$$
\begin{aligned}
\bar{x}(\delta) &= \frac{y}{1 - f(\bar{p}(\delta))} \\[2mm]
&= \frac{y}{1 - f_{aa} - \bar{p}(\delta)(\bar{p}(\delta) + 2\delta - 2\delta\bar{p}(\delta))(f_{AA} - f_{aa})} \\[2mm]
&= \frac{1}{1 - 1.5 - \frac{5}{8\delta}\left(\frac{5}{8\delta} + 2\delta - 2\delta\frac{5}{8\delta}\right)(0.7 - 1.5)} \\[2mm]
&= \frac{1}{-0.5 + \left(\frac{1}{2\delta}\right)\left(\frac{5}{8\delta} + 2\delta - \frac{5}{4}\right)} \\[2mm]
&= \frac{1}{-0.5 + \left(\frac{5}{16\delta^2} + 1 - \frac{5}{8\delta}\right)} \\[2mm]
&= \frac{16\delta^2}{8\delta^2 - 10\delta + 5}.
\end{aligned}
$$

When $\delta = 0.4$, $\bar{p}(0.4) = \dfrac{25}{16} \approx 1.563$ and $\bar{x}(0.4) = \dfrac{64}{57} = \dfrac{2.56}{2.28} \approx 1.123$. When $\delta = 0.8$, $\bar{p}(0.8) = \dfrac{25}{32} \approx 0.781$ and $\bar{x}(0.8) = \dfrac{256}{53} = \dfrac{10.24}{2.12} \approx 4.830$.

In order to determine the stability of E, we look at the eigenvalues. Using constant fitnesses and $q = 1$, (4.16) becomes

$$
\begin{aligned}
D(E) &= \begin{bmatrix} f_A + \bar{p}\left(\frac{\partial f_A}{\partial p} - \frac{\partial f}{\partial p}\right) & h'(\bar{x})(1 - \bar{p}) \\[2mm] \bar{x}\frac{\partial f}{\partial p} & 1 + \bar{x}\left(\frac{\partial f}{\partial x} + h'(\bar{x})\right) \end{bmatrix} \\[3mm]
&= \begin{bmatrix} f_{aa} + (2\bar{p} - 2\bar{p}^2 + \delta - 4\delta\bar{p} + 4\delta\bar{p}^2)(f_{AA} - f_{aa}) & \frac{y(\bar{p}-1)}{\bar{x}^2} \\[2mm] 2\bar{x}(\bar{p} + \delta - 2\delta\bar{p})(f_{AA} - f_{aa}) & 1 - \frac{y}{\bar{x}} \end{bmatrix}.
\end{aligned}
\tag{5.14}
$$

When $\delta = 0.4$, the Jacobian (5.14) for $E(0.4) \approx (1.563, 1.123)$ is

$$
D(E(0.4)) = \begin{bmatrix} \frac{1169}{800} & -\frac{32}{25} \\[2mm] \frac{29241}{65536} & \frac{7}{64} \end{bmatrix}.
$$

The eigenvalues are $\dfrac{2513}{3200} \pm \dfrac{3}{3200}\sqrt{-129959}$. And,

$$|\lambda_1| = |\lambda_2| = \sqrt{\left(\frac{2513}{3200}\right)^2 + \left(\frac{3\sqrt{129959}}{3200}\right)^2} \approx 0.855.$$

Thus, when $\delta = 0.4$, $E = (\bar{p}(\delta), \bar{x}(\delta)) \approx (1.563, 1.123)$ is a stable equilibrium. Therefore, for $\delta < 0.625$, when $\bar{p} = \dfrac{5}{8\delta}$, E is a stable equilibrium.

For $\delta = 0.8$, the Jacobian for $E(0.8) \approx (0.781, 4.830)$ is

$$D(E(0.8)) = \begin{bmatrix} \frac{3277}{3200} & -\frac{64}{25} \\ -\frac{19663}{2097152} & \frac{203}{256} \end{bmatrix}.$$

The eigenvalues are $\dfrac{11629}{12800} \pm \dfrac{1}{12800}\sqrt{6120041}$. So, $\lambda_1 \approx 1.102$ and $\lambda_2 \approx 0.715$. When $\delta = 0.8$, $E = (\bar{p}(\delta), \bar{x}(\delta)) \approx (0.781, 4.830)$ is an unstable equilibrium. Thus, for $\delta > 0.625$, when $\bar{p}(\delta) = \dfrac{5}{8\delta}$, E is an unstable equilibrium. And a bifurcation occurs at $(\delta, \bar{p}) = (0.625, 1)$.
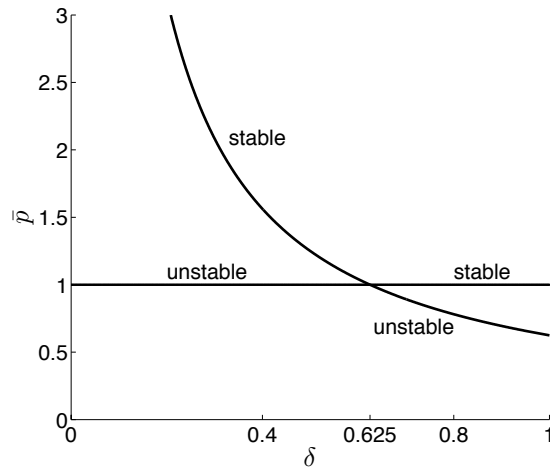

Figure 5.2: Transcritical bifurcation in Example 5.2. For $f_{AA} = 0.7$, $f_{aa} = 1.5$, $y = 1$, and $q = 1$, the bifurcation occurs at $(\delta, p) = (0.625, 1)$.

5.3   Summary

We examined how the degree of dominance affects the position of the equilibrium. We took the derivatives of $\bar{p}$ and $\bar{x}$ with respect to δ to determine how increasing δ would change $\bar{p}$ and $\bar{x}$. Without enforcing other assumptions, a proof to show general behavior was not possible.

From numerical simulations, when the fitness of the homozygote AA is greater than the fitness of the homozygote aa we noted what happened to the equilibrium $E = (\bar{p}, \bar{x})$ as δ increased and offered some possible explanations. From our examples, we saw that the population size at equilibrium increases as the degree of dominance increases. When more than half of the migrant population is A ($\frac{1}{2} \leq q \leq 1$), examples showed that as the degree of dominance increased, the frequency of A in the island population decreased to q. When slightly less than half of the migrant population was the A allele ($0 \leq q \leq \frac{1}{2}$, but q close to $\frac{1}{2}$), we found examples for which $\bar{p}$ increased as well as examples for which $\bar{p}$ decreased as δ increased. For small q, our examples demonstrated that an increase in the degree of dominance leads to an increase in $\bar{p}$.

The migration of a less fit allele may lead to the prevalence of that allele in the island population. This phenomenon is the result of a transcritical bifurcation. We assume that the A allele is the less fit allele and it is the only allele migrating into the island population. If the degree of dominance is large enough, then there is a stable equilibrium that appears as a result of a transcritical bifurcation. In fact, the frequency of the allele at equilibrium is 1. Hence, after many generations, the less fit allele excludes the other allele.

Chapter 6

Attracting Regions

In this chapter, we study the existence of attractors. The results are similar to those found by Selgrade and Roberds [33] for complete dominance ($\delta = 1$) and no dominance ($\delta = 0.5$) and extend to the case of periodic immigration the results found by Selgrade, Bostic, and Roberds [29] for general dominance. We assume that either $f_{AA}(x) \geq f_{aa}(x)$ or $f_{AA}(x) \leq f_{aa}(x)$. To save space, we will suppress some state variables when it will not cause confusion. For results in this chapter, (4.5) does not need to be assumed.

6.1   Location of Attractor

For any set Λ, the topological interior of Λ is denoted by $\text{Int}\,\Lambda$ and the closure of Λ is denoted by $\text{Cl}\,\Lambda$. A set Λ is invariant if for each $(p_0, x_0) \in \Lambda$ then $(p_n, x_n) \in \Lambda$ for all $n \geq 0$. Equilibria and cycles are examples of invariant sets. A compact invariant set Λ is an attractor [25] if there is an open set $\mathcal{U} \supset \Lambda$ where $\text{Cl}\,\mathcal{U}$ is compact and so that for each $(p_0, x_0) \in \text{Cl}\,\mathcal{U}$ then $\lim_{n \to \infty} (p_n, x_n) \in \Lambda$.

It is biologically reasonable to assume that one homozygote is more fit than the other, i.e., either $f_{AA} \geq f_{aa}$ or $f_{AA} \leq f_{aa}$. This is typically the case considering the effects of transgenes in natural populations. When we assume the fitness of the

homozygote AA is greater than the fitness of the homozygote aa and that the A allele enters the island population at a frequency q, we show that where the frequency of A in the island population initially is above q, it never falls below q. If the homozygote AA is less fit, we show that if the frequency of A starts below q, then it will remain below q.

Lemma 6.1. *Assume (3.5) for all $x > 0$ and $0 \leq \delta \leq 1$ and $0 < q < 1$. If $f_{AA}(x) \geq f_{aa}(x)$ for all $x > 0$, then $Int\,\mathcal{S}^+$ and $\mathcal{S}^+$ are invariant regions. If $f_{AA}(x) \leq f_{aa}(x)$ for all $x > 0$, then $Int\,\mathcal{S}^-$ and $\mathcal{S}^-$ are invariant regions.*

Proof. We want to show that for $f_{AA}(x) \geq f_{aa}(x)$, $Int\,\mathcal{S}^+$ and $\mathcal{S}^+$ are invariant regions. To show $Int\,\mathcal{S}^+$ is an invariant region we first need to show that if $p_n > q$ then $p_{n+1} > q$ for $n \geq 0$. From (3.3), we have

$$p_{n+1} = \frac{p_n f_A + qh(1 + \alpha g_k(n))}{f + h(1 + \alpha g_k(n))} = q \left[\frac{\frac{p_n}{q} f_A + h(1 + \alpha g_k(n))}{f + h(1 + \alpha g_k(n))} \right]. \tag{6.1}$$

We want $p_{n+1} > q$, so we need the bracketed term in (6.1) to be greater than 1. Hence, we should show $\dfrac{p_n}{q} f_A > f$, which is equivalent to showing $\dfrac{p_n}{q} f_A - f > 0$. Since we assumed $p_n > q$, then $\dfrac{p_n}{q} f_A - f > f_A - f$. And,

$$
\begin{aligned}
f_A - f &= f_{aa} + (p_n + \delta - \delta p_n)(f_{AA} - f_{aa}) - [f_{aa} + p_n(p_n + 2\delta - 2\delta p_n)(f_{AA} - f_{aa})] \\
&= (p_n + \delta - \delta p_n)(f_{AA} - f_{aa}) + (-p_n^2 - 2\delta p_n + 2\delta p_n^2)(f_{AA} - f_{aa}) \\
&= (p_n - p_n^2 + \delta - \delta p_n - 2\delta p_n + 2\delta p_n^2)(f_{AA} - f_{aa}) \\
&= (1 - p_n)(p_n + \delta - 2\delta p_n)(f_{AA} - f_{aa}) \\
&= (1 - p_n)(p_n(1 - \delta) + \delta(1 - p_n))(f_{AA} - f_{aa}).
\end{aligned}
$$

Since $f_{AA} \geq f_{aa}$, we have $f_A - f \geq 0$ and thus $p_{n+1} > q$. Also, if $p_n < 1$, then $p_{n+1} < 1$. Thus $Int\,\mathcal{S}^+$ is invariant. Similarly, if $p_n \geq q$, then $p_{n+1} \geq q$ and $\mathcal{S}^+$ is invariant.

For $f_{AA}(x) \leq f_{aa}(x)$, we want to prove that $\text{Int}\,\mathcal{S}^-$ and $\mathcal{S}^-$ are invariant regions. We need to show that if $p_n < q$ then $p_{n+1} < q$ for $n \geq 0$. We need the bracketed term in

$$p_{n+1} = \frac{p_n f_A + qh(1 + \alpha g_k(n))}{f + h(1 + \alpha g_k(n))} = q\left[\frac{\frac{p_n}{q} f_A + h(1 + \alpha g_k(n))}{f + h(1 + \alpha g_k(n))}\right]$$

to be less than 1. Hence, we should show $\dfrac{p_n}{q}\, f_A < f$, which is equivalent to showing $\dfrac{p_n}{q}\, f_A - f < 0$. Since $p_n > q$, then $\dfrac{p_n}{q}\, f_A - f < f_A - f$. And, as before,

$$f_A - f = (1 - p_n)(p_n(1 - \delta) + \delta(1 - p_n))(f_{AA} - f_{aa}).$$

Since $f_{aa} \geq f_{AA}$, we have $f_A - f \leq 0$ and thus $p_{n+1} < q$. Also, if $p_n > 0$, then $p_{n+1} > 0$. Thus, $\text{Int}\,\mathcal{S}^-$ is invariant. Similarly, if $p_n \leq q$ then $p_{n+1} \leq q$, and $\mathcal{S}^-$ is invariant.

Note that because of immigration, $x_n \geq y(1 - \alpha)$ for $n \geq 1$. Thus, after the first iterate we need the inequalities on fitnesses to hold only for $x \geq y(1 - \alpha)$, as shown in the following corollary.

Corollary 6.2. *Assume (3.5) for all $x > 0$ and $0 \leq \delta \leq 1$ and $0 < q < 1$. If $f_{AA}(x) \geq f_{aa}(x)$ for all $x \geq y(1 - \alpha)$ and $q < p_n < 1$, then $p_{n+1} > q$ for all $n \geq 1$. If $f_{AA}(x) \leq f_{aa}(x)$ for all $x \geq y(1 - \alpha)$ and $0 < p_n < q$, then $p_{n+1} < q$ for all $n \geq 1$.*

Solution orbits in the complement of $\mathcal{S}^+$ or $\mathcal{S}^-$ iterate monotonically towards $\mathcal{S}^+$ or $\mathcal{S}^-$ as we now demonstrate.

Lemma 6.3. *Assume (3.5) for all $x > 0$ and $0 \leq \delta \leq 1$ and $0 < q < 1$. If $f_{AA}(x) \geq f_{aa}(x)$ for all $x \geq y(1 - \alpha)$ and $p_n < q$ for $n \geq 1$ then $p_n < p_{n+1}$. If $f_{aa}(x) \geq f_{AA}(x)$ for all $x \geq y(1 - \alpha)$ and $p_n > q$ for $n \geq 1$ then $p_n > p_{n+1}$.*

Proof. For $f_{AA} \geq f_{aa}$, we want to prove that for all $x \geq y(1 - \alpha)$ and $p_n < q$ for

$n \geq 1$, $p_n < p_{n+1}$. Thus, we want to show that

$$p_{n+1} = \frac{p_n f_A + qh(1 + \alpha g_k(n))}{f + h(1 + \alpha g_k(n))} = p_n \left[\frac{f_A + \frac{q}{p_n} h (1 + \alpha g_k(n))}{f + h (1 + \alpha g_k(n))} \right] > p_n. \qquad (6.2)$$

We require the bracketed term in equation (6.2) to be greater than 1. So, we need to verify that $f_A + \frac{q}{p_n} h (1 + \alpha g_k(n)) > f + h (1 + \alpha g_k(n))$ and, thus,

$$f_A - f + \left(\frac{q}{p_n} - 1 \right) h(1 + \alpha g_k(n)) > 0. \qquad (6.3)$$

In the previous lemma, we proved that $f_A - f \geq 0$ when $f_{AA}(x) \geq f_{aa}(x)$. Also, since $q > p_n$, $\frac{q}{p_n} - 1 > 0$, we see that (6.3) holds and thus $p_n < p_{n+1}$.

For $f_{AA} \leq f_{aa}$, we want to show for all $x \geq y(1 - \alpha)$ and $p_n > q$ for $n \geq 1$ that $p_n > p_{n+1}$. We want to demonstrate that

$$p_{n+1} = p_n \left[\frac{f_A + \frac{q}{p_n} h (1 + \alpha g_k(n))}{f + h (1 + \alpha g_k(n))} \right] < p_n. \qquad (6.4)$$

We propose to verify that the bracketed term in equation (6.4) is less than 1. This is equivalent to showing $f_A + \frac{q}{p_n} h (1 + \alpha g_k(n)) < f + h (1 + \alpha g_k(n))$ and thus,

$$f - f_A + (1 - \frac{q}{p_n}) h (1 + \alpha g_k(n)) > 0. \qquad (6.5)$$

From the previous lemma, $f_A - f \leq 0$ when $f_{AA}(x) \leq f_{aa}(x)$ and hence $f - f_A \geq 0$. Also, since $q < p_n$ then $1 - \frac{q}{p_n} > 0$. Therefore, we have demonstrated that (6.5) holds and $p_{n+1} < p_n$.

Biologically it makes sense to assume that the population size x is bounded for all generations. More specifically, the assumption we make on genotypic fitnesses is:

$$\text{There exists } B > 0 \text{ so that } x f_{AA} < B \text{ and } x f_{aa} < B \text{ for all } x > 0. \qquad (6.6)$$

From (6.6), we see that the genotype fitnesses are bounded and that they approach zero as the $x \to \infty$. Also, (6.6) implies that $x_n f(p_n, x_n) + y(1 + \alpha g_k(n)) \leq B + y(1 + \alpha)$ for all n and solutions to (3.3) are bounded. For the closed interval $\mathcal{J} \equiv [y(1 - \alpha), y(1 + \alpha) + B]$, it follows that:

Lemma 6.4. *Assume (6.6), (3.5), $0 \leq \delta \leq 1$, and $0 < q < 1$. Then each solution (p_n, x_n) to (3.3) is contained in the rectangle $\mathcal{R} = [0, 1] \times \mathcal{J}$ for all $n \geq 1$.*

Example 6.5. Take $y = 1$, $\delta = 0.5$, $k = 5$, $g_k(n) = \cos\left(\dfrac{2\pi n}{k}\right)$ and genotype fitnesses

$$f_{AA}(x) = e^{1.8 - 0.5x} \text{ and } f_{aa}(x) = e^{1 - 0.5x}.$$

Clearly, $f_{AA}(x) > f_{aa}(x)$ for all $x > 0$. We can determine $B \approx 4.451$. For $\alpha = 0$ and $q = 0.2$, there is an equilibrium point at $(\bar{p}, \bar{x}) \approx (0.4484, 3.5399)$. We have that the p-coordinate of the fixed point is greater than q. Also, we compute $\mathcal{J} \approx [1, 5.451]$. Clearly, the attractor is contained in the rectangle $\mathcal{R}$.

For $\alpha = 0.5$, the attractor is a 5-cycle. We compute $\mathcal{J} \approx [0.5, 5.951]$. The points in the five cycle are in Table 6.1 and Figure 6.1(a), and we see that the attractor is contained in the rectangle $\mathcal{R}$. Also, all the p-coordinates are greater than $q = 0.2$.

Table 6.1: Points in 5-cycle when $q = 0.2$ for Example 6.5. For $f_{AA}(x) = e^{1.8 - 0.5x}$, $f_{aa}(x) = e^{1 - 0.5x}$, $y = 1$, $\delta = 0.5$, $k = 5$, $g_k(n) = \cos\left(\dfrac{2\pi n}{k}\right)$, and $\alpha = 0.5$ the p values in the attractor are greater than $q = 0.2$.

p	x
0.4706	3.8720
0.4259	3.8943
0.4159	3.4532
0.4544	3.1164
0.4898	3.3719

For $\alpha = 0$ and $q = 0.8$, there is an equilibrium point at $(\bar{p}, \bar{x}) \approx (0.8884, 4.0417)$. We have that the p-coordinate of the fixed point is greater than $q = 0.8$. Also, we compute $\mathcal{J} \approx [1, 5.451]$. Clearly, the attractor is contained in the rectangle $\mathcal{R}$.

For $\alpha = 0.5$, the attractor is a 5-cycle. We compute $\mathcal{J} \approx [0.5, 5.951]$. The points in the five cycle are in Table 6.2 and Figure 6.1(b). The attractor is contained in the rectangle $\mathcal{R}$. Also, all the p-coordinates are greater than $q = 0.8$.

Table 6.2: Points in 5-cycle when $q = 0.8$ for Example 6.5. For $f_{AA}(x) = e^{1.8-0.5x}$, $f_{aa}(x) = e^{1-0.5x}$, $y = 1$, $\delta = 0.5$, $k = 5$, $g_k(n) = \cos\left(\dfrac{2\pi n}{k}\right)$, and $\alpha = 0.5$, the p values in the attractor are greater than $q = 0.8$.

p	x
0.8936	4.3175
0.8794	4.3393
0.8784	3.9538
0.8921	3.6864
0.9020	3.9164

6.2 Approach Rates of Attractors

Since solutions to (3.3) are bounded and the orbits are monotonic, we can prove the behavior of p_n in the complement of Int $\mathcal{S}^+$ or Int $\mathcal{S}^-$ is exponential.

Lemma 6.6. *Assume (6.6), (3.5) for all $x > 0$, $0 \leq \delta \leq 1$, and $0 < q < 1$. If $f_{AA}(x) > f_{aa}(x)$ for all $x \in \mathcal{J}$ then there is $r > 0$ so that $p_n \leq q$ where $n \geq 1$ implies that $p_{n+1} \geq p_n(1 + r)$. If $f_{AA}(x) < f_{aa}(x)$ for all $x \in \mathcal{J}$ then there is $s > 0$ so that $p_n \geq q$ where $n \geq 1$ implies that $1 - p_{n+1} \geq (1 - p_n)(1 + s)$.*

Proof. Part 1: $f_{AA}(x) > f_{aa}(x)$

Assume that $f_{AA}(x) > f_{aa}(x)$ for all $x \in \mathcal{J}$. From (3.3) we have

$$p_{n+1} = p_n \left[1 + \frac{f_A - f + (\frac{q}{p_n} - 1)h(1 + \alpha g_k(n))}{f + h(1 + \alpha g_k(n))} \right]. \tag{6.7}$$

For the fraction in (6.7), we want to make it as small as possible, so we will minimize the numerator and maximize the denominator. Let min_1 denote $\min\limits_{x \in \mathcal{J}}(f_{AA}(x) - f_{aa}(x))$.

(a) $q = 0.2$ (b) $q = 0.8$
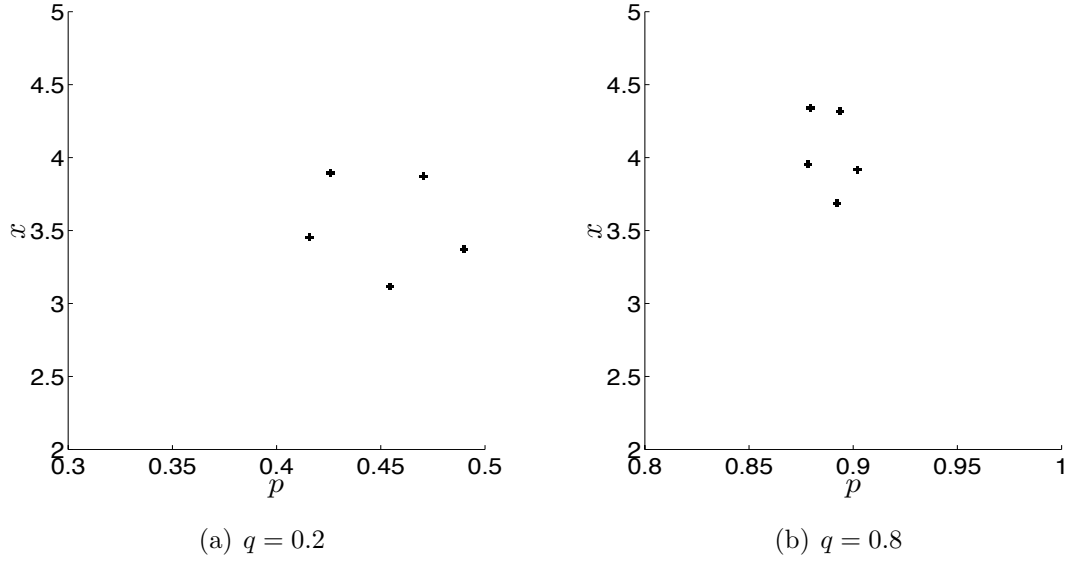
Figure 6.1: Global attractors in Example 6.5. For $f_{AA}(x) = e^{1.8-0.5x}$, $f_{aa}(x) = e^{1-0.5x}$, $y = 1$, $\delta = 0.5$, $k = 5$, $g_k(n) = \cos\left(\dfrac{2\pi n}{k}\right)$, $\alpha = 0.5$, the attractor is a 5-cycle. When $q = 0.2$ and when $q = 0.8$, the attractor is contained in the rectangle $[0,1] \times [0.5, 5.951]$.

Since $(p_n, x_n) \in \mathcal{R}$ for $n \geq 1$ and $p_n \leq q$, for $0 < \delta \leq 1$ and ignoring the non-negative h term, we have

$$f_A - f + \left(\frac{q}{p_n} - 1\right)h(1 + \alpha g_k(n)) \geq (1 - p_n)(p_n + \delta - 2\,\delta\,p_n)(f_{AA}(x_n) - f_{aa}(x_n))$$

$$\geq (1 - p_n)(p_n(1 - \delta) + \delta\,(1 - p_n))min_1$$

$$= (\delta(1 - p_n)^2 + p_n(1 - p_n)(1 - \delta))min_1$$

$$\geq \delta(1 - p_n)^2 min_1$$

$$\geq \delta(1 - q)^2 min_1.$$

When $\delta = 0$, for $n \geq 1$, note that a lower bound for p_n is found by

$$
\begin{aligned}
p_{n+1} &= \frac{x_n(p_n f_A + qh(1 + \alpha g_k(n)))}{x_n(f + h(1 + \alpha g_k(n)))} \\
&= \frac{x_n p_n f_A + qx_n h(1 + \alpha g_k(n))}{x_n f + x_n h(1 + \alpha g_k(n))} \\
&\geq \frac{qy(1 + \alpha g_k(n))}{x_n f + y(1 + \alpha g_k(n))} \\
&\geq \frac{qy(1 - \alpha)}{B + y(1 + \alpha)}.
\end{aligned}
\tag{6.8}
$$

Thus, using (6.8), the numerator of the fraction in (6.7) becomes

$$
\begin{aligned}
f_A - f + \left(\frac{q}{p_n} - 1 \right) h(1 + \alpha g_k(n)) &= p_n(1 - p_n)(f_{AA} - f_{aa}) + \left(\frac{q}{p_n} - 1 \right) h(1 + \alpha g_k(n)) \\
&\geq p_n(1 - p_n)(f_{AA} - f_{aa}) \\
&\geq \frac{qy(1 - \alpha)}{B + y(1 + \alpha)}(1 - q)min_1 \\
&= \frac{q(1 - q)y(1 - \alpha)min_1}{B + y(1 + \alpha)}.
\end{aligned}
$$

In the denominator, because $x \in \mathcal{J}$ we have that

$$
h(1 + \alpha\ g_k(n)) = \frac{y}{x_n}(1 + \alpha g_k(n)) \leq \frac{y}{x_n}(1 + \alpha) \leq \frac{1 + \alpha}{1 - \alpha}.
\tag{6.9}
$$

since $y(1 - \alpha) \leq x_n$. Also, note that

$$
\begin{aligned}
f &= (p_n^2 + 2\delta p_n - 2\delta p_n^2)f_{AA} + (1 - p_n^2 - 2\delta p_n + 2\delta p_n^2)f_{aa} \\
&= (p_n^2 + 2\delta p_n - 2\delta p_n^2)f_{AA} + (1 - p_n)(1 + p_n - 2\delta p_n)f_{aa} \\
&\leq (p_n^2 + 2\delta p_n - 2\delta p_n^2)f_{AA} + (1 - p_n)(1 + p_n - 2\delta p_n)f_{AA} \\
&= (p_n^2 + 2\delta p_n - 2\delta p_n^2)f_{AA} + (1 - p_n^2 - 2\delta p_n + 2\delta p_n^2)f_{AA} \\
&= f_{AA} \\
&\leq \max_{x \in \mathcal{J}} f_{AA}(x).
\end{aligned}
$$

Hence,

$$f + h\left(1 + \alpha\, g_k(n)\right) \leq \frac{1+\alpha}{1-\alpha} + \max_{x\in\mathcal{J}} f_{AA}(x). \tag{6.10}$$

Thus, for $0 < \delta \leq 1$, $r > 0$ is defined by

$$r = \frac{\delta(1-q)^2 min_1}{\frac{1+\alpha}{1-\alpha} + \max_{x\in\mathcal{J}} f_{AA}(x)}. \tag{6.11}$$

And for $\delta = 0$, $r > 0$ can be expressed as

$$r = \frac{q(1-q)y(1-\alpha)min_1}{\left(B + y(1+\alpha)\right)\left(\frac{1+\alpha}{1-\alpha} + \max_{x\in\mathcal{J}} f_{AA}(x)\right)}.$$

We then have $p_{n+1} \geq p_n(1+r)$ for $0 \leq \delta \leq 1$.

Part II: $f_{AA}(x) < f_{aa}(x)$

Assume that $f_{aa}(x) > f_{AA}(x)$ for all $x \in \mathcal{J}$. Define $v_n = 1 - p_n$ which is the frequency of a. The difference equation we require is

$$v_{n+1} = \frac{v_n f_a + (1-q)h\left(1 + \alpha\, g_k(n)\right)}{f + h\left(1 + \alpha\, g_k(n)\right)}. \tag{6.12}$$

We can rewrite (6.12) as

$$v_{n+1} = v_n\left[1 + \frac{f_a - f + \left(\frac{1-q}{v_n} - 1\right)h(1 + \alpha\, g_k(n))}{f + h(1 + \alpha\, g_k(n))}\right]. \tag{6.13}$$

We now proceed to minimize the fraction in (6.13). Let min_2 denote $\min_{x\in\mathcal{J}}(f_{aa}(x) - f_{AA}(x))$. Since $(p_n, x_n) \in \mathcal{R}$ for $n \geq 1$ and $p_n \geq q$ which is equivalent to

$1 - v_n \geq q$, when $0 \leq \delta < 1$, by ignoring the non-negative h term, we obtain

$$f_a - f + \left(\frac{1-q}{v_n} - 1\right) h(1 + \alpha g_k(n))$$

$$= f_a - f + \left(\frac{1 - q - v_n}{v_n}\right) h(1 + \alpha g_k(n))$$

$$\geq f_a - f$$

$$= (-(1 - v_n)^2 - \delta(1 - v_n) + 2\delta(1 - v_n)^2)(f_{AA} - f_{aa})$$

$$= (1 - v_n)((1 - v_n) + \delta - 2\delta(1 - v_n))(f_{aa} - f_{AA})$$

$$= (1 - v_n)((1 - v_n) - \delta(1 - v_n) + \delta - \delta(1 - v_n))(f_{aa} - f_{AA})$$

$$\geq (1 - v_n)((1 - v_n)(1 - \delta) + \delta - \delta + \delta v_n)min_2$$

$$\geq (1 - v_n)((1 - v_n)(1 - \delta) + \delta v_n)min_2$$

$$\geq (1 - v_n)^2(1 - \delta)min_2$$

$$\geq q^2(1 - \delta)min_2.$$

Furthermore, when $\delta = 1$, note that

$$v_{n+1} = \frac{v_n f_a + (1 - q)h(1 + \alpha g_k(n))}{f + h(1 + \alpha g_k(n))}$$

$$= \frac{x_n v_n f_a + (1 - q)x_n h(1 + \alpha g_k(n))}{x_n f + x_n h(1 + \alpha g_k(n))}$$

$$\geq \frac{x_n v_n f_a + (1 - q)y(1 - \alpha)}{x_n f + y(1 + \alpha)}$$

$$\geq \frac{(1 - q)y(1 - \alpha)}{B + y(1 + \alpha)}.$$

Therefore, for $\delta = 1$, the numerator of the fraction in (6.12) becomes

$$f_a - f + \left(\frac{1-q}{v_n} - 1\right)h(1 + \alpha g_k(n)) \geq f_a - f$$

$$\geq (1 - v_n)(1 - v_n - 1)(f_{AA} - f_{aa})$$

$$\geq (1 - v_n)v_n min_2$$

$$\geq q\frac{(1-q)y(1-\alpha)}{B + y(1+\alpha)}min_2$$

$$= \frac{q(1-q)y(1-\alpha)\,min_2}{B + y(1+\alpha)}.$$

It is also clear that

$$f = (p_n^2 + 2\delta\ p_n - 2\delta p_n^2)f_{AA} + (1 - p_n^2 - 2\delta p_n + 2\delta p_n^2)f_{aa}$$

$$\leq (p_n^2 + 2\delta\ p_n - 2\delta p_n^2)f_{aa} + (1 - p_n^2 - 2\delta p_n + 2\delta p_n^2)f_{AA}$$

$$= f_{aa}$$

$$\leq \max_{x \in \mathcal{J}} f_{aa}(x).$$

(6.14)

Hence, for $0 \leq \delta < 1$, using (6.9), $s > 0$ is defined by

$$s = \frac{q^2(1-\delta)min_2}{\frac{1+\alpha}{1-\alpha} + \max_{x \in \mathcal{J}} f_{aa}(x)}.$$

And for $\delta = 0$, $s > 0$ is defined by

$$s = \frac{q(1-q)y(1-\alpha)min_2}{(B + y(1+\alpha))\left(\frac{1+\alpha}{1-\alpha} + \max_{x \in \mathcal{J}} f_{aa}(x)\right)}$$

and $v_{n+1} \geq v_n(1 + s)$ so $1 - p_{n+1} \geq (1 - p_n)(1 + s)$.

This completes the proof of Lemma 6.6.

Example 6.7. Take $y = 1$, $q = 0.9$, $\delta = 0.6$, $k = 2$, $g_k(n) = (-1)^n$ and genotype fitnesses

$$f_{AA}(x) = e^{1.5 - 0.5x} \text{ and } f_{aa}(x) = e^{1 - 0.5x}.$$

Clearly, $f_{AA}(x) > f_{aa}(x)$ for all $x > 0$. Take $\alpha = 0$. We assume that the population originally consists of only the aa genotype, i.e. $p_0 = 0$. Then, using (3.1), we see

$$p_1 = \frac{qy}{x_0 f_{aa}(x_0) + y} \geq \frac{qy}{y + \max_{x \geq 0} x f_{aa}(x)}, \tag{6.15}$$

and find that $\max\limits_{x \geq 0} x f_{aa}(x) = 2$. Thus, from (6.15), $p_1 \geq 0.3$. From (6.11), we compute $r \approx 0.00332$. An orbit starting with $p = 0.3$ would require 3311 iterates before p_n is larger than $q = 0.9$. However, numerical simulations indicate that an orbit with initial frequency $p_0 = 0$ reaches frequency 0.9 in about 9 iterations.

For $\alpha = 0.4$, we again assume that $p_0 = 0$. Using (3.2),

$$p_1 = \frac{qy(1 + \alpha g_k(n))}{x_0 f_{aa}(x_0) + y(1 + \alpha g_k(n))} \geq \frac{qy(1 - \alpha)}{y(1 + \alpha) + \max_{x \geq 0} x f_{aa}(x)}. \tag{6.16}$$

Since $\max\limits_{x \geq 0} x f_{aa}(x) = 2$, from (6.16), $p_1 > 0.159$. Using (6.11), we compute $r \approx 0.000179$. An orbit starting with $p = 0.16$ would require 9707 iterates before p_n is greater than $q = 0.9$. Numerical simulations indicate that an orbit with initial frequency $p_0 = 0$ reaches frequency 0.9 in about 9 iterations.

6.3   Existence of Global Attractors

The existence of the bounds r and s in Lemma 6.6 allows us to prove the existence of global attractors. An open set $\mathcal{U}$ for a dynamical system $\mathcal{F}$ is a trapping region if $\mathcal{F}(\text{Cl}\,\mathcal{U}) \subset \mathcal{U}$ [25].

Theorem 6.8. *Assume (6.6), (3.5), $0 \leq \delta \leq 1$, and $0 < q < 1$. If $f_{AA}(x) > f_{aa}(x)$ for all $x \in \mathcal{J}$ then (3.3) has a global attractor in $Int\,\mathcal{S}^+$. If $f_{AA}(x) < f_{aa}(x)$ for all $x \in \mathcal{J}$ then (3.3) has a global attractor in $Int\,\mathcal{S}^-$.*

Proof. Lemma 6.4 ensures that $(p_n, x_n) \in \mathcal{R}$ for all $n \geq 1$. Assume $f_{AA}(x) > f_{aa}(x)$ and $p_n \leq q$ for all n. Lemma 6.6 says that there is $r > 0$ so that p_n grows like $(1+r)^n$. This is a contradiction to p_n being bounded above by 1. Hence, there exists N so

(a) $\alpha = 0$ (b) $\alpha = 0.4$
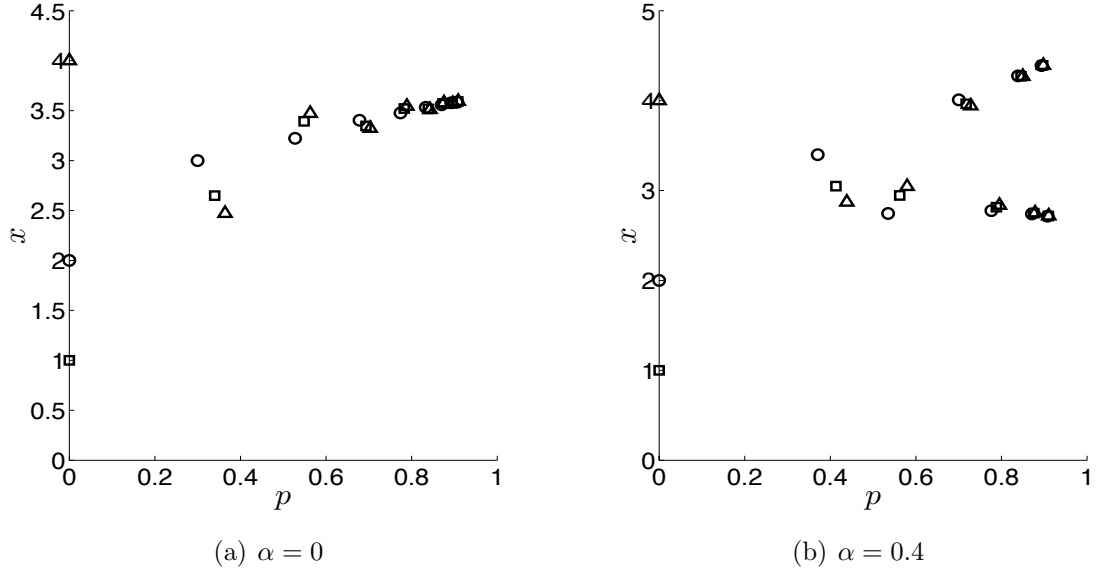
Figure 6.2: Nine iterates of three orbits with $p_0 = 0$ approaching the attractor for both $\alpha = 0$ and $\alpha = 0.4$ in Example 6.7. For $f_{AA}(x) = e^{1.5-0.5x}$, $f_{aa}(x) = e^{1-0.5x}$, $y = 1$, $q = 0.9$, $\delta = 0.6$, $k = 2$, $g_k(n) = (-1)^n$ for $p_0 = 0$ with $x_0 = 1$ ($\square$), $x_0 = 2$ ($\circ$), and $x_0 = 4$ ($\triangle$), the approach to the attractor is shown. When $\alpha = 0$, the fixed point is $(\bar{p}, \bar{x}) = (0.9287, 3.6038)$. When $\alpha = 0.4$, there exists a two cycle that oscillates between $(p, x) = (0.9308, 2.6945)$ and $(p, x) = (0.9285, 4.4696)$.

that $p_N > q$. By Corollary 6.2, it follows that $p_n > q$ for all $n \geq N$. Thus, the open set $\mathcal{U} = (q, 1) * (y(1 - \alpha), y(1 + \alpha) + B)$ is a trapping region and the intersection of all forward iterates of Cl $\mathcal{U}$ is the global attractor and is contained in Int $\mathcal{S}^+$ [25].

Assume $f_{AA}(x) < f_{aa}(x)$ and $p_n \geq q$ for all n. Lemma 6.6 says that p_n decreases exponentially, which is not possible. Hence, there is N so that $p_N < q$. By Corollary 6.2, it follows that $p_n < q$ for all $n \geq N$. Thus, the open set $\mathcal{V} = (0, q) * (y(1 - \alpha), y(1 + \alpha) + B)$ is a trapping region and the intersection of all forward iterates of Cl $\mathcal{V}$ is the global attractor Int $\mathcal{S}^-$.

6.4 Summary

In this chapter, we have demonstrated the existence of attractors. When the fitness of the homozygote AA is superior to the fitness of the homozygote aa, we have developed results that indicate the position of such an attractor. We showed that if the frequency of allele A in the island population is ever above the frequency in which it is carried by migration into the population, then the frequency of A can not fall below its migration frequency. Also, if the frequency of A in the island population is initially below q, the solution orbit will monotonically increase. We developed a method to approximate approach rates of the solution orbits to these attractors. We proved that for all degrees of dominance, a global attractor exists and is in the region defined by $p > q$. These results assert that if the transgenic allele homozygote is more fit than the nontransgenic homozygote, the transgene will persist in a natural population at an allele frequency higher than the allele frequency at which it migrates.

When the homozygote AA is inferior in fitness to the fitness of the homozygote aa, we found analogous results. If the frequency of A in the island population is initially below q, then it never rises above q. If the initial frequency of A is above q, then the solution orbit for the frequency of A will monotonically decrease. Approach rates of solution orbits to these attractors were approximated. Approximations indicate that these attractors are fairly rapidly approached in solution orbits. For all degrees of dominance that we studied, we were able to prove that a global attractor exists in the region where $p < q$.

Chapter 7

Allelic Diversity

We examine how the amplitude of the oscillatory migration factor affects the attractor. Then, we investigate how for periodic migration, the attractor decomposes into multiple pieces. We also introduce the concept of allelic diversity and investigate how changing the degree of dominance affects allelic diversity.

7.1 Amplitude of Oscillatory Migration

We explore the effect of changing the amplitude of oscillatory migration on the attractor. As introduced in Section 3.2, for $\alpha \in \mathbb{R}$, $0 \leq \alpha < 1$, we multiply the constant immigration y by a factor of $1 + \alpha g_k(n)$ where $-1 \leq g_k(n) \leq 1$ and $g_k(n+k) = g_k(n)$ for $n = 0, 1, 2, \ldots$. We know that the constant migration factor of y varies between $y(1-\alpha)$ and $y(1+\alpha)$ and the maximum variation from y is αy. Thus, for a given $g_k(n)$, the larger the α, the more variation in the amount of migration. For a k-periodic dynamical system the attractor is the union of k attractor subsets. Each of these subsets is the attractor of an autonomous system and may be homeomorphic to the attractor from the corresponding system that does not have periodic migration [9], i.e. where $\alpha = 0$.

Including periodic migration in the model changes the attractor. From the second

equation in our system of difference equations (3.2), we see that the population size has more variation for larger α values. The parameter α occurs in both the numerator and denominator of the computation of the allele frequency in the next generation. No general conclusion can be made about how α affects allele frequency. Graphical simulations demonstrate how the amplitude of the oscillatory migration can affect the position and dynamics of the attractor.

Example 7.1. Take $k = 2$ and $g_k(n) = (-1)^n$ and genotype fitnesses

$$f_{AA}(x) = e^{3.1-0.5x} \text{ and } f_{aa}(x) = e^{1-0.5x}.$$

Clearly, $f_{AA}(x) > f_{aa}(x)$ for all $x > 0$. Fix $\delta = 0$ to examine how varying α changes the attractor.

For $y = 1$, $q = 0.6$, and $\alpha = 0$, the attractor is a 4-cycle. When $\alpha = 0.4$, there is an 8-cycle. The x values and p values expand in both directions when compared to their values when $\alpha = 0$. When $\alpha = 0.5$, the behavior of the attractor is more chaotic. The p and x values expand from when $\alpha = 0.4$. When $\alpha = 0.95$, the attractor appears even more chaotic. The x values expanded but the p values contracted from their values at $\alpha = 0.5$ (see Table 7.1). As the amplitude of the oscillatory migration factor increases, the attractor expands in the x direction. The allele frequency expands and then contracts as the amplitude increases. The attractor has a higher degree of chaos as α increases (see Figure 7.1).

Table 7.1: Minimum and maximum values of allele frequency and population size for attractor as α varies for $y = 1$, $q = 0.6$ in Example 7.1. For $f_{AA}(x) = e^{3.1-0.5x}$, $f_{aa}(x) = e^{1-0.5x}$, $\delta = 0$, $k = 2$, and $g_k(n) = (-1)^n$, the population size interval increases as α increases. The allele frequency both expands and contracts as α increases.

α	min p value	max p value	min x value	max x value
0	0.756	0.928	1.670	11.652
0.4	0.705	0.947	0.818	14.378
0.5	0.699	0.948	0.668	14.986
0.95	0.759	0.978	0.103	17.641

When $y = 0.1$, $q = 0.1$, and $\alpha = 0$, there is a chaotic attractor. When $\alpha = 0.2$, there is migration of period two and there are two pieces of the attractor. When $\alpha = 0.5$, the attractor expands in both the p and x directions. The pieces of the chaotic attractor also spread apart. When $\alpha = 0.95$, the shape of the attractor changes, but the two pieces of the attractor can still be seen. In this particular example, the attractor has more variation in both the p and x direction as α increases (see Table 7.2 and Figure 7.2).

Table 7.2: Minimum and maximum values of allele frequency and population size for attractor as α varies for $y = 0.1$, $q = 0.1$ in Example 7.1. For $f_{AA}(x) = e^{3.1-0.5x}$, $f_{aa}(x) = e^{1-0.5x}$, $\delta = 0$, $k = 2$, and $g_k(n) = (-1)^n$, the population size interval and the allele frequency interval increase as α increases.

α	min p value	max p value	min x value	max x value
0	0.662	0.9896	0.267	15.175
0.2	0.646	0.9902	0.230	15.422
0.5	0.630	0.9915	0.177	15.800
0.95	0.621	0.9957	0.103	16.392

7.2 Subsets Comprising the Attractor

The periodic migration produces subsets in the structure of the attractor. As seen in the previous example, including period 2 migration can produce additional pieces in the attractor that are similar in form to what the attractor looked like when there was no periodic migration (i.e. when $\alpha = 0$). The attractor of the system that incorporates the period two migration is the union of these subsets of attractors [9].

When we include period two migration, we can get two similar copies of the attractor as compared to what occurs when $\alpha = 0$ creating one attractor with two homeomorphic pieces. We can view the even iterates and odd iterates separately and see the parts of the attractor that are due to the periodicity of the migration. If the attractor is a j-cycle when $\alpha = 0$, this period two migration can lead to an

Figure 7.1: Attractor movement as α varies for $y = 1$, $q = 0.6$ in Example 7.1. For $f_{AA}(x) = e^{3.1-0.5x}$, $f_{aa}(x) = e^{1-0.5x}$, $\delta = 0$, $k = 2$, and $g_k(n) = (-1)^n$, the attractor changes from a 4-cycle to a chaotic attractor as α increases from 0 to 0.95.

(a) $\alpha = 0$

(b) $\alpha = 0.2$
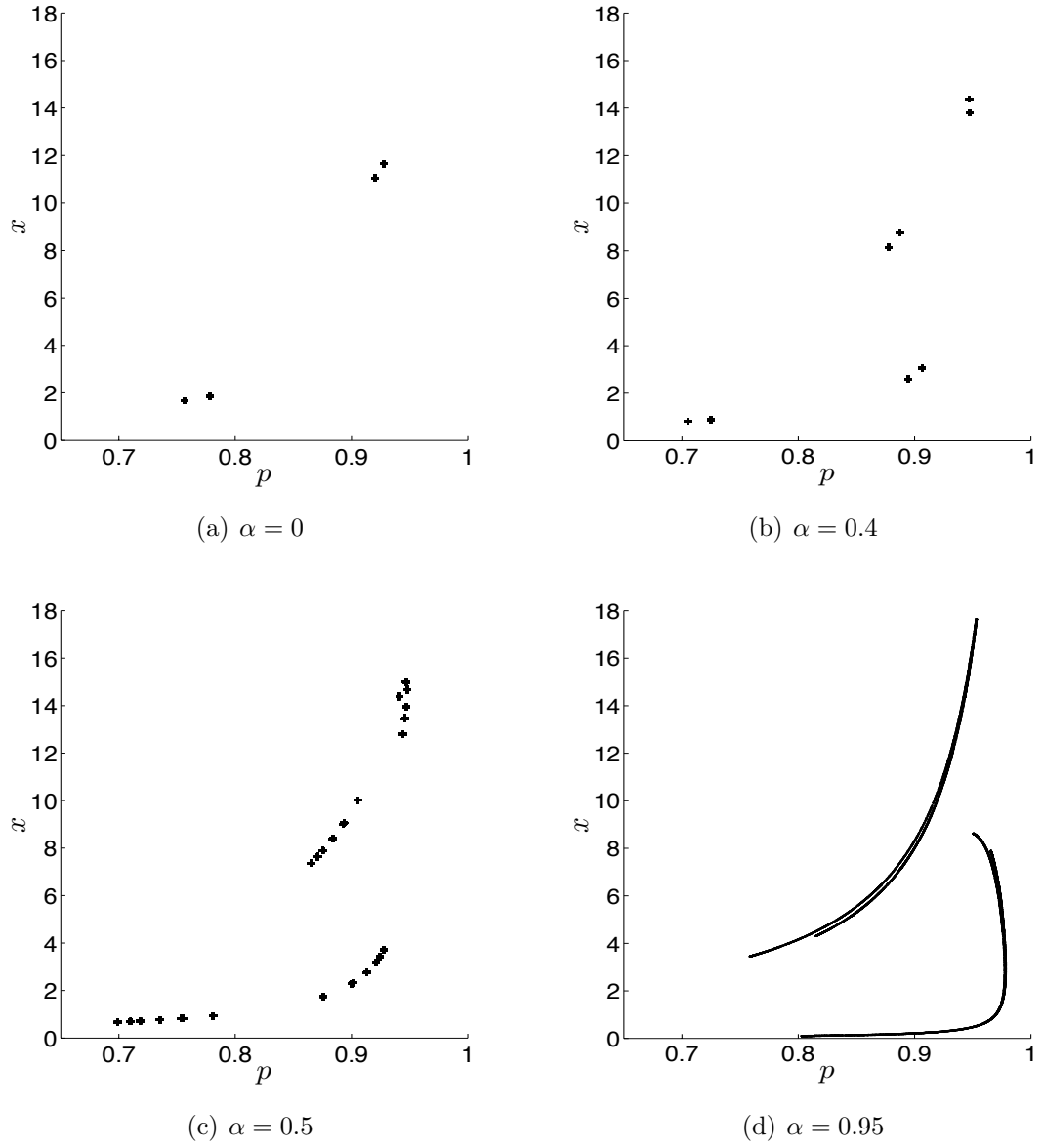
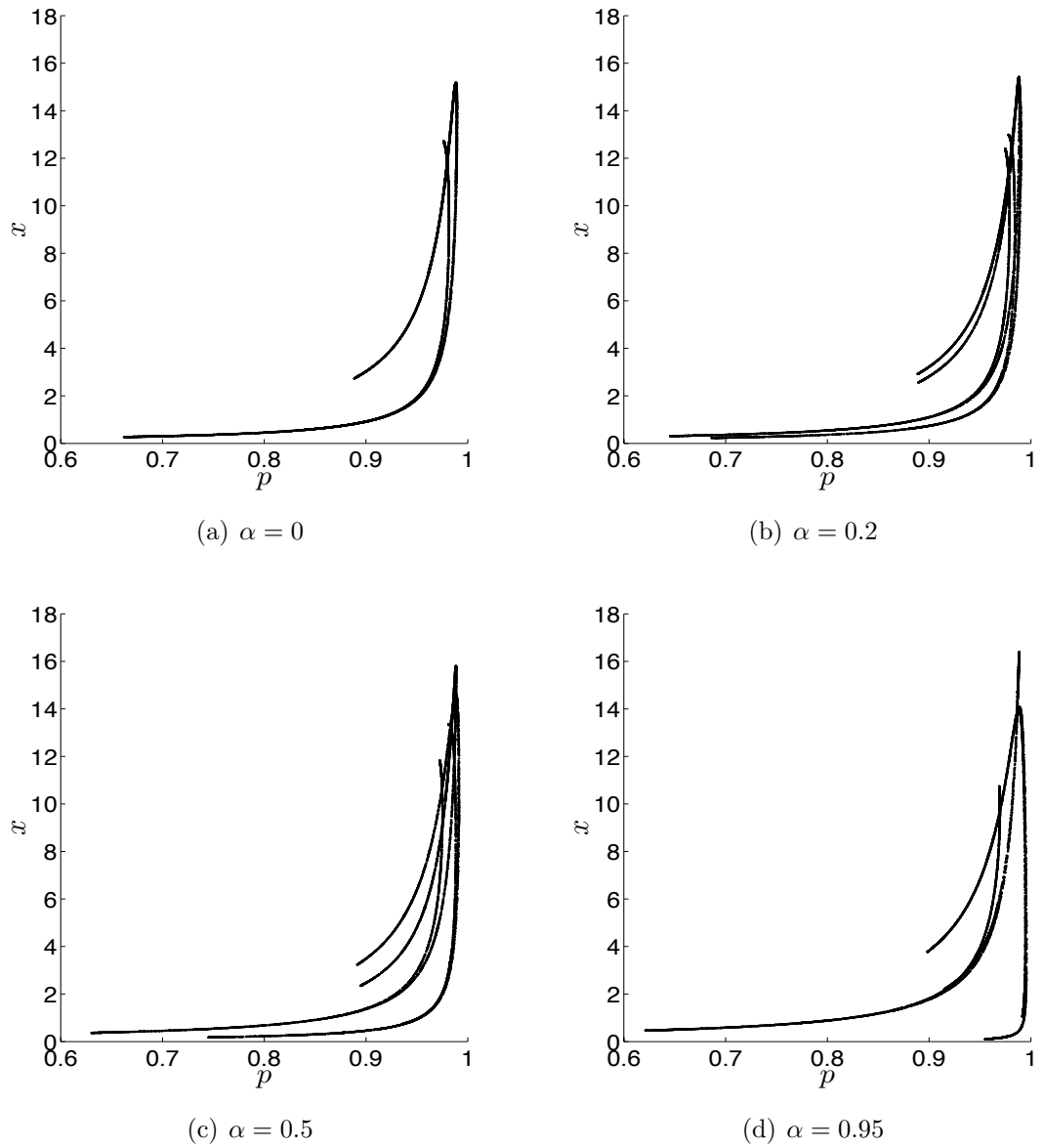(c) $\alpha = 0.5$

(d) $\alpha = 0.95$

Figure 7.2: Attractor movement as α varies for $y = 0.1$, $q = 0.1$ in Example 7.1. For $f_{AA}(x) = e^{3.1-0.5x}$, $f_{aa}(x) = e^{1-0.5x}$, $\delta = 0$, $k = 2$, and $g_k(n) = (-1)^n$, the attractor can be viewed as two subsets when $\alpha \neq 0$ and it expands in both directions as α increases from 0 to 0.95.

attractor composed of a $2j$-cycle. If viewed in terms of even and odd iterates, there are two separate j-cycles that when considered together form the attractor. Likewise, when we include period two oscillatory migration for what was a chaotic attractor when $\alpha = 0$, two chaotic pieces that are homeomorphic to the original are formed. Even and odd iterates form two separate pieces of the attractor. These findings are demonstrated in the following example.

Example 7.2. Take $y = 0.1$, $q = 0.1$, $\delta = 0.5$, $\alpha = 0.2$, $k = 2$, $g_k(n) = (-1)^n$, and genotype fitnesses

$$f_{AA}(x) = e^{3.1-0.5x} \text{ and } f_{aa}(x) = e^{1-0.5x}.$$

Clearly, $f_{AA}(x) > f_{aa}(x)$ for all $x > 0$. This example illustrates the effects that result from period two migration. The pieces of the attractor exist apart from each other. We view the odd iterates as the blue curve (Figure 7.3(a)) and the even iterates as the red curve (Figure 7.3(b)). The union of the two subsets gives the attractor for this system (Figure 7.3(c)).

When we include period k migration, we can get k similar copies of the attractor that was obtained when $\alpha = 0$. We examine the iterates of the attractor using a modulo argument. We let $n \mod k \equiv a$ so $n = mk + a$ for an integer m where $0 \leq a < k$. We look at the iterates based on the various values of a and can see the different attractor for each of these. Again, the result of putting all these iterations together is the attractor for the whole system.

Example 7.3. Take $y = 0.1$, $q = 0.3$, $\alpha = 0.3$, $k = 3$, $g_k(n) = \cos\left(\dfrac{2\pi n}{k}\right)$, $\delta = 0.8$, and genotype fitnesses

$$f_{AA}(x) = e^{2.1-0.7x} \text{ and } f_{aa}(x) = e^{1.1-0.7x}.$$

Clearly, $f_{AA}(x) > f_{aa}(x)$ for all $x > 0$. When $\alpha = 0$, the attractor for this system is a 2-cycle. We have included period three migration as a factor and get an example

(a) odd iterates

(b) even iterates
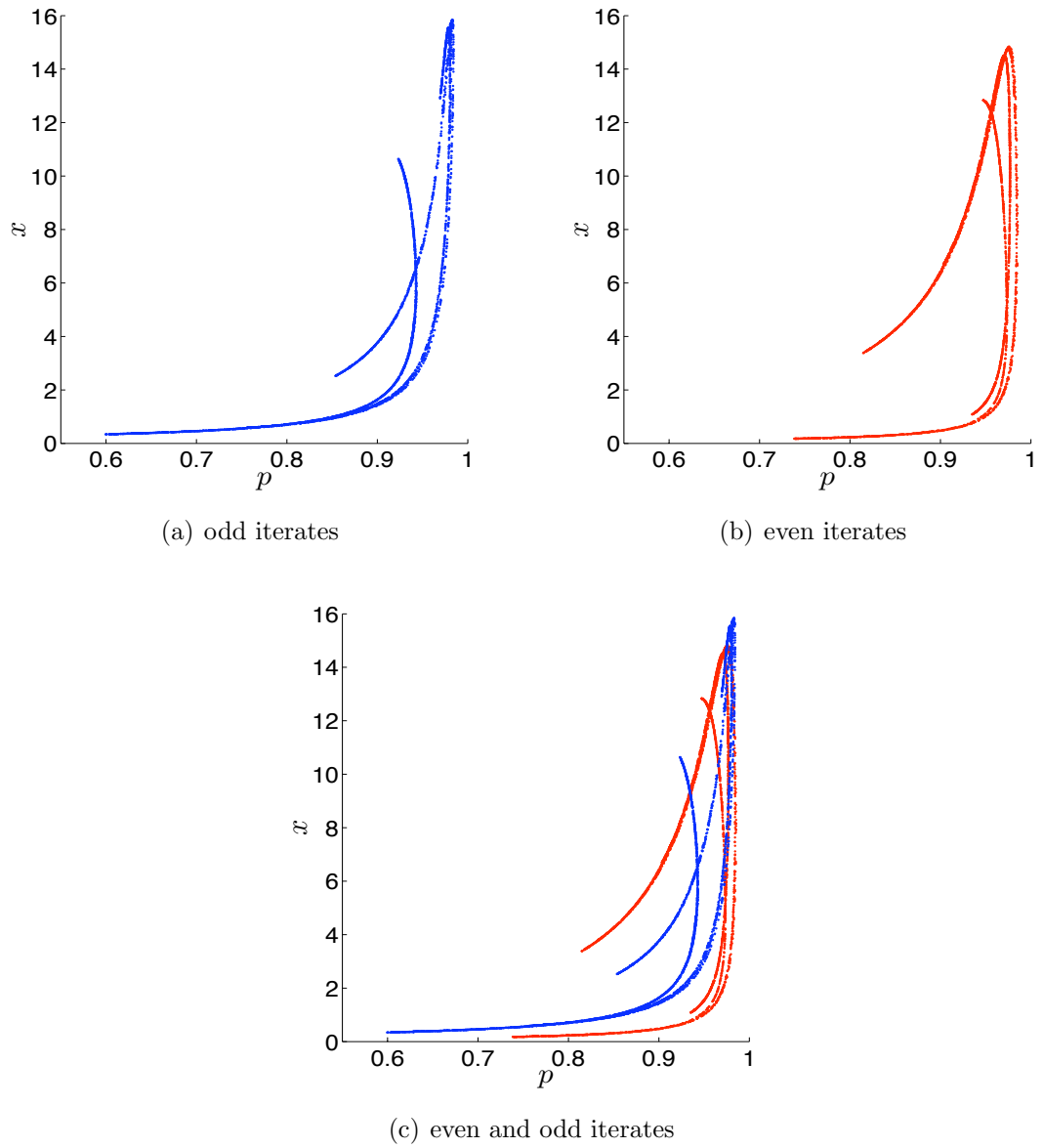
(c) even and odd iterates

Figure 7.3: Two subsets of attractor for system with period 2 migration in Example 7.2. For $f_{AA}(x) = e^{3.1-0.5x}$, $f_{aa}(x) = e^{1-0.5x}$, $y = 0.1$, $q = 0.1$, $\delta = 0.5$, $\alpha = 0.2$, $k = 2$, and $g_k(n) = (-1)^n$, the even and odd iterates can be interpreted as two separate subsets of attractors or considered together as the overall attractor.
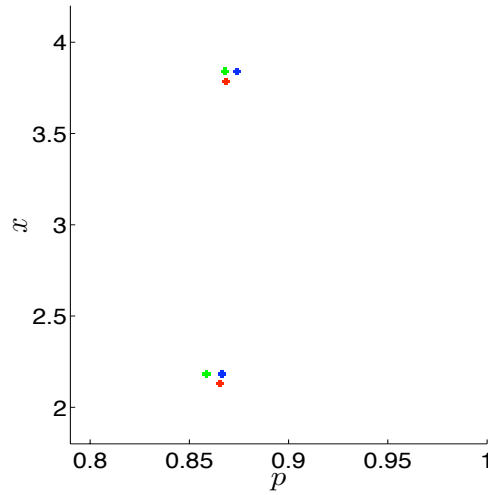
Figure 7.4: Three subsets of attractor for system with period 2 migration in Example 7.3. For $f_{AA}(x) = e^{2.1-0.7x}$, $f_{aa}(x) = e^{1.1-0.7x}$, $y = 0.1$, $q = 0.3$, $\delta = 0.8$, $\alpha = 0.3$, $k = 3$, and $g_k(n) = \cos\left(\dfrac{2\pi n}{k}\right)$, the attractor is a 6-cycle that can also be viewed as three 2-cycles for the appropriate compositions.

that is a 6-cycle. We can also interpret this attractor as three 2-cycles by using the appropriate compositions [9]. We take the attractor that is produced from the iterates that are modulo 0 and plot them in red, the iterates that are modulo 1 and plot them in green and the iterates that are modulo 2 and plot them blue (Figure 7.4). We can see the individual 2-cycles. Taking the union of these three subsets, we get the attractor for the original system.

7.3   Allelic Diversity

The maximal allelic diversity for a population at equilibrium occurs when $\bar{p} = 0.5$ because there are equal frequencies for the A and a alleles. We will consider a measure allelic diversity (AD) that yields a number between 0 and 1, scaled so the 0 indicates no diversity and 1 indicates the highest level of diversity. For an equilibrium,

$E = (\bar{p}, \bar{x})$, we define allelic diversity as

$$AD(E) = 1 - 2|\bar{p} - 0.5|.$$

If $\bar{p} = 0$ or $\bar{p} = 1$, then $AD(E) = 0$ and there is no allelic diversity as only either the A allele or the a allele exists in the population. If $\bar{p} = 0.5$ then $AD(E) = 1$ and there is maximal allelic diversity as equal numbers of the A allele and the a allele occur in the population.

As in Selgrade, Bostic, and Roberds [29], we extend this notion to an invariant set Λ by considering the time-average of the distance to 0.5 along a solution orbit in Λ and scaling it to be between 0 and 1, i.e.,

$$AD(\Lambda) = 1 - \lim_{k \to \infty} \frac{2}{k} \sum_{n=0}^{k-1} |p_n - 0.5| \tag{7.1}$$

provided this limit exists and is the same for almost all initial points in Λ.

This nonnegative number, $AD(\Lambda)$ measures the departure from maximal allelic diversity for Λ. The closer $AD(\Lambda)$ is to 1, the more allelic diverse Λ is. If $E = (\bar{p}, \bar{x})$ is the equilibrium solution, then clearly $AD(\Lambda) = 1 - 2|\bar{p} - 0.5|$.

If Λ is a j-cycle, then we show $AD(\Lambda)$ is the average distance to 0.5 scaled between 0 and 1.

Proposition 7.4. *If Λ is a j-cycle, then*

$$AD(\Lambda) = 1 - \frac{2}{j}[|p_0 - 0.5| + |p_1 - 0.5| + \ldots |p_{j-1} - 0.5|].$$

Proof. We use a modulo argument to prove this. We let $k \mod j \equiv a$ so $k = Mj + a$

for an integer M where $0 \le a < j$. Thus, we compute

$$
\begin{aligned}
AD(\Lambda) &= 1 - \lim_{k \to \infty} \frac{2}{k} \sum_{n=0}^{k-1} |p_n - 0.5| \\
&= 1 - \lim_{k \to \infty} \frac{2}{k} [|p_0 - 0.5| + |p_1 - 0.5| + \cdots + |p_{j-1} - 0.5| + |p_j - 0.5| + \ldots \\
&\qquad\qquad + |p_{k-1} - 0.5|] \\
&= 1 - 2 \lim_{k \to \infty} \frac{1}{k} [|p_0 - 0.5| + |p_1 - 0.5| + \cdots + |p_{j-1} - 0.5| + |p_0 - 0.5| + \ldots \\
&\qquad\qquad + |p_0 - 0.5| + \cdots + |p_{a-1} - 0.5|] \\
&= 1 - 2 \lim_{k \to \infty} \frac{1}{k} [|p_0 - 0.5| \left(\frac{k-a}{j}\right) + |p_1 - 0.5| \left(\frac{k-a}{j}\right) + \ldots \\
&\qquad\qquad + |p_{j-1} - 0.5| \left(\frac{k-a}{j}\right) + |p_0 - 0.5| + \cdots + |p_{a-1} - 0.5|] \\
&= 1 - 2 \lim_{k \to \infty} [|p_0 - 0.5| \left(\frac{k}{jk}\right) + |p_1 - 0.5| \left(\frac{k}{jk}\right) + \cdots + |p_{j-1} - 0.5| \left(\frac{k}{jk}\right) \\
&\qquad\qquad - |p_0 - 0.5| \left(\frac{a}{jk}\right) - |p_1 - 0.5| \left(\frac{a}{jk}\right) - \cdots - |p_{j-1} - 0.5| \left(\frac{a}{jk}\right) \\
&\qquad\qquad + |p_0 - 0.5| \left(\frac{1}{k}\right) + \cdots + |p_{a-1} - 0.5| \left(\frac{1}{k}\right)] \\
&= 1 - 2[|p_0 - 0.5| \left(\frac{1}{j}\right) + |p_1 - 0.5| \left(\frac{1}{j}\right) + \cdots + |p_{j-1} - 0.5| \left(\frac{1}{j}\right)]
\end{aligned}
$$

Example 7.5. Take $y = 0.1$, $q = 0.3$, and genotype fitnesses

$$
f_{AA}(x) = e^{2.1 - 0.7x} \text{ and } f_{aa}(x) = e^{1.1 - 0.7x}.
$$

Clearly, $f_{AA}(x) > f_{aa}(x)$ for all $x > 0$. Let $g_k(n) = \cos\left(\frac{2\pi n}{k}\right)$. First, we examine the attractor when there is no periodic migration with the system ($\alpha = 0$). For $\delta = 0$, the attractor is a 2-cycle. The attractor oscillates between the points $(0.964, 3.580)$ and $(0.957, 2.379)$. Using Proposition 7.4, we compute $AD(\Lambda) \approx 0.0782$. Clearly, with the high values of p, there is not much allelic diversity because of the high frequency of the A allele (Figure 7.5(a)).

For $\delta = 1$ (Figure 7.5(d)), the attractor oscillates between $(0.804, 2.053)$ and $(0.811, 3.986)$. And, $AD(\Lambda) \approx 0.386$. When there is no periodic migration, we see in Figure 7.5 that as δ increases, the 2-cycle moves to the left (p decreases) and the allelic diversity increases. In addition, the interval between the x values increases (see Table 7.3).

Table 7.3: Allelic Diversity for various δ when $\alpha = 0$ in Example 7.5. For $f_{AA}(x) = e^{2.1-0.7x}$, $f_{aa}(x) = e^{1.1-0.7x}$, $y = 0.1$, $q = 0.3$, allelic diversity increases as δ increases. Allele frequency decreases and the interval between the population sizes expands as δ increases.

δ	$AD(\Lambda)$	min p value	max p value	min x value	max x value
0	0.078	0.957	0.964	2.379	3.580
0.5	0.151	0.921	0.928	2.252	3.712
0.8	0.267	0.863	0.870	2.164	3.823
1	0.386	0.804	0.811	2.053	3.986

We now include period three migration with the same fitnesses. Letting $k = 3$, $g_k(n) = \cos\left(\frac{2\pi n}{k}\right)$, and $\alpha = 0.3$, the attractor is a 6-cycle. For $\delta = 0$, we compute $AD(\Lambda) \approx 0.0782$. The attractor is within the p-interval $0.950 < p < 0.968$ and within the x-interval $2.340 < x < 3.614$ (see Figure 7.6 and Table 7.4).

For $\delta = 1$, the attractor is a 6-cycle. The attractor is within the p-interval $0.799 < p < 0.814$ and the x-interval $2.021 < x < 4.006$. In addition, $AD(\Lambda) \approx 0.386$ (see Table 7.4). Note that as δ increases from 0 to 1, allele frequency values in the attractor decrease and allelic diversity increases. Also, the interval that contains the population sizes expands (see Table 7.4 and Figure 7.6).

Numerical simulations indicate that for a j-cycle when $f_{AA}(x) > f_{aa}(x)$ for all $x > 0$ regardless of if periodic migration is included or not that as δ increases, the attractor moves to the left and allelic diversity increases. Also, the interval that includes the population size expands in both directions as δ increases.

(a) $\delta = 0$ (b) $\delta = 0.5$

(c) $\delta = 0.8$ (d) $\delta = 1$

Figure 7.5: Location of 2-cycle for various δ when $\alpha = 0$ in Example 7.5. For $f_{AA}(x) = e^{2.1-0.7x}$, $f_{aa}(x) = e^{1.1-0.7x}$, $y = 0.1$, $q = 0.3$, the 2-cycle moves left as δ increases.

(a) $\delta = 0$

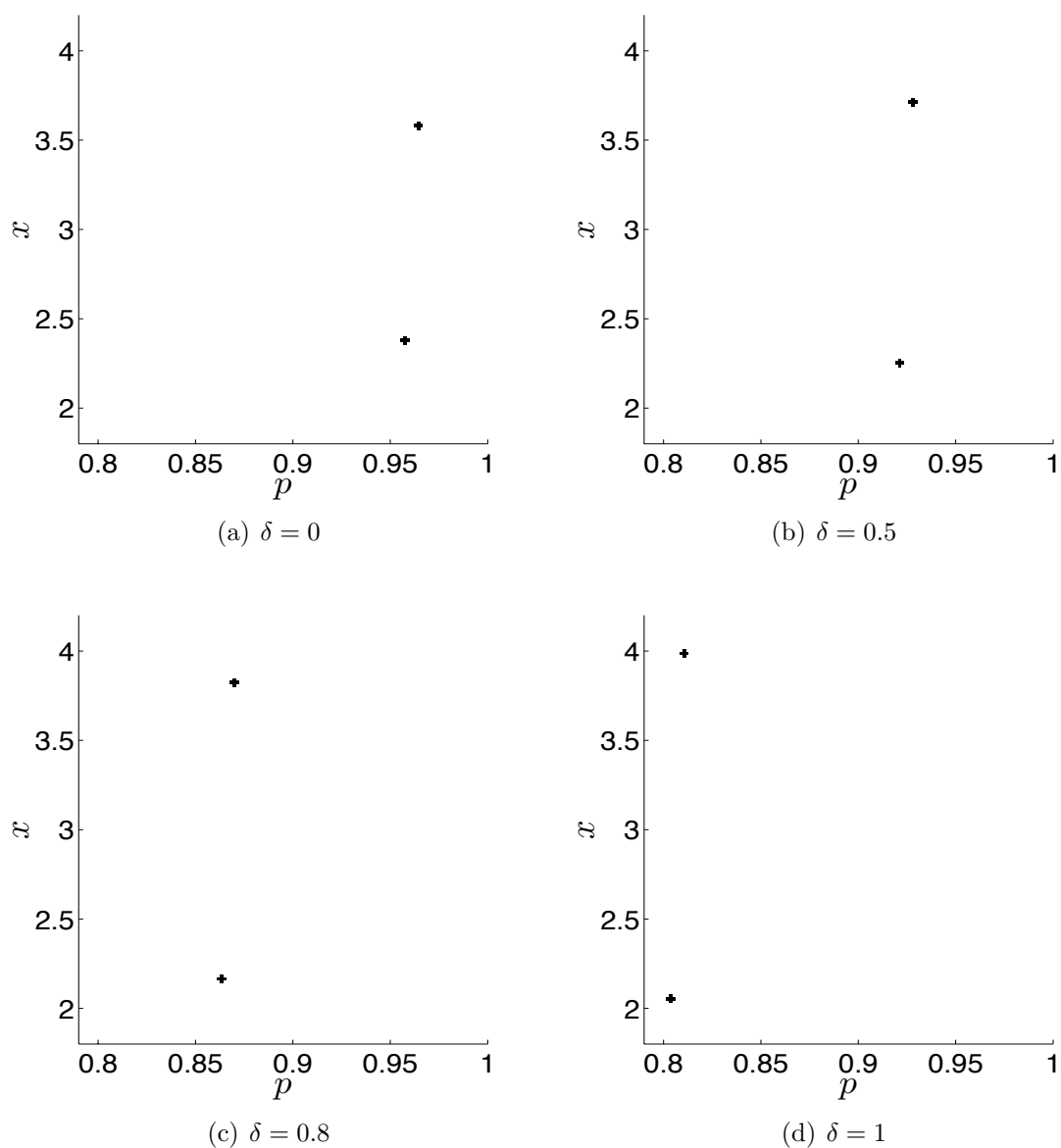(b) $\delta = 0.5$

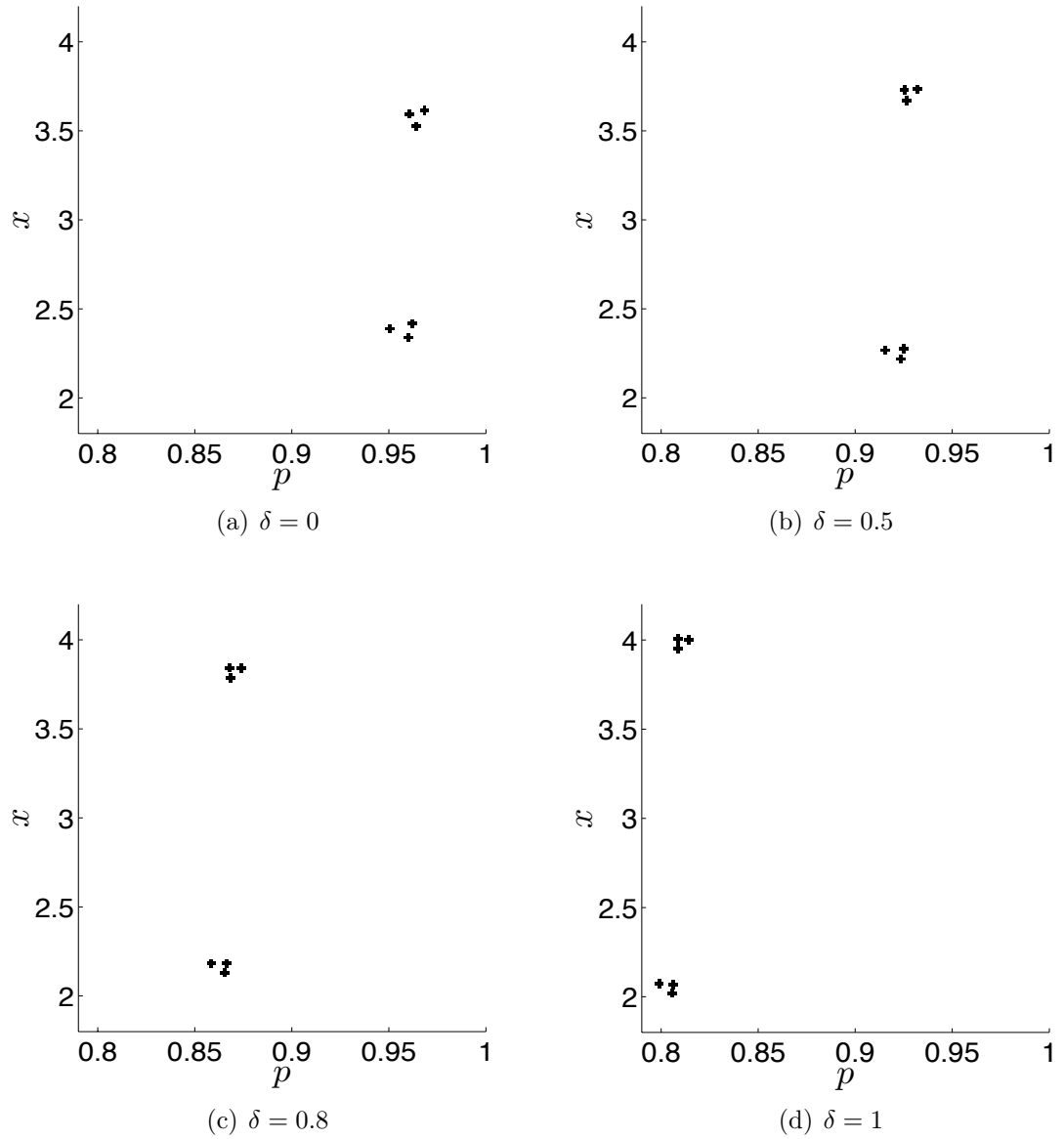(c) $\delta = 0.8$

(d) $\delta = 1$

Figure 7.6: Location of 6-cycle for various δ when $\alpha = 0.3$ in Example 7.5. For $f_{AA}(x) = e^{2.1-0.7x}$, $f_{aa}(x) = e^{1.1-0.7x}$, $y = 0.1$, $q = 0.3$, $k = 3$, and $g_k(n) = \cos\left(\frac{2\pi n}{k}\right)$ the 6-cycle moves left as δ increases.

Table 7.4: Allelic Diversity for various δ when $\alpha = 0.3$ in Example 7.5. For $f_{AA}(x) = e^{2.1-0.7x}$, $f_{aa}(x) = e^{1.1-0.7x}$, $y = 0.1$, $q = 0.3$, $k = 3, g_k(n) = \cos\left(\dfrac{2\pi n}{k}\right)$ allelic diversity increases as δ increases. Allele frequency decreases and the interval that contains the population size expands as δ increases.

δ	$AD(\Lambda)$	min p value	max p value	min x value	max x value
0	0.078	0.950	0.968	2.340	3.614
0.5	0.151	0.916	0.932	2.218	3.734
0.8	0.266	0.859	0.874	2.131	3.841
1	0.386	0.799	0.814	2.021	4.006

Example 7.6. Take $y = 0.1$, $q = 0.1$, $k = 2$, $g_k(n) = (-1)^n$, and genotype fitnesses

$$f_{AA}(x) = e^{3.1-0.5x} \text{ and } f_{aa}(x) = e^{1-0.5x}.$$

Clearly, $f_{AA}(x) > f_{aa}(x)$ for all $x > 0$. For $\alpha = 0$ and $\delta = 0$, we have a chaotic attractor which is within the p-interval $0.662 < p < 0.990$, the x-interval $0.267 < x < 15.175$, and $AD(\Lambda) \approx 0.148$. As δ increases, the attractor moves to the left. When $\delta = 0.7$, the attractor is an island grouping. The p-interval and x-interval which contain the attractor have decreased in size. When $\delta = 1$, the attractor moves to the left and the region that contains the attractor expands. For $\alpha = 0$, as δ increases from 0 to 1, the attractor moves left (except $\delta = 0.7$) and allelic diversity increases (see Figure 7.7 and Table 7.5).

Table 7.5: Allelic Diversity for various δ when $\alpha = 0$ in Example 7.6. For $f_{AA}(x) = e^{3.1-0.5x}$, $f_{aa}(x) = e^{1-0.5x}$, $y = 0.1$, $q = 0.1$, $k = 2$, $g_k(n) = (-1)^n$ allelic diversity increases as δ increases.

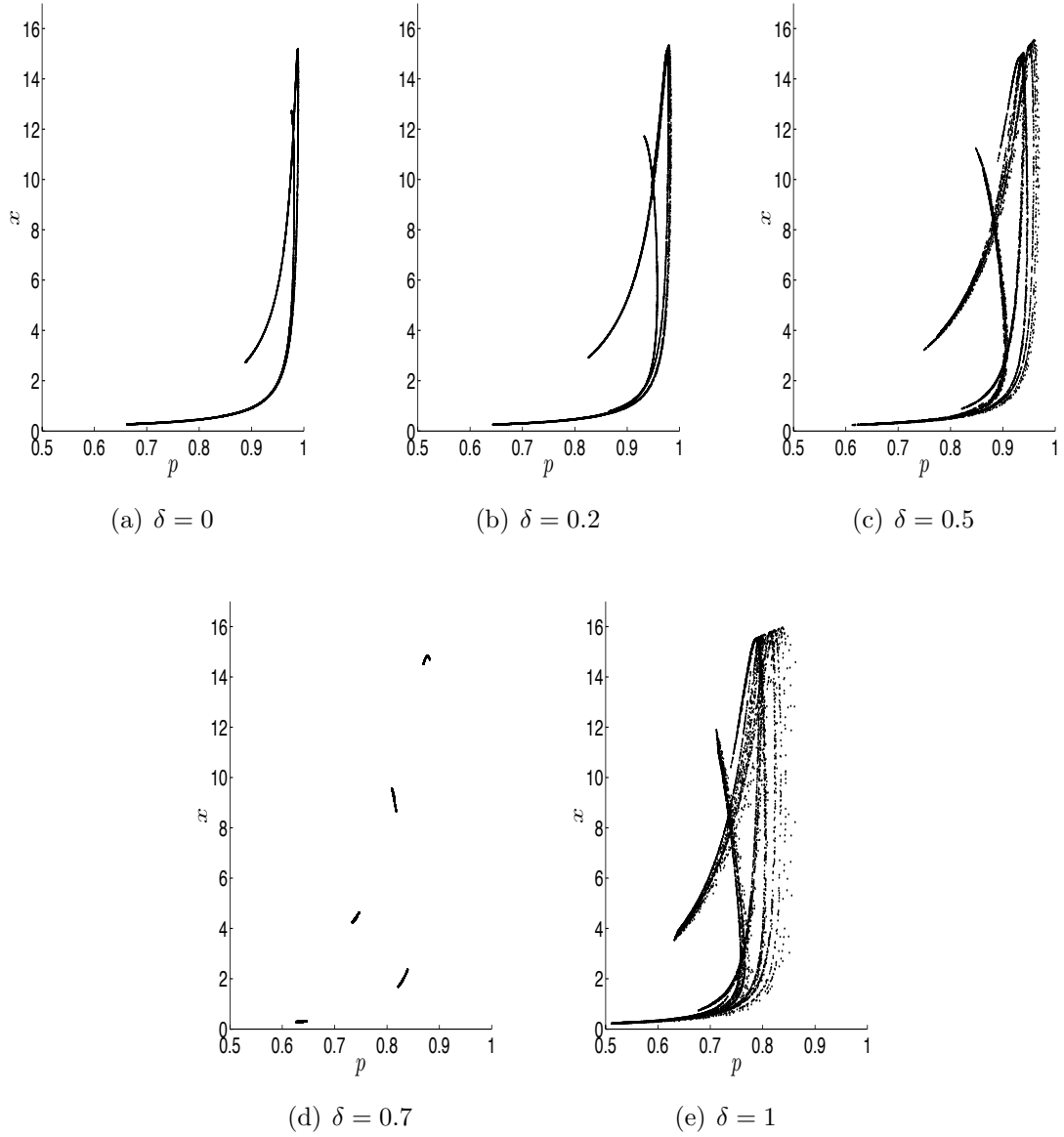| δ	$AD(\Lambda)$	min p value	max p value	min x value	max x value
0	0.148	0.662	0.990	0.267	15.175
0.2	0.184	0.643	0.984	0.255	15.331
0.5	0.280	0.613	0.970	0.240	15.541
0.7	0.443	0.627	0.882	0.285	14.828
1	0.560	0.510	0.865	0.216	16.009

Figure 7.7: Attractor for various δ when $\alpha = 0$ in Example 7.6. For $f_{AA}(x) = e^{3.1-0.5x}$, $f_{aa}(x) = e^{1-0.5x}$, $y = 0.1$, $q = 0.1$, $k = 2$, and $g_k(n) = (-1)^n$, as δ increases the attractor moves left and the region that contains the attractor expands (except when $\delta = 0.7$ when the attractor is an island grouping).

When $\alpha = 0.5$, period two migration is included in the model. When $\delta = 0$, there are two homeomorphic copies of the attractor. The p-interval is $0.630 < p < 0.992$, the x-interval is $0.177 < x < 15.800$, and $AD(\Lambda) \approx 0.136$. As δ increases, the attractor expands in both the p and x direction and the pieces of the attractor separate. When $\delta = 1$, the attractor is a 12-cycle that is in the p-interval is $0.442 < p < 0.860$, the x-interval is $0.163 < x < 16.091$ and $AD(\Lambda) \approx 0.591$. As δ increases, the attractor moves left and allelic diversity increases (see Figure 7.8 and Table 7.6).

Table 7.6: Allelic Diversity for various δ when $\alpha = 0.5$ in Example 7.6. For $f_{AA}(x) = e^{3.1-0.5x}$, $f_{aa}(x) = e^{1-0.5x}$, $y = 0.1$, $q = 0.1$, $k = 2$, $g_k(n) = (-1)^n$ allelic diversity increases as δ increases.

δ	$AD(\Lambda)$	min p value	max p value	min x value	max x value
0	0.136	0.630	0.992	0.177	15.800
0.2	0.193	0.599	0.985	0.175	15.839
0.5	0.282	0.554	0.972	0.174	15.844
0.7	0.376	0.519	0.951	0.174	15.825
1	0.591	0.442	0.860	0.163	16.091

When $\alpha = 0.95$, the amplitude of the oscillatory migration is high. When $\delta = 0$, the p-interval is $0.621 < p < 0.996$, the x-interval is $0.103 < x < 16.389$ and $AD(\Lambda) \approx 0.138$. As δ increases, the attractor moves left and the allelic diversity increases. There is not much difference in the interval that contains the population size. When $\delta = 1$, the p-interval is $0.398 < p < 0.889$, the x-interval is $0.107 < x < 16.233$ and $AD(\Lambda) \approx 0.534$.

From the previous examples, we have seen that for $f_{AA}(x) > f_{aa}(x)$ for all $x > 0$ that regardless of whether periodic migration is included and whether the attractor is a j-cycle or chaotic, that as the degree of dominance increases, the allelic diversity of the attractor increases. A possible explanation for this is that as δ increases, the heterozygote fitness becomes more similar to the homozygote AA fitness. Thus, the heterozygote fitness is increasing, leading to an increase in the heterozygote Aa in the population and an increase in allelic diversity.
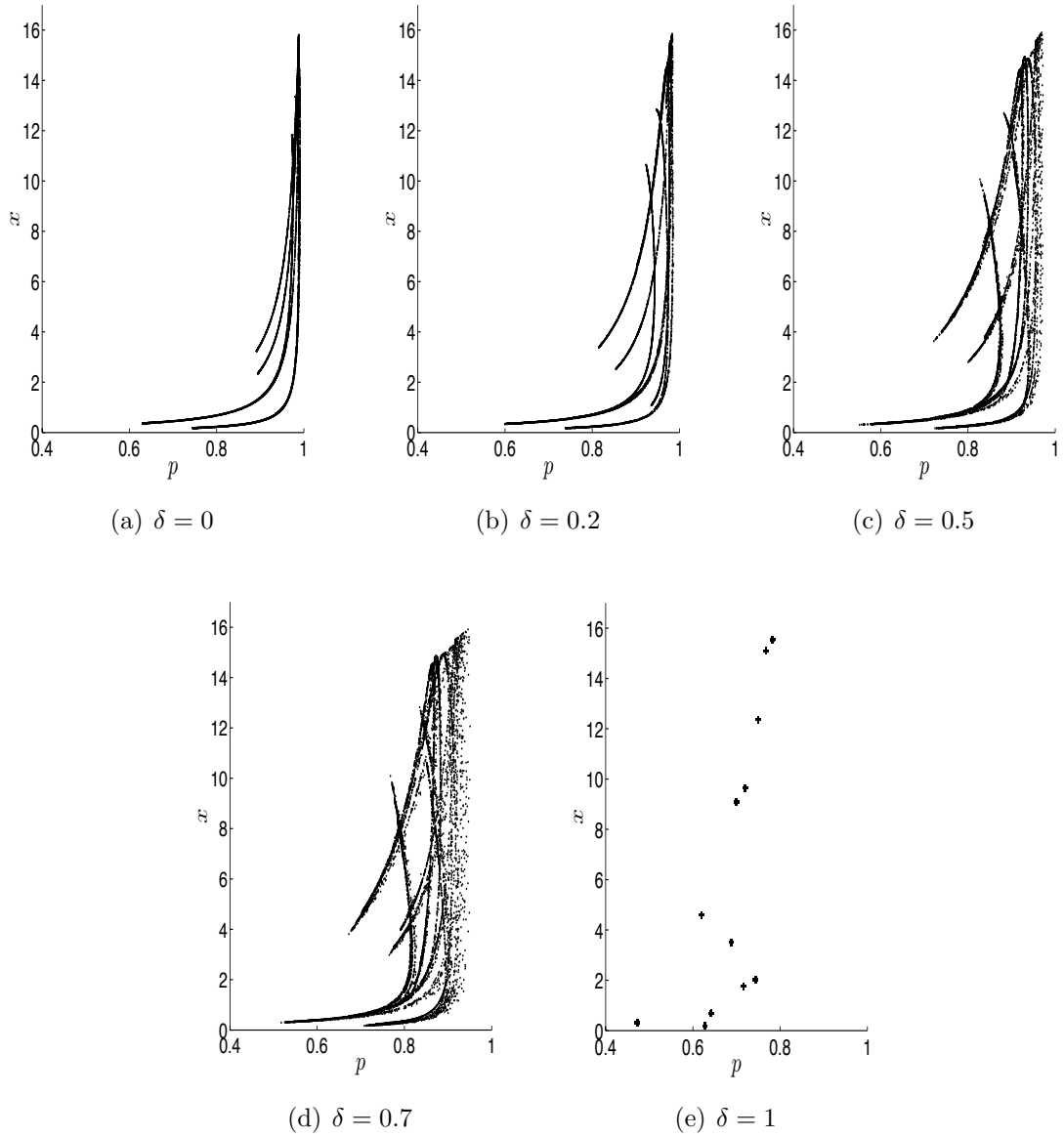
Figure 7.8: Attractor for various δ when $\alpha = 0.5$ in Example 7.6. For $f_{AA}(x) = e^{3.1-0.5x}$, $f_{aa}(x) = e^{1-0.5x}$, $y = 0.1$, $q = 0.1$, $k = 2$, and $g_k(n) = (-1)^n$ the attractor moves left and the region that contains the attractor expands as δ increases. The attractor is chaotic until $\delta = 1$ when it becomes a 12-cycle.

(a) $\delta = 0$ (b) $\delta = 0.2$ (c) $\delta = 0.5$

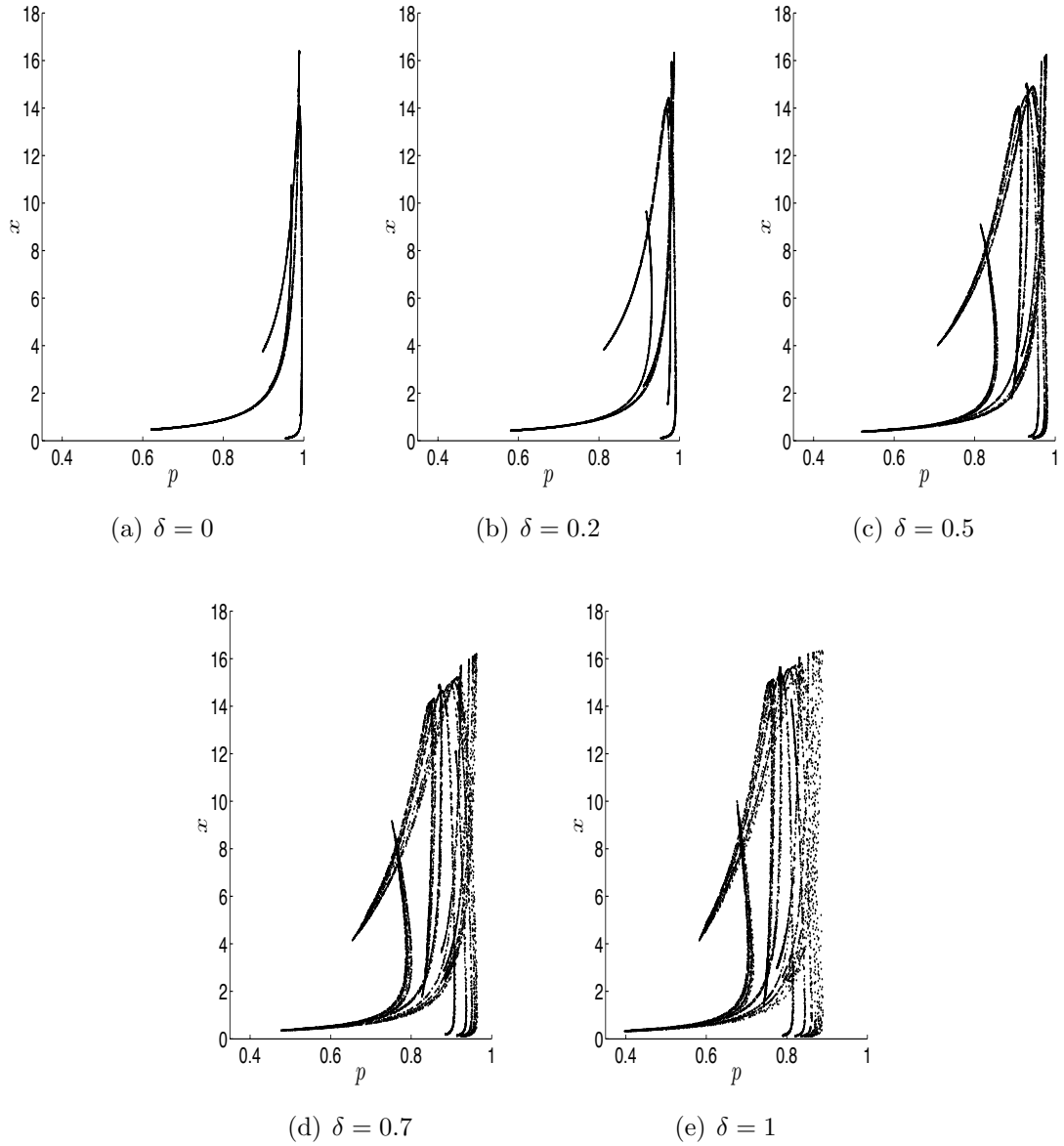(d) $\delta = 0.7$ (e) $\delta = 1$

Figure 7.9: Attractor for various δ when $\alpha = 0.95$ in Example 7.6. For $f_{AA}(x) = e^{3.1-0.5x}$, $f_{aa}(x) = e^{1-0.5x}$, $y = 0.1$, $q = 0.1$, $k = 2$, and $g_k(n) = (-1)^n$ the attractor moves left as δ increases.

Table 7.7: Allelic Diversity for various δ when $\alpha = 0.95$ in Example 7.6. For $f_{AA}(x) = e^{3.1-0.5x}$, $f_{aa}(x) = e^{1-0.5x}$, $y = 0.1$, $q = 0.1$, $k = 2$, $g_k(n) = (-1)^n$ allelic diversity increases as δ increases.

δ	$AD(\Lambda)$	min p value	max p value	min x value	max x value
0	0.138	0.621	0.996	0.103	16.389
0.2	0.169	0.581	0.991	0.107	16.318
0.5	0.250	0.520	0.980	0.110	16.239
0.7	0.349	0.478	0.966	0.112	16.200
1	0.534	0.398	0.889	0.107	16.327

7.4 Summary

We investigated the effect that the magnitude of oscillatory migration has on the attractor. From examples, we noted that when the fitness for the homozygote AA is greater than the fitness for the homozygote aa, the population size has more variation as the amplitude increases. No general conclusion can be made about how allele frequency is affected.

Often the attractor expands in both the x and p directions and the pieces of the attractor separate as the amplitude of the oscillatory migration increases. When k-periodic migration is included in the model, an attractor results that is composed of k subsets, each of which is an attractor for a corresponding autonomous system.

We devised a method to measure allelic diversity for an attractor that is a j-cycle. We found that we could scale the average of the distances the allele frequency of each of the j points deviates from $p = 0.5$. For the case when the fitness of the homozygote AA is superior to that of the homozygote aa, we studied various examples of attractors and observed that allelic diversity increases as the degree of dominance increases. As the degree of dominance improves, the fitness of the heterozygote improves, leading to increased frequency of the Aa genotype. Therefore the value of p moves toward $\frac{1}{2}$ and the value of the defined allelic diversity measure increases.

Chapter 8

Conclusion and Future Directions

8.1 Summary

In this research, we used a two-dimensional time-dependent dynamical system to study the behavior of gene frequencies and population size in island populations that undergo both selection and migration. We expanded the results of Selgrade and Roberds [24, 34, 32, 33] to include the effects that result when the degree of dominance is allowed to widely vary.

Let $E = (\bar{p}, \bar{x})$ denote a polymorphic equilibrium. We found conditions that ensure that a polymorphic equilibrium is unique and stable. When the fitness of the homozygote AA is greater than the fitness of the homozygote aa ($f_{AA}(\bar{x}) > f_{aa}(\bar{x})$), if the frequency q of A in the population of migrants is greater than 0.5 and if the heterozygote fitness is closer to the fitness of the homozygote AA than to the homozygote aa ($0.5 \leq \delta \leq 1$), then there is a unique polymorphic equilibrium which is stable under additional conditions.

These results can be applied to a study of transgenes. If A represents a transgene which imparts greater fitness than its null state and the heterozygote carrying the transgene has fitness closer to the fitness of the transgenic homozygote, and the transgene makes up more than half of the migrating alleles, then a unique equilibrium

exists. This equilibrium will have an allele frequency that is greater than the allele frequency at which the transgene enters the population ($\bar{p} > q$).

Formulas for how E varies as the degree of dominance δ changes (i.e. $d\bar{p}/d\delta$ and $d\bar{x}/d\delta$) were derived. When the AA homozygote is more fit than the aa homozygote ($f_{AA} > f_{aa}$), examples demonstrated that an increase in δ causes the equilibrium population size ($\bar{x}$) to increase. If the frequency of the A allele at equilibrium starts above the frequency of the A allele migrating into the population (i.e. $\bar{p} > q$), then $\bar{p}$ decreases toward the migrant frequency q as the degree of dominance increases. Also, examples showed that if $q < 0.5$, then the equilibrium allele frequency goes to 0.5 as the degree of dominance increases.

We proved how the migration of a less fit allele can lead to the exclusion of the alternate allele in the island population because of a transcritical bifurcation. If the transgene is the less fit allele and is the only allele migrating into the population, then, provided the degree of dominance is high enough, the transgene is the only allele remaining in the population.

Positions for global attractors as well as approximate approach rates to these attractors were established. We proved that a global attractor exists and is in the region where the allele frequency is greater than the allele frequency of the migrants (i.e. $p > q$) when $f_{AA}(x) > f_{aa}(x)$. These results can also be expanded to the behavior of transgenes. If the transgene homozygote has greater fitness than the null allele homozygote, then the transgene will persist in the population at a frequency higher than that at which it enters the population.

The amplitude of oscillatory migration leads to increased variation in population size. Including periodic migration in our model leads to the attractor consisting of similar attractor subsets (corresponding in number to the period), the union of which forms the overall attractor. The notion of allelic diversity was defined. If $f_{AA}(x) > f_{aa}(x)$, an increase in the degree of dominance appears to lead to an increase in the allelic diversity for the population. As the heterozygote fitness becomes more similar to the fitness of the homozygote with the highest fitness, allelic diversity

increases. Therefore we conclude that a reasonably fit heterozygote is important for allelic diversity.

8.2 Future Directions

In future work, there is a need to expand the conditions that ensure a unique polymorphic equilibrium or find counterexamples to uniqueness. For a global attractor, when the fitness for the homozygote AA is greater than the fitness for the homozygote aa, the lower bound for the p-coordinate of the attractor is q. In many, if not all cases, this bound can be improved and will probably depend on the degree of dominance. In Example 6.7, we compute that it will take over 3000 iterations for a solution to reach the attractor, but numerical simulations show that it takes about nine iterates. Thus, improving the rate of approach of a solution to an attractor given by Lemma 6.6 is also an area for further research.

The theory behind the notion of allelic diversity needs to be developed. How changes in the degree of dominance affect the position of a chaotic attractor and its allelic diversity needs to be investigated in general.

Finally, it would be interesting to determine how migration occurring prior to selection affects the model. Removing the dominance relationship would also be of interest.

Bibliography

[1] W. W. ANDERSON, *Genetic equilibrium and population growth under density-regulated selection*, The American Naturalist, 105 (1971), pp. 489–498.

[2] R. F. COSTANTINO, J. M. CUSHING, B. DENNIS, R. A. DESHARNAIS, AND S. M. HENSON, *Resonant population cycles in temporally fluctuating habitats*, Bulletin of Mathematical Biology, 60 (1998), pp. 247–273.

[3] J. M. CUSHING, *Periodic time-dependent predatorprey systems*, SIAM Journal on Applied Mathematics, 32 (1977), pp. 82–95.

[4] D. S. DOERING, *Designing genes: aiming for safety and sustainability in US agriculture and biotechnology*, World Resources Institute, Washington, DC, 2004.

[5] L. EDELSTEIN-KESHET, *Mathematical Models in Biology*, McGraw-Hill, New York, NY, 1988.

[6] N. C. ELLSTRAND, *When transgenes wander, should we worry?*, Plant Physiology, 125 (2001), p. 1543.

[7] ——, *Dangerous Liaisons?: When Cultivated Plants Mate with their Wild Relatives*, Johns Hopkins University Press, Baltimore, MD, 2003.

[8] D. S. FALCONER AND T. F. MACKAY, *Introduction to Quantitative Genetics*, Longman, Essex, England, 4th ed., 1996.

[9] J. E. Franke and J. F. Selgrade, *Attractors for discrete periodic dynamical systems*, Journal of Mathematical Analysis and Applications, 286 (2003), pp. 64–79.

[10] D. J. Futuyma, *Evolution*, Sinauer Associates, Sunderland, MA, 2005.

[11] J. Haldane, *A mathematical theory of natural and artificial selection. part vi. isolation*, Proceedings of the Cambridge Philosophical Society, 26 (1929-1930).

[12] ——, *The theory of a cline*, Journal of Genetics, 48 (1948), pp. 277–284.

[13] D. L. Hartl, *A Primer of Population Genetics*, Sinauer Associates, Sunderland, MA, 2000.

[14] D. L. Hartl and A. G. Clark, *Principles of Population Genetics*, Sinauer Associates, Sunderland, MA, 2007.

[15] P. W. Hedrick, *Genetics of Populations*, Jones and Bartlett Publishers, Boston, MA, 2nd ed., 2000.

[16] S. Henson and J. Cushing, *The effect of periodic habitat fluctuations on a nonlinear insect population model*, Journal of Mathematical Biology, 36 (1997), pp. 201–226.

[17] S. Herrera, *Struggling to see the forest through the trees*, Nature Biotechnology, 23 (2005), pp. 165–167.

[18] D. A. Jillson, *Insect populations respond to fluctuating environments*, Nature, 288 (1980), pp. 699–700.

[19] R. C. King and W. D. Stansfield, *A Dictionary of Genetics*, Oxford University Press, New York, NY, 6th ed., 2002.

[20] J. Li, *Simple mathematical models for interacting wild and transgenic mosquito populations*, Mathematical Biosciences, 189 (2004), pp. 39–59.

[21] ——, *Heterogeneity in modelling of mosquito populations with transgenic mosquitos*, Journal of Difference Equations and Applications, 11 (2005), pp. 443–457.

[22] T. NAGYLAKI, *Introduction to Theoretical Population Genetics*, Springer-Verlag, New York, NY, 1992.

[23] H. A. ORR, *Fitness and its role in evolutionary genetics*, Nature Reviews Genetics, 10 (2009), pp. 531–539.

[24] J. H. ROBERDS AND J. F. SELGRADE, *Dynamical analysis of density-dependent selection in a discrete one-island migration model*, Mathematical Biosciences, 164 (2000), pp. 1–15.

[25] C. ROBINSON, *Dynamical Systems: Stability, Symbolic Dynamics, and Chaos*, CRC Press, Boca Raton, FL, 1995.

[26] J. ROUGHGARDEN, *Density-dependent natural selection*, Ecology, 52 (1971), pp. 453–468.

[27] ——, *Theory of Population Genetics and Evolutionary Ecology: An Introduction*, Macmillan, New York, NY, 1979.

[28] R. A. SEDJO, *Global agreements and US forestry: genetically modified trees*, Journal of Forestry, 103 (2005), pp. 109–113.

[29] J. F. SELGRADE, J. W. BOSTIC, AND J. H. ROBERDS, *Dynamical behaviour of a discrete selection-migration model with arbitrary dominance*, Journal of Difference Equations and Applications, 15 (2009), pp. 371–385.

[30] J. F. SELGRADE AND G. NAMKOONG, *Dynamical behavior for population genetics models of differential and difference equations with nonmonotone fitnesses*, Journal of Mathematical Biology, 30 (1992), pp. 815–826.

[31] J. F. SELGRADE AND J. H. ROBERDS, *Lumped-density population models of pioneer-climax type and stability analysis of hopf bifurcations*, Mathematical Biosciences, 137 (1996), pp. 1–21.

[32] ——, *Equilibrium and nonequilibrium attractors for a discrete, selection-migration model*, Canadian Applied Mathematics Quarterly, 11 (2003), pp. 195–211.

[33] ——, *Global attractors for a discrete selection model with periodic immigration*, Journal of Difference Equations and Applications, 13 (2007), pp. 275–287.

[34] ——, *Uniqueness of polymorphism for a discrete, selection-migration model with genetic dominance*, Advanced Studies in Pure Mathematics, 53 (2009), pp. 319–331.

[35] R. F. SERVICE, *A growing threat down on the farm*, Science, 316 (2007), pp. 1114–1117.

[36] A. A. SNOW, *Transgenic crops - why gene flow matters*, Nature Biotechnology, 20 (2002), p. 542.

[37] A. E. TAYLOR AND W. R. MANN, *Advanced Calculus*, John Wiley and Sons, Inc., New York, NY, 3rd ed., 1983.

[38] C. G. WILLIAMS, *Framing the issues on transgenic forests*, Nature Biotechnology, 23 (2005), pp. 530–532.

[39] ——, *Landscapes, Genomics and Transgenic Conifers*, Springer, Dordrecht, 2006.

[40] S. WRIGHT, *Evolution in mendelian populations*, Genetics, 16 (1931), pp. 97–159.

Appendices

Appendix A

Chapter 4 Computations

In this appendix, we give details for the computations made in Chapter 4.

A.1   Uniqueness for $f_{AA}(\bar{x}) > f_{aa}(\bar{x})$ at each equilibrium

In order to prove uniqueness of the equilibrium for the case where $f_{AA}(\bar{x}) > f_{aa}(\bar{x})$ at each equilibrium, we want to show that where the isoclines $\mathcal{C}$ and $\mathcal{C}_A$ cross,

$$\frac{d\tilde{x}_A}{dp} < \frac{d\tilde{x}}{dp}.$$

For $0 < p < 1$, this is equivalent to showing

$$\frac{p\left(1 - f_A - p\frac{\partial f_A}{\partial p}\right)}{p\frac{\partial f_A}{\partial x} + qh'} = p\frac{d\tilde{x}_A}{dp} < p\frac{d\tilde{x}}{dp} < \frac{d\tilde{x}}{dp} = \frac{-2p(f_A - f_a)}{\frac{\partial f}{\partial x} + h'}.$$

We cross multiply the first and last terms to obtain

$$\left[p\left(1 - f_A - p\frac{\partial f_A}{\partial p}\right)\right]\left[\frac{\partial f}{\partial x} + h'\right] < [-2p(f_A - f_a)]\left[p\frac{\partial f_A}{\partial x} + qh'\right].$$

Then moving all terms to one side we obtain the inequality

$$\left[p\left(1 - f_A - p\frac{\partial f_A}{\partial p}\right)\right]\left[\frac{\partial f}{\partial x} + h'\right] - [-2p(f_A - f_a)]\left[p\frac{\partial f_A}{\partial x} + qh'\right] < 0.$$

We want to show that this inequality holds at each equilibrium $E = (\bar{p}, \bar{x})$. Using (4.10) to substitute $qh(\bar{x})$ for $\bar{p}(1 - f_A(\bar{p}, \bar{x}))$, the inequality we want to show is

$$\left[qh(\bar{x}) - \bar{p}^2\frac{\partial f_A}{\partial p}\right]\left[\frac{\partial f}{\partial x} + h'\right] + [2p(f_A - f_a)]\left[\bar{p}\frac{\partial f_A}{\partial x} + qh'\right] < 0.$$

Using (3.6) and (3.7), we substitute for the allelic and mean fitnesses and their derivatives and rearrange terms by genotype fitness derivatives to obtain

$$
\begin{aligned}
&[qh(\bar{x}) - \bar{p}^2(1 - \delta)(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))] \\
&\quad * [(\bar{p}^2 + 2\delta\bar{p} - 2\delta\bar{p}^2)f'_{AA}(\bar{x}) + (1 - \bar{p}^2 - 2\delta\bar{p} + 2\delta\bar{p}^2)f'_{aa}(\bar{x}) + h'(\bar{x})] \\
&\quad + 2\bar{p}[(\bar{p} + \delta - 2\delta\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))] \\
&\quad * [\bar{p}(\bar{p} + \delta - \delta\bar{p})f'_{AA}(\bar{x}) + \bar{p}(1 - \bar{p} - \delta + \delta\bar{p})f'_{aa}(\bar{x}) + qh'(\bar{x})] \\
&= f'_{AA}(\bar{x})\{(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))\bar{p}^2[(\delta - 1)(\bar{p}^2 + 2\delta\bar{p} - 2\delta\bar{p}^2) + 2(\bar{p} + \delta - 2\delta\bar{p})(\bar{p} + \delta - \delta\bar{p})] \\
&\qquad + q\bar{p}h(\bar{x})(\bar{p} + 2\delta - 2\delta\bar{p})\} \\
&\quad + f'_{aa}(\bar{x})\{(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))[(1 - \bar{p}^2 - 2\delta\bar{p} + 2\delta\bar{p}^2)(-\bar{p}^2(1 - \delta)) \\
&\qquad + 2(\bar{p} + \delta - 2\delta\bar{p})\bar{p}^2(1 - \bar{p})(1 - \delta)] + (1 - \bar{p}^2 - 2\delta\bar{p} + 2\delta\bar{p}^2)qh(\bar{x})\} \\
&\quad + h'(\bar{x})\{qh(\bar{x}) + (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))(-\bar{p}^2(1 - \delta) + 2\bar{p}q(\bar{p} + \delta - 2\delta\bar{p}))\} < 0.
\end{aligned}
$$
$$(A.1)$$

We assume (4.5), so we want to show that each of the terms in curly brackets in (A.1) is positive.

First, the terms multiplied by $f'_{AA}(\bar{x})$ can be rewritten as

$$(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))\bar{p}^2[(\delta - 1)(\bar{p}^2 + 2\delta\bar{p} - 2\delta\bar{p}^2) + 2(\bar{p} + \delta - 2\delta\bar{p})(\bar{p} + \delta - \delta\bar{p})]$$
$$+ q\bar{p}h(\bar{x})(\bar{p} + 2\delta - 2\delta\bar{p})$$
$$= (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))\bar{p}^2[\delta\bar{p}^2 + 2\delta^2\bar{p} - 2\delta^2\bar{p}^2 - \bar{p}^2 - 2\delta\bar{p} + 2\delta\bar{p}^2$$
$$+ 2\bar{p}^2 + 4\delta\bar{p} - 6\delta^2\bar{p} - 6\delta\bar{p}^2 + 2\delta^2 + 4\delta^2\bar{p}^2]$$
$$+ q\bar{p}h(\bar{x})(\bar{p} + 2\delta - 2\delta\bar{p})$$
$$= (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))\bar{p}^2[\bar{p}^2 - 3\delta\bar{p}^2 + 2\delta\bar{p} + 2\delta^2 - 4\delta^2\bar{p} + 2\delta^2\bar{p}^2]$$
$$+ q\bar{p}h(\bar{x})(\bar{p} + 2\delta - 2\delta\bar{p}) \tag{A.2}$$
$$= (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))\bar{p}^2[\bar{p}^2 - \delta\bar{p}^2 + 2\delta\bar{p} - 2\delta\bar{p}^2 + 2\delta^2 - 2\delta^2\bar{p} - 2\delta^2\bar{p} + 2\delta^2\bar{p}^2]$$
$$+ q\bar{p}h(\bar{x})(\bar{p} + 2\delta - 2\delta\bar{p})$$
$$= (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))\bar{p}^2[\bar{p}^2(1 - \delta) + 2\delta\bar{p}(1 - \bar{p}) + 2\delta^2(1 - \bar{p}) + 2\delta^2\bar{p}(\bar{p} - 1)]$$
$$+ q\bar{p}h(\bar{x})(\bar{p} + 2\delta - 2\delta\bar{p})$$
$$= (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))\bar{p}^2[\bar{p}^2(1 - \delta) + 2\delta\bar{p}(1 - \bar{p})(1 - \delta) + 2\delta^2(1 - \bar{p})]$$
$$+ q\bar{p}h(\bar{x})(\bar{p} + 2\delta(1 - \bar{p}))$$

Since we are assuming $f_{AA}(\bar{x}) > f_{aa}(\bar{x})$ at each equilibrium, $0 < \bar{p} < 1$, $0 \le \delta \le 1$, and $0 \le q \le 1$ clearly (A.2) is positive. These appear in the first two lines in (A.5) and (4.11).

Similarly, for the terms multiplied by $f'_{aa}(\bar{x})$, we simplify and obtain

$$(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))\bar{p}^2(1-\delta)[(-1 + \bar{p}^2 + 2\delta\bar{p} - 2\delta\bar{p}^2)$$
$$+ 2(\bar{p} + \delta - 2\delta\bar{p})(1-\bar{p})]$$
$$+ (1 - \bar{p}^2 - 2\delta\bar{p} + 2\delta\bar{p}^2)qh(\bar{x})$$
$$= (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))\bar{p}^2(1-\delta)[-1 + \bar{p}^2 + 2\delta\bar{p} - 2\delta\bar{p}^2$$
$$+ 2(\bar{p} + \delta - 2\delta\bar{p} - \bar{p}^2 - \delta\bar{p} + 2\delta\bar{p}^2)]$$
$$+ (1 - \bar{p}^2 - 2\delta\bar{p} + 2\delta\bar{p}^2)qh(\bar{x})$$
$$= (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))\bar{p}^2(1-\delta)[-1 + \bar{p}^2 + 2\delta\bar{p} - 2\delta\bar{p}^2 + 2\bar{p} + 2\delta - 6\delta\bar{p} - 2\bar{p}^2 + 4\delta\bar{p}^2]$$
$$+ (1 - \bar{p}^2 - 2\delta\bar{p} + 2\delta\bar{p}^2)qh(\bar{x})$$
$$= (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))\bar{p}^2(1-\delta)[-1 + 2\bar{p} - \bar{p}^2 + 2\delta - 4\delta\bar{p} + 2\delta\bar{p}^2]$$
$$+ (1 - \bar{p})(1 + \bar{p} - 2\delta\bar{p})qh(\bar{x})$$
$$= (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))\bar{p}^2(1-\delta)[-(1-\bar{p})^2 + 2\delta(1-\bar{p})^2]$$
$$+ (1 - \bar{p})(1 - \delta\bar{p} + \bar{p}1 - \delta\bar{p})qh(\bar{x})$$
$$= (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))\bar{p}^2(1-\delta)(1-\bar{p})^2(2\delta - 1) + (1 - \bar{p})(1 - \delta\bar{p} + \bar{p}(1-\delta))qh(\bar{x}).$$
$$\text{(A.3)}$$

With the assumptions of $f_{AA}(\bar{x}) > f_{aa}(\bar{x})$ at each equilibrium, $0 < \bar{p} < 1$, $0 \le q \le 1$, then (A.3) is positive if $\dfrac{1}{2} \le \delta \le 1$. These terms appear in the second and third lines of (A.5) and (4.11).

Looking at all the terms multiplied by $h'(\bar{x})$, we simplify and get

$$(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))\bar{p}[-\bar{p}(1-\delta) + 2q(\bar{p} + \delta - 2\delta\bar{p})] + qh(\bar{x})$$
$$= f_{AA}(\bar{x}) - f_{aa}(\bar{x}))\bar{p}[-\bar{p} + \delta\bar{p} + 2\bar{p}q + 2\delta q - 4\delta\bar{p}q] + qh(\bar{x})$$
$$= (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))\bar{p}[2\bar{p}q - \bar{p} + \delta\bar{p} - 2\delta\bar{p}q + 2\delta q - 2\delta\bar{p}q] + qh(\bar{x}) \qquad \text{(A.4)}$$
$$= (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))\bar{p}[\bar{p}(2q-1) + \delta\bar{p}(1-2q) + 2\delta q(1-\bar{p})] + qh(\bar{x})$$
$$= (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))\bar{p}[\bar{p}(1-\delta)(2q-1) + 2\delta q(1-\bar{p})] + qh(\bar{x}).$$

For $f_{AA}(\bar{x}) > f_{aa}(\bar{x})$ at each equilibrium, (A.4) is positive if we assume $0 < \bar{p} < 1$, $0 \leq \delta \leq 1$, and $\frac{1}{2} \leq q \leq 1$. These terms appear as the final line in (A.5) and (4.11).

Therefore, the inequality we want to hold is

$$
\begin{aligned}
& f'_{AA}(\bar{x})\{(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))\bar{p}^2[\bar{p}^2(1 - \delta) + 2\delta\bar{p}(1 - \bar{p})(1 - \delta) + 2\delta^2(1 - \bar{p})]\} \\
& + f'_{AA}(\bar{x})\{q\bar{p}h(\bar{x})(\bar{p} + 2\delta(1 - \bar{p}))\} + f'_{aa}(\bar{x})\{qh(\bar{x})(1 - \bar{p})(1 - \delta\bar{p} + \bar{p}(1 - \delta))\} \\
& + f'_{aa}(\bar{x})\{(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))\bar{p}^2(1 - \delta)(1 - \bar{p})^2(2\delta - 1)\} \\
& + h'(\bar{x})\{qh(\bar{x}) + (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))\bar{p}[\bar{p}(1 - \delta)(2q - 1) + 2\delta q(1 - \bar{p})]\} < 0.
\end{aligned}
\tag{A.5}
$$

We have if $f_{AA}(\bar{x}) > f_{aa}(\bar{x})$ that (A.5) holds if $\frac{1}{2} \leq \delta \leq 1$ and $\frac{1}{2} \leq q \leq 1$ and that the polymorphic equilibrium is unique.

A.2 Uniqueness for $f_{AA}(\bar{x}) < f_{aa}(\bar{x})$ at each equilibrium

In order to prove uniqueness of the equilibrium for the case where $f_{AA}(\bar{x}) < f_{aa}(\bar{x})$ at each equilibrium, we want to show that where the isoclines $\mathcal{C}$ and $\mathcal{C}_a$ cross,

$$
\frac{d\tilde{x}}{dp} < \frac{d\tilde{x}_a}{dp}.
\tag{A.6}
$$

Equivalently, we look at

$$
(1 - p)\frac{d\tilde{x}}{dp} < (1 - p)\frac{d\tilde{x}_a}{dp}.
\tag{A.7}
$$

For $0 < p < 1$, substituting (3.7), (A.7) is the same as showing

$$
\frac{-2(1 - p)(f_A - f_a)}{\frac{\partial f}{\partial x} + h'} = (1 - p)\frac{d\tilde{x}}{dp} < (1 - p)\frac{d\tilde{x}_a}{dp} = \frac{(1 - p)\left(f_a - 1 - (1 - p)\frac{\partial f_a}{\partial p}\right)}{(1 - p)\frac{\partial f_a}{\partial x} + (1 - q)h'}.
\tag{A.8}
$$

Cross multiplying the first and last terms in (A.8) we obtain the inequality

$$[-2(1-p)(f_A - f_a)] \left[(1-p)\frac{\partial f_a}{\partial x} + (1-q)h' \right]$$
$$< \left[(1-p)\left(f_a - 1 - (1-p)\frac{\partial f_a}{\partial p} \right) \right] \left[\frac{\partial f}{\partial x} + h' \right].$$

Then moving all terms to one side, we obtain the inequality

$$[-2(1-p)(f_A - f_a)] \left[(1-p)\frac{\partial f_a}{\partial x} + (1-q)h' \right]$$
$$- \left[(1-p)\left(f_a - 1 - (1-p)\frac{\partial f_a}{\partial p} \right) \right] \left[\frac{\partial f}{\partial x} + h' \right] < 0.$$

We want to show that this inequality holds at each equilibrium $E = (\bar{p}, \bar{x})$. Using (4.3) to substitute $(q-1)h(\bar{x})$ for $(1-\bar{p})(f_a(\bar{p}, \bar{x}) - 1)$, the inequality we want to show is

$$[2(1-\bar{p})(f_A(\bar{p}, \bar{x}) - f_a(\bar{p}, \bar{x}))] \left[(1-\bar{p})\frac{\partial f_a}{\partial x} + (1-q)h'(\bar{x}) \right]$$
$$- \left[\left((q-1)h(\bar{x}) - (1-\bar{p})^2 \frac{\partial f_a}{\partial p} \right) \right] \left[\frac{\partial f}{\partial x} + h'(\bar{x}) \right] < 0.$$

Using (3.6) and (3.7), we substitute for the allelic and mean fitnesses and their derivatives and rearrange terms by genotype fitness derivatives to obtain

$$
\begin{aligned}
& [-2(1-\bar{p})(\bar{p}+\delta-2\delta\bar{p})(f_{AA}(\bar{x})-f_{aa}(\bar{x}))] \\
& \qquad * [(1-\bar{p})\delta\bar{p}f'_{AA}(\bar{x})+(1-\bar{p})(1-\delta\bar{p})f'_{aa}(\bar{x})+(1-q)h'(\bar{x})] \\
& \quad + [\bar{p}(\bar{p}+2\delta-2\delta\bar{p})f'_{AA}(\bar{x})+(1-\bar{p}^2-2\delta\bar{p}+2\delta\bar{p}^2)f'_{aa}(\bar{x})+h'(\bar{x})] \\
& \qquad * [(1-q)h(\bar{x})+(1-\bar{p})^2\delta(f_{AA}(\bar{x})-f_{aa}(\bar{x}))] \\
& = f'_{AA}(\bar{x})\{-2(\bar{p}+\delta-2\delta\bar{p})\delta\bar{p}(1-\bar{p})^2+(1-\bar{p})^2\delta\bar{p}(\bar{p}+2\delta-2\delta\bar{p})](f_{AA}(\bar{x})-f_{aa}(\bar{x})) \\
& \qquad\qquad + \bar{p}(1-q)(\bar{p}+2\delta-2\delta\bar{p})h(\bar{x})\} \\
& \quad + f'_{aa}(\bar{x})\{[-2(1-\bar{p})^2(1-\delta\bar{p})(\bar{p}+\delta-2\delta\bar{p}) \\
& \qquad\qquad + \delta(1-\bar{p})^2(1-\bar{p}^2-2\delta\bar{p}+2\delta\bar{p}^2)](f_{AA}(\bar{x})-f_{aa}(\bar{x})) \\
& \qquad + (1-\bar{p}^2-2\delta\bar{p}+2\delta\bar{p}^2)(1-q)h(\bar{x})\} \\
& \quad + h'(\bar{x})\{[-2(\bar{p}+\delta-2\delta\bar{p})(1-q)(1-\bar{p})+(1-\bar{p})^2\delta](f_{AA}(\bar{x})-f_{aa}(\bar{x})) \\
& \qquad + (1-q)h(\bar{x})\}.
\end{aligned}
$$

(A.9)

We assume (4.5), so we want to show that each of the terms in curly brackets in (A.9) are positive.

The terms multiplied by $f'_{AA}(\bar{x})$ can be rewritten as

$$
\begin{aligned}
& (f_{AA}(\bar{x})-f_{aa}(\bar{x}))[-2(\bar{p}+\delta-2\delta\bar{p})\delta\bar{p}(1-\bar{p})^2+(1-\bar{p})^2\delta\bar{p}(\bar{p}+2\delta-2\delta\bar{p})] \\
& \quad + \bar{p}(1-q)(\bar{p}+2\delta-2\delta\bar{p})h(\bar{x}) \\
& = (f_{AA}(\bar{x})-f_{aa}(\bar{x}))\delta\bar{p}(1-\bar{p})^2[-2\bar{p}-2\delta+4\delta\bar{p}+\bar{p}+2\delta-2\delta\bar{p}] \\
& \quad + \bar{p}(1-q)(\bar{p}+2\delta-2\delta\bar{p})h(\bar{x}) \\
& = (f_{AA}(\bar{x})-f_{aa}(\bar{x}))\delta\bar{p}(1-\bar{p})^2[-\bar{p}+2\delta\bar{p}]+\bar{p}(1-q)(\bar{p}+2\delta-2\delta\bar{p})h(\bar{x}) \\
& = (f_{AA}(\bar{x})-f_{aa}(\bar{x}))\delta\bar{p}^2(1-\bar{p})^2(2\delta-1)+\bar{p}(1-q)(\bar{p}+2\delta(1-\bar{p}))h(\bar{x})
\end{aligned}
$$

(A.10)

Since we are assuming $f_{AA}(\bar{x}) < f_{aa}(\bar{x})$ at each equilibrium, $0 < \bar{p} < 1$, $0 \leq q \leq 1$, if $0 \leq \delta \leq \dfrac{1}{2}$ then (A.10) is positive. These terms appear in the first two lines of (A.13)

and (4.15).

The $f'_{aa}(\bar{x})$ terms can be rewritten as

$$(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))[-2(1-\bar{p})^2(\bar{p} + \delta - 2\delta\bar{p})(1 - \delta\bar{p}) + (1 - \bar{p})^2\delta(1 - \bar{p}^2 - 2\delta\bar{p} + 2\delta\bar{p}^2)]$$
$$+ (1 - \bar{p}^2 - 2\delta\bar{p} + 2\delta\bar{p}^2)(1 - q)h(\bar{x})$$
$$= (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))(1 - \bar{p})^2[-2(\bar{p} + \delta - 2\delta\bar{p} - \delta\bar{p}^2 - \delta^2 + 2\delta^2\bar{p}^2)$$
$$+ \delta - \delta\bar{p}^2 - 2\delta^2\bar{p} + 2\delta^2\bar{p}^2]$$
$$+ (1 - \bar{p}^2 - 2\delta\bar{p} + 2\delta\bar{p}^2)(1 - q)h(\bar{x})$$
$$= (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))(1 - \bar{p})^2[-2\bar{p} - 2\delta + 4\delta\bar{p} + 2\delta\bar{p}^2 + 2\delta^2 - 4\delta^2\bar{p}^2$$
$$+ \delta - \delta\bar{p}^2 - 2\delta^2\bar{p} + 2\delta^2\bar{p}^2]$$
$$+ (1 - \bar{p}^2 - 2\delta\bar{p} + 2\delta\bar{p}^2)(1 - q)h(\bar{x})$$
$$= (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))(1 - \bar{p})^2[-2\bar{p} - \delta + 4\delta\bar{p} + \delta\bar{p}^2 - 2\delta^2\bar{p}^2]$$
$$+ ((1 - \bar{p})(1 + \bar{p}) - 2\delta\bar{p}(1 - \bar{p}))(1 - q)h(\bar{x})$$
$$= (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))(1 - \bar{p})^2[-\delta + 2\delta\bar{p} - \delta\bar{p}^2 - 2\bar{p} + 2\delta\bar{p} + 2\delta\bar{p}^2 - 2\delta^2\bar{p}^2]$$
$$+ (1 - \bar{p})(1 + \bar{p} - 2\delta\bar{p})(1 - q)h(\bar{x})$$
$$= (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))(1 - \bar{p})^2[-\delta(1 - \bar{p})^2 - 2\bar{p}(1 - \delta) + 2\delta\bar{p}^2(1 - \delta)]$$
$$+ (1 - \bar{p})(1 - \delta\bar{p} + \bar{p} - \delta\bar{p})(1 - q)h(\bar{x})$$
$$= (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))(1 - \bar{p})^2[-\delta(1 - \bar{p})^2 - 2\bar{p}(1 - \delta)(1 - \delta\bar{p})]$$
$$+ (1 - \bar{p})(1 - \delta\bar{p} + \bar{p}(1 - \delta))(1 - q)h(\bar{x}).$$

$$(A.11)$$

With the assumptions of $f_{AA}(\bar{x}) < f_{aa}(\bar{x})$ at each equilibrium, $0 < \bar{p} < 1$, $0 \leq \delta \leq 1$, and $0 \leq q \leq 1$ then (A.11) is positive. These terms appear on lines three and four of (A.13) and (4.15).

The terms multiplied by $h'(\bar{x})$ can be rewritten as

$$(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))[-2(\bar{p} + \delta - 2\delta\bar{p})(1 - \bar{p})(1 - q) + (1 - \bar{p})^2\delta] + (1 - q)h(\bar{x})$$

$$= (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))(1 - \bar{p})[-2(\bar{p} + \delta - 2\delta\bar{p} - \bar{p}q - \delta q + 2\delta\bar{p}q) + \delta - \delta\bar{p}]$$

$$\quad + (1 - q)h(\bar{x})$$

$$= (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))(1 - \bar{p})[-2\bar{p} - 2\delta + 4\delta\bar{p} + 2\bar{p}q + 2\delta q - 4\delta\bar{p}q + \delta - \delta\bar{p}]$$

$$\quad + (1 - q)h(\bar{x})$$

$$= (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))(1 - \bar{p})[-2\bar{p} + 3\delta\bar{p} - \delta + 2\bar{p}q + 2\delta q - 4\delta\bar{p}q]$$

$$\quad + (1 - q)h(\bar{x})$$

$$= (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))(1 - \bar{p})[2\bar{p}(\delta - 1) + \delta(\bar{p} - 1) + 2\bar{p}q(1 - \delta) + 2\delta q(1 - \bar{p})]$$

$$\quad + (1 - q)h(\bar{x})$$

$$= (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))(1 - \bar{p})[2\bar{p}(\delta - 1)(1 - q) + \delta(\bar{p} - 1)(1 - 2q)] + (1 - q)h(\bar{x}).$$
$$\tag{A.12}$$

Since we assume $f_{AA}(\bar{x}) < f_{aa}(\bar{x})$ at each equilibrium, $0 < \bar{p} < 1$ and $0 \le \delta \le 1$ (A.12) is positive if $0 \le q \le \dfrac{1}{2}$. These terms appear as the fifth line in (A.13) and (4.15).

Thus, the inequality we want to hold is

$$f'_{AA}(\bar{x})\{((f_{AA}(\bar{x}) - f_{aa}(\bar{x}))\delta\bar{p}^2(1 - \bar{p})^2(2\delta - 1)\}$$
$$+ f'_{AA}(\bar{x})\{\bar{p}(1 - q)(\bar{p} + 2\delta(1 - \bar{p}))h(\bar{x})\}$$
$$+ f'_{aa}(\bar{x})\{(1 - \bar{p})(1 - \delta\bar{p} + \bar{p}(1 - \delta))(1 - q)h(\bar{x})\}$$
$$+ f'_{aa}(\bar{x})\{((f_{AA}(\bar{x}) - f_{aa}(\bar{x}))(1 - \bar{p})^2[-\delta(1 - \bar{p})^2 - 2\bar{p}(1 - \delta)(1 - \delta\bar{p})]\}$$
$$+ h'(\bar{x})[(1 - q)h(\bar{x}) + (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))(1 - \bar{p})[2\bar{p}(\delta - 1)(1 - q) + \delta(\bar{p} - 1)(1 - 2q)]]$$
$$< 0.$$
$$\tag{A.13}$$

For $f_{AA}(\bar{x}) < f_{aa}(\bar{x})$ at each equilibrium, we have that (A.13) holds if $0 \le \delta \le \dfrac{1}{2}$ and $0 \le q \le \dfrac{1}{2}$ and the polymorphic equilibrium is unique.

A.3 Jury Conditions

In order to determine the local stability of the polymorphic equilibrium, we need to examine the Jury conditions. We examine these conditions in parts.

A.3.1 Determinant of Jacobian

To determine the local stability of the polymorphic equilibrium, we need to look at the Jacobian matrix, $D(E)$, of the right hand side of (3.4). The Jacobian is

$$D(E) = \begin{bmatrix} f_A + \bar{p}\left(\frac{\partial f_A}{\partial p} - \frac{\partial f}{\partial p}\right) & \bar{p}(1-\bar{p})\left(\frac{\partial f_A}{\partial x} - \frac{\partial f_a}{\partial x}\right) + h'(\bar{x})(q - \bar{p}) \\ \bar{x}\frac{\partial f}{\partial p} & 1 + \bar{x}\left(\frac{\partial f}{\partial x} + h'(\bar{x})\right) \end{bmatrix}.$$

Using $\dfrac{\partial f_A}{\partial p} - \dfrac{\partial f}{\partial p} = (1 - 3\delta - 2\bar{p} + 4\delta\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))$ and

$\dfrac{\partial f_A}{\partial x} - \dfrac{\partial f_a}{\partial x} = (\bar{p} + \delta - 2\delta\bar{p})(f'_{AA}(\bar{x}) - f'_{aa}(\bar{x}))$.

Using (3.6) and (3.7), for any δ, we compute that the determinant of $D(E)$ in terms of genotype fitness derivatives is

$$\begin{aligned} \det[D(E)] &= \left[f_A + \bar{p}\left(\frac{\partial f_A}{\partial p} - \frac{\partial f}{\partial p}\right)\right]\left[1 + \bar{x}\left(\frac{\partial f}{\partial x} + h'(\bar{x})\right)\right] \\ &\quad - \bar{x}\frac{\partial f}{\partial p}\left[\bar{p}(1-\bar{p})\left(\frac{\partial f_A}{\partial x} - \frac{\partial f_a}{\partial x}\right) + h'(\bar{x})(q - \bar{p})\right] \\ &= f_A + \bar{p}\left(\frac{\partial f_A}{\partial p} - \frac{\partial f}{\partial p}\right) + x\frac{\partial f}{\partial x}\left(f_A + \bar{p}\left(\frac{\partial f_A}{\partial p} - \frac{\partial f}{\partial p}\right)\right) \\ &\quad - xp(1-p)\frac{\partial f}{\partial p}\left(\frac{\partial f_A}{\partial x} - \frac{\partial f_a}{\partial x}\right) \\ &\quad + xh'(x)\left(f_A + \bar{p}\left(\frac{\partial f_A}{\partial p} - \frac{\partial f}{\partial p}\right)\right) + xh'(x)\frac{\partial f}{\partial p}(p - q) \end{aligned}$$

$$
\begin{aligned}
=& f_{aa}(\bar{x}) + (\bar{p} + \delta - \delta\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) \\
& + \bar{p}(1 - 2\bar{p} - 3\delta + 4\delta\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) \\
& + \bar{x}[f'_{aa}(\bar{x}) + \bar{p}(\bar{p} + 2\delta - 2\delta\bar{p})(f'_{AA}(\bar{x}) - f'_{aa}(\bar{x}))] \\
& \quad * [f_{aa}(\bar{x}) + (2\bar{p} - 2\bar{p}^2 + \delta - 4\delta\bar{p} + 4\delta\bar{p}^2)(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))] \\
& - \bar{x}(f'_{AA}(\bar{x}) - f'_{aa}(\bar{x}))\bar{p}(1 - \bar{p})2(\bar{p} + \delta - 2\delta\bar{p})^2(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) \\
& + \bar{x}h'(\bar{x})[f_{aa}(\bar{x}) + (2\bar{p} - 2\bar{p}^2 + \delta - 4\delta\bar{p} + 4\delta\bar{p}^2)(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) \\
& \qquad + 2(\bar{p} + \delta - 2\delta\bar{p})(\bar{p} - q)(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))] \\
=& f_{aa}(\bar{x}) + (2\bar{p} - 2\bar{p}^2 + \delta - 4\delta\bar{p} + 4\delta\bar{p}^2)(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) \\
& + \bar{x}(f'_{AA}(\bar{x}) - f'_{aa}(\bar{x}))(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))[-2\bar{p}(1 - \bar{p})(\bar{p} + \delta - 2\delta\bar{p})^2 \\
& \qquad\qquad\qquad\qquad + \bar{p}(\bar{p} + 2\delta - 2\delta\bar{p})(2\bar{p} - 2\bar{p}^2 + \delta - 4\delta\bar{p} + 4\delta\bar{p}^2)] \\
& + \bar{x}(f'_{AA}(\bar{x}) - f'_{aa}(\bar{x}))f_{aa}(\bar{x})\bar{p}(\bar{p} + 2\delta - 2\delta\bar{p}) \\
& + \bar{x}f'_{aa}(\bar{x})[f_{aa}(\bar{x}) + (2\bar{p} - 2\bar{p}^2 + \delta - 4\delta\bar{p} + 4\delta\bar{p}^2)(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))] \\
& + \bar{x}h'(\bar{x})[f_{aa}(\bar{x}) + (2\bar{p} - 2\bar{p}^2 + \delta - 4\delta\bar{p} + 4\delta\bar{p}^2 \\
& \qquad\qquad + 2\bar{p}^2 + 2\delta\bar{p} - 4\delta\bar{p}^2 + 4\delta\bar{p}q - 2\bar{p}q - 2\delta q)(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))] \\
=& f_{aa}(\bar{x}) + \delta(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) + (2\bar{p} - 2\bar{p}^2 - 4\delta\bar{p} + 4\delta\bar{p}^2)(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) \\
& + \bar{x}(f'_{AA}(\bar{x}) - f'_{aa}(\bar{x}))(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))[\bar{p}(\bar{p} + \delta - 2\delta\bar{p})(2\bar{p} - 2\bar{p}^2 + \delta - 4\delta\bar{p} + 4\delta\bar{p}^2 \\
& \qquad\qquad\qquad\qquad - 2\bar{p} - 2\delta + 4\delta\bar{p} + 2\bar{p}^2 + 2\delta\bar{p} - 4\delta\bar{p}^2) \\
& \qquad\qquad\qquad\qquad + \delta\bar{p}(2\bar{p} - 2\bar{p}^2 + \delta - 4\delta\bar{p} + 4\delta\bar{p}^2)] \\
& + \bar{x}(f'_{AA}(\bar{x}) - f'_{aa}(\bar{x}))f_{aa}(\bar{x})\bar{p}(\bar{p} + 2\delta - 2\delta\bar{p}) \\
& + \bar{x}f'_{aa}(\bar{x})[f_{aa}(\bar{x}) + (2\bar{p} - 2\bar{p}^2 + \delta - 4\delta\bar{p} + 4\delta\bar{p}^2)(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))] \\
& + \bar{x}h'(\bar{x})[f_{aa}(\bar{x}) + (\bar{p} + \delta - 2\delta q + \bar{p} - 2\delta\bar{p} - 2\bar{p}q + 4\delta\bar{p}q)(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))]
\end{aligned}
$$

$$
\begin{aligned}
=& f_{Aa}(\bar{x}) + 2\bar{p}(1-\bar{p})(1-2\delta)(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) \\
& + \bar{x}(f'_{AA}(\bar{x}) - f'_{aa}(\bar{x}))(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))[\bar{p}(\bar{p}+\delta-2\delta\bar{p})(-\delta+2\delta\bar{p}) \\
& \hspace{6cm} + \delta\bar{p}(2\bar{p} - 2\bar{p}^2 + \delta - 4\delta\bar{p} + 4\delta\bar{p}^2)] \\
& + \bar{x}(f'_{AA}(\bar{x}) - f'_{aa}(\bar{x}))f_{aa}(\bar{x})\bar{p}(\bar{p}+2\delta-2\delta\bar{p}) \\
& + \bar{x}f'_{aa}(\bar{x})(f_{aa}(\bar{x}) + (2\bar{p} - 2\bar{p}^2 + \delta - 4\delta\bar{p} + 4\delta\bar{p}^2)(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))) \\
& + \bar{x}h'(\bar{x})[f_{aa}(\bar{x}) + (\bar{p}+\delta-2\delta q + \bar{p}(1-2\delta-2q+4\delta q))(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))] \\
=& f_{Aa}(\bar{x}) + 2\bar{p}(1-\bar{p})(1-2\delta)(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) \\
& + \bar{x}(f'_{AA}(\bar{x}) - f'_{aa}(\bar{x}))(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))\bar{p}(\delta\bar{p} + 2\delta\bar{p}^2 - \delta^2 + 2\delta^2\bar{p} + 2\delta^2\bar{p} - 4\delta^2\bar{p}^2 \\
& \hspace{6cm} + 2\delta\bar{p} - 2\delta\bar{p}^2 + \delta^2 - 4\delta^2\bar{p} + 4\delta^2\bar{p}^2) \\
& + \bar{x}(f'_{AA}(\bar{x}) - f'_{aa}(\bar{x}))f_{aa}(\bar{x})\bar{p}(\bar{p}+2\delta-2\delta\bar{p}) \\
& + \bar{x}f'_{aa}(\bar{x})(f_{aa}(\bar{x}) + (2\bar{p} - 2\bar{p}^2 + \delta - 4\delta\bar{p} + 4\delta\bar{p}^2)(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))) \\
& + \bar{x}h'(x)[f_{aa}(\bar{x}) + (\bar{p}+\delta-2\delta q + \bar{p}(1-2\delta)(1-2q))(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))] \\
=& f_{Aa}(\bar{x}) + 2\bar{p}(1-\bar{p})(1-2\delta)(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) \\
& + \bar{x}(f'_{AA}(\bar{x}) - f'_{aa}(\bar{x}))(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))\bar{p}(\delta\bar{p}) \\
& + \bar{x}(f'_{AA}(\bar{x}) - f'_{aa}(\bar{x}))f_{aa}(\bar{x})\bar{p}(\bar{p}+2\delta-2\delta\bar{p}) \\
& + \bar{x}f'_{aa}(\bar{x})(f_{aa}(\bar{x}) + (2\bar{p} - 2\bar{p}^2 + \delta - 4\delta\bar{p} + 4\delta\bar{p}^2)(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))) \\
& + \bar{x}h'(x)[f_{aa}(\bar{x}) + (\bar{p}+\delta-2\delta q + \bar{p}(1-2\delta)(1-2q))(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))]
\end{aligned}
$$

$$
\begin{aligned}
=& f_{Aa}(\bar{x}) + 2\bar{p}(1-\bar{p})(1-2\delta)(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) \\
& + \bar{x}f'_{AA}(\bar{x})[f_{AA}(\bar{x})\delta\bar{p}^2 + f_{aa}(\bar{x})(\bar{p}^2 + 2\delta\bar{p} - 3\delta\bar{p}^2)] \\
& + \bar{x}f'_{aa}(\bar{x})[f_{AA}(\bar{x})(-\delta\bar{p}^2 + 2\bar{p} - 2\bar{p}^2 + \delta - 4\delta\bar{p} + 4\delta\bar{p}^2) \\
& \hspace{2cm} + f_{aa}(\bar{x})(\delta\bar{p}^2 - \bar{p}^2 - 2\delta\bar{p} + 2\delta\bar{p}^2 + 1 - 2\bar{p} + 2\bar{p}^2 - \delta + 4\delta\bar{p} - 4\delta\bar{p}^2)] \\
& + \bar{x}h'(\bar{x})[f_{aa}(\bar{x}) + (\bar{p}+\delta-2\delta q + \bar{p}(1-2\delta)(1-2q))(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))]
\end{aligned}
$$

$$= f_{Aa}(\bar{x}) + 2\bar{p}(1 - \bar{p})(1 - 2\delta)(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))$$
$$+ \bar{x} f'_{AA}(\bar{x})[f_{AA}(\bar{x})\delta\bar{p}^2 + f_{aa}(\bar{x})(\bar{p}^2 + 2\delta\bar{p} - 3\delta\bar{p}^2)]$$
$$+ \bar{x} f'_{aa}(\bar{x})[f_{AA}(\bar{x})(2\bar{p} - 2\bar{p}^2 + \delta - 4\delta\bar{p} + 3\delta\bar{p}^2)$$
$$+ f_{aa}(\bar{x})(1 - 2\bar{p} + \bar{p}^2 - \delta + 2\delta\bar{p} - \delta\bar{p}^2)]$$
$$+ \bar{x} h'(\bar{x})[f_{aa}(\bar{x}) + (\bar{p} + \delta - 2\delta q + \bar{p}(1 - 2\delta)(1 - 2q))(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))]$$
$$= f_{Aa}(\bar{x}) + 2\bar{p}(1 - \bar{p})(1 - 2\delta)(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))$$
$$+ \bar{x} f'_{AA}(\bar{x})[f_{AA}(\bar{x})\delta\bar{p}^2 + f_{aa}(\bar{x})\bar{p}(\bar{p}(1 - \delta) + 2\delta(1 - \bar{p}))]$$
$$+ \bar{x} f'_{aa}(\bar{x})[f_{AA}(\bar{x})(2\bar{p}(1 - \bar{p}) + \delta(1 - \bar{p}) - 3\delta\bar{p}(1 - \bar{p}))$$
$$+ f_{aa}(\bar{x})((1 - \bar{p})^2 - \delta(1 - \bar{p})^2)]$$
$$+ \bar{x} h'(\bar{x})[f_{aa}(\bar{x}) + (\bar{p} + \delta - 2\delta q + \bar{p}(1 - 2\delta)(1 - 2q))(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))]$$
$$= f_{Aa}(\bar{x}) + 2\bar{p}(1 - \bar{p})(1 - 2\delta)(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))$$
$$+ \bar{x} f'_{AA}(\bar{x})[f_{AA}(\bar{x})\delta\bar{p}^2 + f_{aa}(\bar{x})\bar{p}(\bar{p}(1 - \delta) + 2\delta(1 - \bar{p}))]$$
$$+ \bar{x} f'_{aa}(\bar{x})[f_{AA}(\bar{x})(1 - \bar{p})(2\bar{p} + \delta - 3\delta\bar{p}) + f_{aa}(\bar{x})(1 - \bar{p})^2(1 - \delta)]$$
$$+ \bar{x} h'(\bar{x})[f_{aa}(\bar{x}) + (\bar{p} + \delta - 2\delta q + \bar{p}(1 - 2\delta)(1 - 2q))(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))]$$
$$= f_{Aa}(\bar{x}) + 2\bar{p}(1 - \bar{p})(1 - 2\delta)(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))$$
$$+ \bar{x} f'_{AA}(\bar{x})[f_{AA}(\bar{x})\delta\bar{p}^2 + f_{aa}(\bar{x})\bar{p}(\bar{p}(1 - \delta) + 2\delta(1 - \bar{p}))]$$
$$+ \bar{x} f'_{aa}(\bar{x})[f_{AA}(\bar{x})(1 - \bar{p})(2\bar{p}(1 - \delta) + \delta(1 - \bar{p})) + f_{aa}(\bar{x})(1 - \bar{p})^2(1 - \delta)]$$
$$+ \bar{x} h'(\bar{x})[f_{aa}(\bar{x}) + (\bar{p} + \delta - 2\delta q + \bar{p}(1 - 2\delta)(1 - 2q))(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))].$$

We will use $\det[D(E)]$ to help determine the stability of the equilibrium.

A.3.2 $1 - \mathbf{tr}[D(E)] + \det[D(E)]$

We also need to look at $1 - \text{tr}[D(E)] + \det[D(E)]$ to help determine the stability of the equilibrium.

$$1 - \text{tr}[D(E)] + \det[D(E)]$$

$$= 1 - \left[f_A + \bar{p} \left(\frac{\partial f_A}{\partial p} - \frac{\partial f}{\partial p} \right) + 1 + \bar{x} \left(\frac{\partial f}{\partial x} + h'(\bar{x}) \right) \right] + \det[D(E)]$$

$$= -f_A - \bar{p} \left(\frac{\partial f_A}{\partial p} - \frac{\partial f}{\partial p} \right) - \bar{x} \left(\frac{\partial f}{\partial x} + h'(\bar{x}) \right) + \det[D(E)]$$

$$= -f_{aa}(\bar{x}) - (\bar{p} + \delta - \delta\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) - \bar{p}(1 - 2\bar{p} - 3\delta + 4\delta\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))$$

$$\quad - \bar{x}f'_{aa}(\bar{x}) - \bar{x}\bar{p}(\bar{p} + 2\delta - 2\delta\bar{p})(f'_{AA}(\bar{x}) - f'_{aa}(\bar{x})) - \bar{x}h'(\bar{x}) + \det[D(E)]$$

$$= -f_{aa}(\bar{x}) + (-\bar{p} - \delta + \delta\bar{p} - \bar{p} + 2\bar{p}^2 + 3\delta\bar{p} - 4\delta\bar{p}^2)(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))$$

$$\quad + \bar{x}(-\bar{p}^2 - 2\delta\bar{p} + 2\delta\bar{p}^2)(f'_{AA}(\bar{x}) - f'_{aa}(\bar{x})) - \bar{x}f'_{aa}(\bar{x}) - \bar{x}h'(\bar{x})$$

$$\quad + f_{aa}(\bar{x}) + [\delta + 2\bar{p} - 2\bar{p}^2 - 4\delta\bar{p} + 4\delta\bar{p}^2](f_{AA}(\bar{x}) - f_{aa}(\bar{x}))$$

$$\quad + \bar{x}f'_{AA}(\bar{x})[f_{AA}(\bar{x})\delta\bar{p}^2 + f_{aa}(\bar{x})\bar{p}(\bar{p}(1 - \delta) + 2\delta(1 - \bar{p}))]$$

$$\quad + \bar{x}f'_{aa}(\bar{x})[f_{AA}(\bar{x})(1 - \bar{p})(2\bar{p}(1 - \delta) + \delta(1 - \bar{p})) + f_{aa}(\bar{x})(1 - \bar{p})^2(1 - \delta)]$$

$$\quad + \bar{x}h'(\bar{x})[f_{aa}(\bar{x}) + (\bar{p} + \delta - 2\delta q + \bar{p}(1 - 2\delta)(1 - 2q))(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))]$$

$$= \bar{x}f'_{AA}(\bar{x})[f_{AA}(\bar{x})\delta\bar{p}^2 + f_{aa}(\bar{x})(\bar{p}^2 + 2\delta\bar{p} - 3\delta\bar{p}^2) - \bar{p}^2 - 2\delta\bar{p} + 2\delta\bar{p}^2]$$

$$\quad + \bar{x}f'_{aa}(\bar{x})[f_{AA}(\bar{x})(2\bar{p} + \delta - 4\delta\bar{p} - 2\bar{p}^2 + 3\delta\bar{p}^2)$$

$$\quad\quad\quad\quad + f_{aa}(\bar{x})(-2\bar{p} - \delta + 2\delta\bar{p} + \bar{p}^2 - \delta\bar{p}^2 + 1) + \bar{p}^2 + 2\delta\bar{p} - 2\delta\bar{p}^2 - 1]$$

$$\quad + \bar{x}h'(\bar{x})[f_{AA}(\bar{x})(2\bar{p} - 2\delta\bar{p} + \delta - 2\bar{p}q - 2\delta q + 4\delta\bar{p}q)$$

$$\quad\quad\quad\quad + f_{aa}(\bar{x})(-2\bar{p} + 2\delta\bar{p} - \delta + 2\bar{p}q + 2\delta q - 4\delta\bar{p}q + 1) - 1].$$

$$\text{(A.14)}$$

In order to have results about stability of the equilibrium, we want $1 - \text{tr}[D(E)] + \det[D(E)]$ to be positive. We will look at terms based on their derivatives. For the terms that are multiplied by $\bar{x}f'_{AA}(\bar{x})$, we denote them by $A(\delta)$ where

$$A(\delta) = f_{AA}(\bar{x})\delta\bar{p}^2 + f_{aa}(\bar{x})(\bar{p}^2 + 2\delta\bar{p} - 3\delta\bar{p}^2) - 2\delta\bar{p} - \bar{p}^2 + 2\delta\bar{p}^2.$$

The terms that are multiplied by $\bar{x}f'_{aa}(\bar{x})$, we denote as $B(\delta)$ where

$$B(\delta) = f_{AA}(\bar{x})(2\bar{p} + \delta - 4\delta\bar{p} - 2\bar{p}^2 + 3\delta\bar{p}^2) + f_{aa}(\bar{x})(-2\bar{p} - \delta + 2\delta\bar{p} + \bar{p}^2 - \delta\bar{p}^2 + 1)$$
$$+ 2\delta\bar{p} - 2\delta\bar{p}^2 - 1 + \bar{p}^2.$$

Denote the terms that are multiplied by $\bar{x}h'(\bar{x})$ as $C(q,\delta)$, with

$$C(q,\delta) = f_{AA}(\bar{x})(2\bar{p} - 2\delta\bar{p} + \delta - 2\bar{p}q - 2\delta q + 4\delta\bar{p}q)$$
$$+ f_{aa}(\bar{x})(-2\bar{p} + 2\delta\bar{p} - \delta + 2\bar{p}q + 2\delta q - 4\delta\bar{p}q + 1) - 1.$$

A.3.2.1   Assume $f_{AA}(\bar{x}) > f_{aa}(\bar{x})$

For $f_{AA}(\bar{x}) > f_{aa}(\bar{x})$, we rewrite the terms multiplied by $\bar{x}f'_{AA}(\bar{x})$ as

$$A(\delta) = \bar{p}[f_{AA}(\bar{x})\delta\bar{p} + f_{aa}(\bar{x})\bar{p}(1-\delta) - \bar{p} + f_{aa}(\bar{x})2\delta(1-\bar{p}) - 2\delta(1-\bar{p})]$$
$$= \bar{p}[\bar{p}(f_{AA}(\bar{x})\delta + f_{aa}(\bar{x})(1-\delta) - 1) + 2\delta(1-\bar{p})(f_{aa}(\bar{x}) - 1)] \qquad \text{(A.15)}$$
$$= \bar{p}[\bar{p}(f_{Aa}(\bar{x}) - 1) + 2\delta(1-\bar{p})(f_{aa}(\bar{x}) - 1)].$$

Since $f_{Aa}(\bar{x}) < 1$ and $f_{aa}(\bar{x}) < 1$ when $f_{AA}(\bar{x}) > f_{aa}(\bar{x})$, then $A(\delta) < 0$ for all δ, $0 \le \delta \le 1$.

For the terms multiplied by $\bar{x}f'_{aa}(\bar{x})$, we have to look both when $f_{AA}(\bar{x}) \le 1$ and when $f_{AA}(\bar{x}) > 1$. First, when $f_{AA}(\bar{x}) \le 1$, we can rewrite $B(\delta)$ as

$$B(\delta) = (1 - \bar{p})[f_{AA}(\bar{x})(2\bar{p} + \delta - 3\delta\bar{p}) + f_{aa}(\bar{x})(1 - \bar{p} - \delta + \delta\bar{p}) + (-1 - \bar{p} + 2\delta\bar{p})]$$
$$= (1 - \bar{p})[f_{AA}(\bar{x})(2\bar{p} + \delta - 3\delta\bar{p}) + (-2\bar{p} - \delta + 3\delta\bar{p})$$
$$+ f_{aa}(\bar{x})(1 - \bar{p} - \delta + \delta\bar{p}) + (-1 + \bar{p} + \delta - \delta\bar{p})]$$
$$= (1 - \bar{p})[(2\bar{p} + \delta - 3\delta\bar{p})(f_{AA}(\bar{x}) - 1) + (1 - \bar{p} - \delta + \delta\bar{p})(f_{aa}(\bar{x}) - 1)]$$
$$= (1 - \bar{p})[(2\bar{p}(1 - \delta) + \delta(1 - \bar{p}))(f_{AA}(\bar{x}) - 1) + (1 - \bar{p})(1 - \delta)(f_{aa}(\bar{x}) - 1)].$$
$$\text{(A.16)}$$

We have for $f_{AA}(\bar{x}) > f_{aa}(\bar{x})$ that $f_{aa}(\bar{x})$ and we assume $f_{AA}(\bar{x}) \le 1$, thus $B(\delta) < 0$ for all δ, $0 \le \delta \le 1$. We also need to show that $B(\delta) < 0$ when $f_{AA}(\bar{x}) > 1$. We will

use that at equilibrium, $f_A(\bar{p}, \bar{x}) - f_{aa}(\bar{x}) = (\bar{p} + \delta - \delta\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))$ and the fact that $f_A(\bar{p}, \bar{x}) - 1 < 0$.

$$
\begin{aligned}
B(\delta) &= (1 - \bar{p})[f_{AA}(\bar{x})(2\bar{p} + \delta - 3\delta\bar{p}) + f_{aa}(\bar{x})(1 - \bar{p} - \delta + \delta\bar{p}) + (-1 - \bar{p} + 2\delta\bar{p})] \\
&= (1 - \bar{p})[(\bar{p} + \delta - \delta\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) + (\bar{p} - 2\delta\bar{p})f_{AA}(\bar{x}) + f_{aa}(\bar{x}) \\
&\qquad + 2\delta\bar{p} - 1 - \bar{p}] \\
&= (1 - \bar{p})[(f_A(\bar{x}) - f_{aa}(\bar{x})) + \bar{p}(1 - 2\delta)f_{AA}(\bar{x}) + \bar{p}(2\delta - 1) + f_{aa}(\bar{x}) - 1] \\
&< (1 - \bar{p})[1 - f_{aa}(\bar{x}) + \bar{p}(1 - 2\delta)(f_{AA}(\bar{x}) - 1) + f_{aa}(\bar{x}) - 1] \\
&= (1 - \bar{p})\bar{p}(1 - 2\delta)(f_{AA}(\bar{x}) - 1).
\end{aligned}
$$
(A.17)

When $f_{AA}(\bar{x}) > 1$, $B(\delta) < 0$ when $\dfrac{1}{2} \leq \delta \leq 1$. If $f_{AA}(\bar{x}) > 1$ or if $f_{AA}(\bar{x}) \leq 1$, for $\dfrac{1}{2} \leq \delta \leq 1$ then $B(\delta) < 0$.

For the terms multiplied by $\bar{x}h'(\bar{x})$, we have

$$
\begin{aligned}
C(q, \delta) &= (2\bar{p} + \delta - 2\delta\bar{p} - 2\bar{p}q - 2\delta q + 4\delta\bar{p}q)(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) - 1 \\
&= (\bar{p} + \delta - \delta\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) + f_{aa}(\bar{x}) - 1 \\
&\qquad + (\bar{p} - \delta\bar{p} - 2\bar{p}q - 2\delta q + 4\delta\bar{p}q)(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) \\
&= -\bar{p} - f_{aa}(\bar{x})) + f_{aa}(\bar{x}) - 1 \\
&\qquad + [\bar{p}(1 - \delta) + 2\bar{p}q(\delta - 1) + 2\delta q(\bar{p} - 1)](f_{AA}(\bar{x}) - f_{aa}(\bar{x})) \\
&< 1 - f_{aa}(\bar{x}) + f_{aa}(\bar{x}) - 1 \\
&\qquad + [\bar{p}(1 - \delta)(1 - 2q) - 2\delta q(1 - \bar{p})](f_{AA}(\bar{x}) - f_{aa}(\bar{x})) \\
&= [\bar{p}(1 - \delta)(1 - 2q) - 2\delta q(1 - \bar{p})](f_{AA}(\bar{x}) - f_{aa}(\bar{x})).
\end{aligned}
$$
(A.18)

And, $C(q, \delta) < 0$ when $\dfrac{1}{2} \leq q \leq 1$ for all δ, $0 \leq \delta \leq 1$.

Thus for $f_{AA}(\bar{x}) > f_{aa}(\bar{x})$ since we are assuming (4.5), when $\dfrac{1}{2} \leq \delta \leq 1$ and $\dfrac{1}{2} \leq q \leq 1$, then $1 - \text{tr}[D(E)] + \det[D(E)] > 0$.

A.3.2.2 Assume $f_{AA}(\bar{x}) < f_{aa}(\bar{x})$

When $f_{AA}(\bar{x}) < f_{aa}(\bar{x})$, we use that at equilibrium,
$\delta\bar{p}(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) = f_a(\bar{p}, \bar{x}) - f_{aa}(\bar{x})$ and the fact that $f_a(\bar{p}, \bar{x}) - 1 < 0$. For the terms
multiplied by $\bar{x}f'_{AA}(\bar{x})$, we need to look both when $f_{aa}(\bar{x}) \leq 1$ and when $f_{aa}(\bar{x}) > 1$.
First, when $f_{aa}(\bar{x}) \leq 1$,

$$
\begin{aligned}
A(\delta) &= \bar{p}^2(\delta f_{AA}(\bar{x}) + (1-\delta)f_{aa}(\bar{x})) - \bar{p}^2 + (2\delta\bar{p} - 2\delta\bar{p}^2)f_{aa}(\bar{x}) - 2\delta\bar{p} + 2\delta\bar{p}^2 \\
&= \bar{p}^2 f_{Aa}(\bar{x}) - \bar{p}^2 + (2\delta\bar{p}(1-\bar{p}))f_{aa}(\bar{x}) - 2\delta p(1-\bar{p}) \\
&= \bar{p}^2(f_{Aa}(\bar{x}) - 1) + 2\delta\bar{p}(1-\bar{p})(f_{aa}(\bar{x}) - 1).
\end{aligned} \tag{A.19}
$$

And $A(\delta) < 0$ if $f_{aa}(\bar{x}) < 1$ for all δ, $0 \leq \delta \leq 1$. When $f_{aa}(\bar{x}) > 1$, we rewrite $A(\delta)$ as

$$
\begin{aligned}
A(\delta) &= \delta\bar{p}^2(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) + (\bar{p}^2 + 2\delta\bar{p} - 2\delta\bar{p}^2)f_{aa}(\bar{x}) + (-\bar{p}^2 - 2\delta\bar{p} + 2\delta\bar{p}^2) \\
&= \bar{p}(f_a(\bar{p}, \bar{x}) - f_{aa}(\bar{x})) + (\bar{p}^2 + 2\delta\bar{p} - 2\delta\bar{p}^2)f_{aa}(\bar{x}) + (-\bar{p}^2 - 2\delta\bar{p} + 2\delta\bar{p}^2) \\
&< \bar{p}(1 - f_{aa}(\bar{x})) + \bar{p}(\bar{p} + 2\delta - 2\delta\bar{p})f_{aa}(\bar{x}) + \bar{p}(-\bar{p} - 2\delta + 2\delta\bar{p}) \\
&= \bar{p}(-1 + \bar{p} + 2\delta - 2\delta\bar{p})(f_{aa}(\bar{x}) - 1) \\
&= \bar{p}(1 - \bar{p})(2\delta - 1)(f_{aa}(\bar{x}) - 1).
\end{aligned} \tag{A.20}
$$

When $f_{aa}(\bar{x}) > 1$, $A(\delta) < 0$ for all δ, $0 \leq \delta \leq \dfrac{1}{2}$. If $f_{aa}(\bar{x}) \leq 1$ or $f_{aa}(\bar{x}) > 1$ when
$0 \leq \delta \leq \dfrac{1}{2}$, then $A(\delta) < 0$.

For the terms multiplied by $\bar{x} f'_{aa}(\bar{x})$, we can rewrite them as

$$
\begin{aligned}
B(\delta) &= (1-\bar{p})[f_{AA}(\bar{x})(2\bar{p}+\delta-3\delta\bar{p}) + f_{aa}(\bar{x})(1-\bar{p}-\delta+\delta\bar{p}) + (-1-\bar{p}+2\delta\bar{p})] \\
&= (1-\bar{p})[(\bar{p}+\delta-\delta\bar{p})(f_{AA}(\bar{x})-f_{aa}(\bar{x})) + f_{AA}(\bar{x})(\bar{p}-2\delta\bar{p}) + f_{aa}(\bar{x}) \\
&\qquad + (-1-\bar{p}+2\delta\bar{p})] \\
&= (1-\bar{p})[f_A(\bar{p},\bar{x}) - f_{aa}(\bar{x}) + f_{AA}(\bar{x})\bar{p}(1-2\delta) + f_{aa}(\bar{x}) - 1 - \bar{p}(1-2\delta)] \\
&< (1-\bar{p})[1 - f_{aa}(\bar{x}) + \bar{p}(1-2\delta)(f_{AA}(\bar{x})-1) + f_{aa}(\bar{x}) - 1] \\
&= (1-\bar{p})\bar{p}(1-2\delta)(f_{AA}(\bar{x})-1).
\end{aligned}
$$
(A.21)

When $f_{AA}(\bar{x}) < f_{aa}(\bar{x})$, we have that $f_{AA}(\bar{x}) < 1$. Thus, $B(\delta) < 0$ when $0 \le \delta \le \dfrac{1}{2}$.

For the terms multiplied by $\bar{x} h'(\bar{x})$, we can rewrite them as

$$
\begin{aligned}
C(q,\delta) =& f_{aa}(\bar{x}) + \delta\bar{p}(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) - 1 \\
& + (2\bar{p} - 3\delta\bar{p} + \delta - 2\bar{p}q - 2\delta q + 4\delta\bar{p}q)(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) \\
=& f_a(\bar{p},\bar{x}) - 1 + (\bar{p} + \delta - 2\delta\bar{p} - 2\bar{p}q - 2\delta q + 4\delta\bar{p}q + \bar{p} - \delta\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) \\
<& ((\bar{p} + \delta - 2\delta\bar{p})(1-2q) + \bar{p}(1-\delta))(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) \\
=& [(\bar{p}(1-\delta) + \delta(1-\bar{p}))(1-2q) + \bar{p}(1-\delta)](f_{AA}(\bar{x}) - f_{aa}(\bar{x})).
\end{aligned}
$$
(A.22)

For $f_{AA}(\bar{x}) < f_{aa}(\bar{x})$, when $0 \le q \le \dfrac{1}{2}$, $C(q,\delta) < 0$.

Thus, for $f_{AA}(\bar{x}) < f_{aa}(\bar{x})$, since we are assuming (4.5) when $0 \le \delta \le \dfrac{1}{2}$ and $0 \le q \le \dfrac{1}{2}$, $1 - \text{tr}[D(E)] + \det[D(E)] > 0$

Appendix B

Chapter 5 Computations

In this appendix, we give details for the computations made in chapter (5).

B.1   Derivative of $\bar{p}$ with respect to δ

We use the system satisfied at equilibrium, (4.2), to define functions F and G as follows:

$$F(p, x, \delta) = pf_A + qh - p$$

$$G(p, x, \delta) = f + h - 1.$$

The values of p, x, and δ at equilibrium are simultaneous solutions of $F = 0$ and $G = 0$. The Implicit Function Theorem permits us to express the p and x coordinates of a solution in terms of the parameter δ in a neighborhood of a solution provided

$$\det \begin{bmatrix} \frac{\partial F}{\partial p} & \frac{\partial F}{\partial x} \\ \frac{\partial G}{\partial p} & \frac{\partial G}{\partial x} \end{bmatrix} \neq 0.$$

The derivative of $\bar{p}$ with respect to δ is

$$\frac{d\bar{p}}{d\delta} = -\det \begin{bmatrix} \frac{\partial F}{\partial \delta} & \frac{\partial F}{\partial x} \\ \frac{\partial G}{\partial \delta} & \frac{\partial G}{\partial x} \end{bmatrix} \Big/ \det \begin{bmatrix} \frac{\partial F}{\partial p} & \frac{\partial F}{\partial x} \\ \frac{\partial G}{\partial p} & \frac{\partial G}{\partial x} \end{bmatrix}. \tag{B.1}$$

We will use

$$\frac{\partial F}{\partial \delta} = \bar{p}\frac{df_A}{d\delta} = \bar{p}(1-\delta)(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))$$

$$\frac{\partial F}{\partial x} = \bar{p}\frac{df_A}{dx} + qh'(\bar{x})$$

$$\frac{\partial F}{\partial p} = f_A + \bar{p}\frac{\partial f_A}{\partial p} - 1$$

$$\frac{\partial G}{\partial \delta} = 2\bar{p}(1-\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))$$

$$\frac{\partial G}{\partial x} = \frac{\partial f}{\partial x} + h'(\bar{x})$$

$$\frac{\partial G}{\partial p} = \frac{\partial f}{\partial p}$$

to simplify.

The numerator of (B.1) is

$$-\frac{\partial F}{\partial \delta}\frac{\partial G}{\partial x} + \frac{\partial F}{\partial x}\frac{\partial G}{\partial \delta}$$

$$= - \left[\bar{p}(1-\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))\right]\left[\frac{\partial f}{\partial x} + h'(\bar{x})\right]$$

$$\quad + \left[2\bar{p}(1-\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))\right]\left[\bar{p}\frac{\partial f_A}{\partial x} + qh'(\bar{x})\right]$$

$$= \bar{p}(1-\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))\left[-\frac{\partial f}{\partial x} - h'(\bar{x}) + 2\bar{p}\frac{\partial f_A}{\partial x} + 2qh'(\bar{x})\right]$$

$$= \bar{p}(1-\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))\left[2\bar{p}\frac{\partial f_A}{\partial x} - \frac{\partial f}{\partial x} + (2q-1)h'(\bar{x})\right]$$

$$= \bar{p}(1-\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))[2\bar{p}f'_{aa}(\bar{x}) + 2\bar{p}(\bar{p} + \delta - \delta\bar{p})(f'_{AA}(\bar{x}) - f'_{aa}(\bar{x}))$$

$$\quad - f'_{aa}(\bar{x}) - \bar{p}(\bar{p} + 2\delta - 2\delta\bar{p})(f'_{AA}(\bar{x}) - f'_{aa}(\bar{x})) + (2q-1)h'(\bar{x})]$$

$$= \bar{p}(1-\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))[(2q-1)h'(\bar{x}) + (2\bar{p} - 1)f'_{aa}(\bar{x})$$

$$\quad + (2\bar{p}^2 + 2\delta\bar{p} - 2\delta\bar{p}^2 - \bar{p}^2 - 2\delta\bar{p} + 2\delta\bar{p}^2)(f'_{AA}(\bar{x}) - f'_{aa}(\bar{x}))]$$

$$= \bar{p}(1-\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))[(2q-1)h'(\bar{x}) + (2\bar{p} - 1)f'_{aa}(\bar{x}) + \bar{p}^2(f'_{AA}(\bar{x}) - f'_{aa}(\bar{x}))]$$

$$= \bar{p}(1-\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))[\bar{p}^2 f'_{AA}(\bar{x}) + (-\bar{p}^2 + 2\bar{p} - 1)f'_{aa}(\bar{x}) + (2q-1)h'(\bar{x})]$$

$$= \bar{p}(1-\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))[\bar{p}^2 f'_{AA}(\bar{x}) - (1-\bar{p})^2 f'_{aa}(\bar{x}) + (2q-1)h'(\bar{x})].$$

$$(B.2)$$

And the denominator of (B.1) is

$$
\frac{\partial F}{\partial p}\frac{\partial G}{\partial x} + \frac{\partial F}{\partial x}\frac{\partial G}{\partial p}
$$

$$
= \left[f_A + \bar{p}\frac{\partial f_A}{\partial p} - 1\right]\left[\frac{\partial f}{\partial x} + h'(\bar{x})\right] - \left[\bar{p}\frac{\partial f_A}{\partial x} + qh'(\bar{x})\right]\left[\frac{\partial f}{\partial p}\right]
$$

$$
= [f_{aa}(\bar{x}) + (\bar{p} + \delta - \delta\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) + \bar{p}(1-\delta)(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) - 1]
$$

$$
* [f'_{aa}(\bar{x}) + \bar{p}(\bar{p} + 2\delta - 2\delta\bar{p})(f'_{AA}(\bar{x}) - f'_{aa}(\bar{x})) + h'(\bar{x})]
$$

$$
- [\bar{p}f'_{aa}(\bar{x}) + \bar{p}(\bar{p} + \delta - \delta\bar{p})(f'_{AA}(\bar{x}) - f'_{aa}(\bar{x})) + qh'(\bar{x})]
$$

$$
* [2(\bar{p} + \delta - 2\delta\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))]
$$

$$
= [f_{aa}(\bar{x}) + (2\bar{p} + \delta - 2\delta\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) - 1]
$$

$$
* [f'_{aa}(\bar{x}) + (\bar{p}^2 + 2\delta\bar{p} - 2\delta\bar{p}^2)(f'_{AA}(\bar{x}) - f'_{aa}(\bar{x})) + h'(\bar{x})]
$$

$$
+ [\bar{p}f'_{aa}(\bar{x}) + (\bar{p}^2 + \delta\bar{p} - \delta\bar{p}^2)(f'_{AA}(\bar{x}) - f'_{aa}(\bar{x})) + qh'(\bar{x})]
$$

$$
* [2(2\delta\bar{p} - \bar{p} - \delta)(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))]
$$

$$
= (f'_{AA}(\bar{x}) - f'_{aa}(\bar{x}))[(\bar{p}^2 + 2\delta\bar{p} - 2\delta\bar{p}^2)(f_{aa}(\bar{x}) - 1) + (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))
$$

$$
* ((2\bar{p} + \delta - 2\delta\bar{p})(\bar{p}^2 + 2\delta\bar{p} - 2\delta\bar{p}^2) + (\bar{p}^2 + \delta\bar{p} - \delta\bar{p}^2)(4\delta\bar{p} - 2\bar{p} - 2\delta))]
$$

$$
+ f'_{aa}(\bar{x})[f_{aa}(\bar{x}) - 1 + (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))(2\bar{p} + \delta - 2\delta\bar{p} + 4\delta\bar{p}^2 - 2\bar{p}^2 - 2\delta\bar{p})]
$$

$$
+ h'(\bar{x})[f_{aa}(\bar{x}) - 1 + (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))(2\bar{p} + \delta - 2\delta\bar{p} + q(4\delta\bar{p} - 2\bar{p} - 2\delta))]
$$

$$
= (f'_{AA}(\bar{x}) - f'_{aa}(\bar{x}))[(\bar{p}^2 + 2\delta\bar{p} - 2\delta\bar{p}^2)(f_{aa}(\bar{x}) - 1) + (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))
$$

$$
* (2\bar{p}^3 + 4\delta\bar{p}^2 - 4\delta\bar{p}^3 + \delta\bar{p}^2 + 2\delta^2\bar{p} - 2\delta^2\bar{p}^2 - 2\delta\bar{p}^3 - 4\delta^2\bar{p}^2 + 4\delta^2\bar{p}^3
$$

$$
+ 4\delta\bar{p}^3 - 2\bar{p}^3 - 2\delta\bar{p}^2 + 4\delta^2\bar{p}^2 - 2\delta\bar{p}^2 - 2\delta^2\bar{p} - 4\delta^2\bar{p}^3 + 2\delta\bar{p}^3 + 2\delta^2\bar{p}^2)]
$$

$$
+ f'_{aa}(\bar{x})[f_{aa}(\bar{x}) - 1 + (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))(2\bar{p} + \delta - 2\delta\bar{p} + 4\delta\bar{p}^2 - 2\bar{p}^2 - 2\delta\bar{p})]
$$

$$
+ h'(\bar{x})[f_{aa}(\bar{x}) - 1 + (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))(2\bar{p} + \delta - 2\delta\bar{p} + 4\delta\bar{p}q - 2\bar{p}q - 2\delta q)]
$$

$$
= (f'_{AA}(\bar{x}) - f'_{aa}(\bar{x}))[(\bar{p}^2 + 2\delta\bar{p} - 2\delta\bar{p}^2)(f_{aa}(\bar{x}) - 1) + (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))(\delta\bar{p}^2)]
$$

$$
+ f'_{aa}(\bar{x})[f_{aa}(\bar{x}) - 1 + (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))(2\bar{p} + \delta - 2\delta\bar{p} + 4\delta\bar{p}^2 - 2\bar{p}^2 - 2\delta\bar{p})]
$$

$$
+ h'(\bar{x})[f_{aa}(\bar{x}) - 1 + (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))(2\bar{p} + \delta - 2\delta\bar{p} + 4\delta\bar{p}q - 2\bar{p}q - 2\delta q)]
$$

$$
\begin{aligned}
=& f'_{AA}(\bar{x})[\delta\bar{p}^2 f_{AA}(\bar{x}) + (\bar{p}^2 + 2\delta\bar{p} - 3\delta\bar{p}^2)f_{aa}(\bar{x}) - \bar{p}^2 - 2\delta\bar{p} + 2\delta\bar{p}^2] \\
&+ f'_{aa}(\bar{x})[(\bar{p}^2 + 2\delta\bar{p} - 2\delta\bar{p}^2 - 1)(1 - f_{aa}(\bar{x})) \\
&\qquad\qquad + (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))(-\delta\bar{p}^2 + 2\bar{p} + \delta - 2\delta\bar{p} + 4\delta\bar{p}^2 - 2\bar{p}^2 - 2\delta\bar{p})] \\
&+ h'(\bar{x})[f_{aa}(\bar{x}) - 1 + (f_{AA}(\bar{x}) - f_{aa}(\bar{x}))(2\bar{p} + \delta - 2\delta\bar{p} + 4\delta\bar{p}q - 2\bar{p}q - 2\delta q)] \\
=& f'_{AA}(\bar{x})[\delta\bar{p}^2 f_{AA}(\bar{x}) + (\bar{p}^2 + 2\delta\bar{p} - 3\delta\bar{p}^2)f_{aa}(\bar{x}) - \bar{p}^2 - 2\delta\bar{p} + 2\delta\bar{p}^2] \\
&+ f'_{aa}(\bar{x})[(2\bar{p} - 2\bar{p}^2 + \delta - 4\delta\bar{p} + 3\delta\bar{p}^2)f_{AA}(\bar{x}) \\
&\qquad\qquad + (-2\bar{p} + \bar{p}^2 - \delta + 2\delta\bar{p} - \delta\bar{p}^2 + 1)f_{aa}(\bar{x}) + (\bar{p}^2 + 2\delta\bar{p} - 2\delta\bar{p}^2 - 1)] \\
&+ h'(\bar{x})[(2\bar{p} + \delta - 2\delta\bar{p} + 4\delta\bar{p}q - 2\bar{p}q - 2\delta q)f_{AA}(\bar{x}) \\
&\qquad\qquad + (1 - 2\bar{p} - \delta + 2\delta\bar{p} - 4\delta\bar{p}q + 2\bar{p}q + 2\delta q)f_{aa}(\bar{x}) - 1].
\end{aligned}
\tag{B.3}
$$

B.2 Derivative of $\bar{x}$ with respect to δ

The derivative of $\bar{x}$ with respect to δ is

$$
\frac{d\bar{x}}{d\delta} = -\det \begin{bmatrix} \frac{\partial F}{\partial p} & \frac{\partial F}{\partial \delta} \\ \frac{\partial G}{\partial p} & \frac{\partial G}{\partial \delta} \end{bmatrix} \bigg/ \det \begin{bmatrix} \frac{\partial F}{\partial p} & \frac{\partial F}{\partial x} \\ \frac{\partial G}{\partial p} & \frac{\partial G}{\partial x} \end{bmatrix}.
\tag{B.4}
$$

The numerator of (B.4) is

$$
\begin{aligned}
-\frac{\partial F}{\partial p}\frac{\partial G}{\partial \delta} &+ \frac{\partial F}{\partial \delta}\frac{\partial G}{\partial p} \\
&= -\left[f_A + \bar{p}\frac{\partial f_A}{\partial p} - 1\right][2\bar{p}(1-\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))] \\
&\quad + [p(1-\delta)(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))]\left[\frac{\partial f}{\partial p}\right] \\
&= -[f_{aa}(\bar{x}) + (\bar{p} + \delta - \delta\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) + p(1-\delta)(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) - 1] \\
&\qquad * [2\bar{p}(1-\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))] \\
&\quad + [\bar{p}(1-\delta)(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))][2(\bar{p} + \delta - 2\delta\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))] \\
&= -[f_{aa}(\bar{x}) + (2\bar{p} + \delta - 2\delta\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x})) - 1][2\bar{p}(1-\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))] \\
&\quad + [\bar{p}(1-\delta)(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))][2(\bar{p} + \delta - 2\delta\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))] \\
&= 2\bar{p}(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))^2[(2\bar{p} + \delta - 2\delta\bar{p})(\bar{p} - 1) + (1-\delta)(\bar{p} + \delta - 2\delta\bar{p})] \\
&\quad + 2\bar{p}(1-\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))(1 - f_{aa}(\bar{x})) \\
&= 2\bar{p}(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))^2[2\bar{p}^2 + \delta\bar{p} - 2\delta\bar{p}^2 - 2\bar{p} - \delta + 2\delta\bar{p} + \bar{p} + \delta - 2\delta\bar{p} - \delta\bar{p} - \delta^2 \\
&\qquad\qquad + 2\delta^2\bar{p}] \\
&\quad + 2\bar{p}(1-\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))(1 - f_{aa}(\bar{x})) \\
&= 2\bar{p}(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))^2[2\bar{p}^2 - 2\delta\bar{p}^2 - \bar{p} - \delta^2 + 2\delta^2\bar{p}] \\
&\quad + 2\bar{p}(1-\bar{p})(f_{AA}(\bar{x}) - f_{aa}(\bar{x}))(1 - f_{aa}(\bar{x})).
\end{aligned}
$$

(B.5)

The denominator for the derivative of $\bar{x}$ with respect to δ is the same as the denominator for the derivative of $\bar{p}$ with respect to δ and can be simplified as the last five lines of (B.3).