Reaction-diffusion equations for population genetics

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Reaction-diffusion equations for population genetics

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by

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This thesis, submitted in fulfilment of the requirements for the award of Doctor of Philosophy, in the School of Mathematics and Applied Statistics, University of Wollongong, is wholly my own work unless otherwise referenced or acknowledged. The document has not been submitted for qualifications at any other academic institution.

Bronwyn Bradshaw-Hajek

May, 2004
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*I get by with a little help from my friends.*

*John Lennon and Paul McCartney*

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Abstract

In this thesis, we reinforce the validity of using reaction-diffusion equations with cubic source terms to describe the change in frequency of alleles in a gene pool. In a population with two possible alleles at the locus in question, the Fitzhugh-Nagumo equation is shown to be appropriate when there is no dominance, whereas the Huxley equation is appropriate when one of the alleles is completely dominant. The difference between the Huxley equation (with cubic source term) and the Fisher-Kolmogorov equation (with quadratic source term) is examined numerically and analytically.

Using the method of nonclassical symmetry analysis, we construct some practical analytic solutions to the Fitzhugh-Nagumo and Huxley equations. The solutions satisfy specific boundary conditions and are different from previously derived travelling wave solutions.

We derive a system of reaction-diffusion equations describing the case of three possible alleles at the locus in question. By introducing a nonlinear transformation, we are able to construct an exact travelling wave solution.

We also extend the model to include the case of spatially dependent reproductive success rates. We use classical and nonclassical symmetry methods to discover what forms of explicit spatial variability will enable us to find exact solutions to our equations. A number of solutions are constructed for various forms of spatial...
variability.

Finally, we demonstrate the benefits of systematic symmetry analysis by studying two related systems of reaction-diffusion equations.
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Chapter 1

Introduction

*If the Lord Almighty had consulted me before embarking upon Creation, I should have recommended something simpler.*

– Alfonso X (1221-1284), Spanish King of Castile and Leon.

Population genetics is that branch of genetics which is concerned with changes in the genetic make-up of a population. In any single population of a sexually reproducing species, the number of possible genotypes is huge, and the genotype of any particular individual is likely to be unique. Therefore, modelling any such situation is extremely complicated and often too difficult to be treated theoretically [43]. However, modelling changes in the frequency of the alleles at one particular locus within the population is feasible. Knowledge of the frequency of each of the alleles enables us to characterise the population by its gene ratio [30]. It is the investigation
of the changes in these allele frequencies that is the motivation for this thesis.

Modelling of gene frequencies is of particular relevance today, especially in light of recent developments in the field of gene technology. Some recent advances and problems in the broad field of gene technology include the following:

- species can develop immunity to viral pathogens that have been introduced to control the species;
- some bacteria have developed a tolerance to widely prescribed antibiotics, rendering them far less useful;
- archaeologists are hoping that the human genome project will enable us to map geographic distributions of signature genes and to deduce historical patterns of migration, and;
- agricultural crops and livestock can now be genetically modified to be more resistant to pests and produce a higher yield (see for example [53, 59]).

The last item has been extremely topical in recent years, and debate has raged on the possible implications of genetically modified crops and animals cross-pollinating or breeding with wild or traditionally farmed members of their species. In order to make use of genetic population data, we need to understand the dynamics of gene patterns through a population. It is therefore timely that the mathematical modelling of changing gene proportions be re-examined.
A change in the gene frequencies in a population is the most elementary step in evolution from a population genetics point of view [43]. Variation exists in a population due to the different possible alleles an individual may possess, and this variation is heritable. Individuals with variations that are best suited to the environment are more likely to survive and pass on those advantageous genes to successive generations [64]. By attempting to model these changes in allele frequencies we hope to determine the probability of the ultimate success of an advantageous gene.

Problems arising in chemistry and physics are usually well defined and the system being considered can often be isolated, so that modelling techniques can easily be applied to many situations. The same is not true for the biological sciences. Biological systems are often extremely complex and the situations under examination are not so clearly defined. In nature, things are far more complicated than can be described by any simple model [29] so that the limitations of any such model must be recognised. The biological sciences are not yet at the stage where it is appropriate to attempt to construct comprehensive and extremely detailed mathematical models [54].

Having recognised this fact, this thesis approaches the problem of changing gene frequencies from a relatively mathematical point of view. We have been primarily interested in developing a number of models to describe slightly different situations, and have attempted to find new analytic solutions to many of the equations.
1.1 Existing models

Models currently used in the study of population genetics can be divided into two broad categories: stochastic and deterministic. Although stochastic models are important, this thesis is solely concerned with deterministic models. For examples of stochastic models in population genetics, the reader is referred to Goel and Richter-Dyn [33], Kelly [42], Kimura [43] or Ludwig [49].

Many of the deterministic models used in the field of population genetics have great similarities with those used in other disciplines. Reaction-diffusion equations of the type

\[ p_t = p_{xx} + Q(p, x) \]

are used in many areas of science and engineering, including models for transmission of nerve impulses [69], heating by microwave radiation [39], chemical reactions [5], the theory of super conductivity [2], as well as other biological situations such as predator-prey systems and the modelling of calcium waves on the surface of amphibian eggs [54]. Countless other examples also exist.

A number of authors have proposed reaction-diffusion equations to model changing gene frequencies in a population. Interest in this field began in earnest in the 1920’s and 1930’s. Contributions of note include those by Haldane (see for example [35] and the ensuing parts), Fisher (for example [27, 28]) and Wright (see for example [79]). One of the earliest and most well known articles devoted to this topic
was that by Fisher. In his 1937 paper [28], Fisher proposed a reaction-diffusion equation with quadratic source term that models the spread of a new recessive advantageous gene through a population that previously had only one allele at the locus in question. Several others have also developed reaction-diffusion equations with a similar quadratic source term, (see for example Slatkin [71]), and others claim to have verified Fisher’s results (see for example Skellam [72]).

Modelling changes in gene frequencies in a population was re-examined in the latter half of the last century. Some authors suggested that a cubic source term was more appropriate than a quadratic source term (see for example Bazykin [9], Piálek & Barton [61]). Although the cubic source term was suggested, a thorough derivation was often not provided. Nagylaki [55] and Nagylaki & Crow [56], however, derived the cubic source term by using Fick’s Laws and a local Hardy-Weinberg property. Although the cubic source term is implicit as one possibility in the general dispersion equations derived by others, its significance has not been highlighted and the difference between cubic and quadratic source terms has not been examined.

Fisher’s equation is

$$\frac{\partial p}{\partial t} = k \frac{\partial^2 p}{\partial x^2} + mp(1 - p),$$

(1.1)

where $p$ is the frequency of the gene in question (in this case a new mutant gene), $k$ is the diffusion constant (dimensions $L^2T^{-1}$) and $m$ is the intensity of selection in favour of the mutant gene (dimensions $T^{-1}$). If we use nondimensional variables $x' = x/l_s$ and $t' = t/t_s$ where $t_s = m^{-1}$ (take-over time) and $l_s = \sqrt{k/m}$ (diffu-
sion length at take-over), then both coefficients $k$ and $m$ are effectively reduced to unity. However, when we compare alternative reaction-diffusion models for the same gene, we cannot in general simultaneously normalise both reaction terms. We will therefore take $k = 1$ but retain $m$ as a parameter.

In many applications, it is convenient to choose the much shorter individual maturation time $t_m$, or time between generations, as the time scale. We can still normalise the diffusivity by choosing the length scale to be the generation diffusion length $\sqrt{kt_m}$ but the factor of the source term will be replaced by the dimensionless parameter $mt_m$.

Equation (1.1) predicts a wave front of increasing allele frequency, propagating through the population. Only original alleles are present in front of the wave, and behind the wave is an area taken over by the mutant allele. Fisher wrote his equation with no formal derivation and very little explanation. Equation (1.1) is now known as the Fisher-Kolmogorov equation, due also to the classic paper written at the same time by Kolmogorov, Petrovsky and Piscounov [44].

In 1969, Bazykin [9] suggested an equation with a cubic source term,

$$\frac{\partial p}{\partial t} = \frac{\partial^2 p}{\partial x^2} + mp(1 - p)(2p - 1).$$

This equation describes the situation in which “the heterozygote is less fit than both homozygotes” and “homozygote fitness is equal”.

Skellam [72] derived a reaction-diffusion equation with cubic source term by
first writing equations for the genotype frequencies, then combining them to write equations describing changes in gene frequencies. By assuming the birthrates of the genotypes to be in arithmetic progression, one of the constants is reduced to zero, and Fisher’s equation is recovered. Aronson and Weinberger [6] use a similar method to derive a related reaction-diffusion equation with a source term which is cubic in the allele frequencies.

Skellam’s method of derivation is the most straight forward and concise, and we use the same method in this thesis to derive equations describing more complicated situations.

1.2 Background information in genetics

We now give a brief explanation of some of the biological and genetical terms used in this thesis. These definitions may not be entirely comprehensive, however they are adequate for the purposes of this thesis.

Unless stated otherwise, throughout this thesis, we consider a diploid population, so that each individual possesses two sets of chromosomes, one set inherited from each parent. We are only interested in the genes located at one particular locus, i.e. the genes at a particular place on a particular chromosome. We consider the situation in which the gene occurs in two or three different forms, called alleles. The Mendelian model of inheritance assumes that parents pass on discrete heritable
units – genes – that remain separate and can be passed on to subsequent generations in undiluted form.

The genetic makeup of an individual is known as its genotype. A homozygote possesses two identical alleles for a given trait, whereas a heterozygote has two different alleles for a given trait.

The physical traits exhibited by an individual is known as its phenotype. In a heterozygote, the allele that is fully expressed by the phenotype is known as the dominant allele, whereas if an allele is completely masked in the phenotype, it is known as recessive.

1.3 Structure and scope of the thesis

In Chapter 2 we develop a model to describe the change in frequency of an allele in a population in which there are two possible alleles at the locus in question. We do this using two different methods. In the first method, we formulate difference equations that describe a spatially homogeneous model with discrete breeding cycles. A reaction-diffusion equation is obtained with a nonlinear growth rate for which the leading term is cubic in the allele frequency.

We also re-examine the direct continuum approaches of Aronson and Weinberger [6] and Skellam [72]. By writing equations that describe changes in the genotype frequencies, we arrive at a single reaction-diffusion equation that describes the change
in frequency of one of the alleles. The same class of reaction-diffusion equations with a cubic source term is obtained. This reaction-diffusion equation is sometimes known as the Fitzhugh-Nagumo equation.

In the case of a completely recessive allele (the case examined by Fisher in [28]), the reaction-diffusion equation has the source term \( gp^2(1 - p) \) where \( g \) is a constant. This equation is sometimes known as the Huxley equation. This cubic source term is in contrast to the quadratic source term originally proposed by Fisher (1.1) in [28]. Analytical and numerical comparisons are made between this cubic equation and the Fisher-Kolmogorov equation, and we show that the cubic term leads to a much delayed spread of the new gene.

In Chapter 3 we look for exact solutions to the Fitzhugh-Nagumo and Huxley equations. We find that these equations belong to a small class of nonlinear reaction-diffusion equations that admit particular exact solutions by Painlevé methods [17, 45] or by nonclassical symmetry reductions [7, 23]. We construct a nontrivial exact solution for each of the Fitzhugh-Nagumo and Huxley equations. Some comments about the stability of these solutions are also made. Limited explanation is given about the methods of classical and nonclassical symmetry analysis in this chapter, however greater detail is provided in Chapter 5.

In Chapter 4 we use similar modelling techniques to extend the model to describe the case in which there are three possible alleles (resulting in six possible genotypes) at the locus in question. By writing equations describing the change in frequency
of each of the genotypes, we derive a new system of coupled cubic reaction-diffusion equations for two of the alleles. Very few authors have examined the situation in which there are greater than two possible alleles at the locus in question (a limited number have studied this situation using stochastic methods, for example [48]).

A new exact travelling wave solution is found using a new method proposed by Rodrigo and Mimura [66]. After transforming to the travelling wave coordinate we introduce a nonlinear transformation which allows us to find solutions that are polynomials in the transformed coordinate. In particular, we examine the particular case of a recessive, advantageous allele. We make some comments about the stability of the travelling wave solution. We also show, using proof by induction, that when any number of pre-existing alleles and one new allele compete for a single locus, in the case of shared disadvantage of pre-existing alleles, the frequency of a new allele is described by the same single equation as that developed in Chapter 2.

In Chapter 5 we extend the model to incorporate spatial dependence in the reproductive success rates. Using the same technique as that used in Chapters 2 and 4, reaction-diffusion equations are developed to describe the change in frequency of the alleles. Spatial variability in the advantage afforded by different alleles has been examined by a number of authors including Fife and Peletier [26], Fisher [29], Nagylaki [55] and Slatkin [71]. The most commonly examined case is the step environment, however the effect of gradual environmental change has also been investigated (where the advantage of one allele is proportional to $x$). The equations
developed in this chapter contain arbitrary spatial dependence.

We then proceed to analyse these equations using classical and nonclassical symmetry analysis to determine what forms of spatial dependence will allow exact solutions to be found. Given that nonclassical symmetry analysis has been successfully used to find solutions to the equations with constant reproductive success rates (Chapter 3), there is some hope that solutions may be found for more interesting reproductive success rates (that contain explicit spatial dependence). Analysis of the equations does indeed show that for some particular forms of spatial dependence, classical and nonclassical symmetries exist. New exact solutions are presented for these different cases. In this chapter, the methods used to find and use classical and nonclassical symmetries are explained in detail.

In Chapter 6, we use classical symmetry analysis to analyse a system of equations related to the system developed in Chapter 4. The concept of an optimal system is explained, and we find the optimal system and a complete set of reductions for two systems of reaction-diffusion equations.

It has already been mentioned that we do not consider stochastic effects in this thesis. Only deterministic models for probability densities will be used.

We are primarily concerned with finding analytical solutions. Although numerical analysis can be a useful tool for examining the characteristics of a differential equation, it has only been used occasionally in this thesis.
Chapter 2

Formulation of the local deterministic model for gene propagation

*All models are wrong — some are useful.*

— source unknown

In this chapter, we present two different approaches to develop a reaction-diffusion equation that describes the change in frequency of a particular allele in a population for which there exist two possible alleles at the locus in question.

In the first approach, we formulate difference equations that describe a spatially homogeneous population with discrete breeding cycles. This approach is summarised
in the text by Fulford, *et al* [31], however we extend their reasoning to develop a reaction-diffusion equation.

The second approach is based on the direct continuum approaches of Skellam [72] and Aronson and Weinberger [6]. This involves first writing equations that describe changes in genotype frequencies, then combining them to find one equation describing the change in frequency of one of the alleles. We include this method because it is concise and it is readily extended to the analysis of more complicated situations and modelling assumptions. It also incorporates a non-uniform total population density. We show that both methods lead us to the same class of reaction-diffusion-convection equations describing the change in frequency of the allele in question.

### 2.1 Developing the reaction-diffusion model

In developing the model we make a number of assumptions about the population, most of which are consistent with assumptions made by other authors (for example see [28, 54, 71]).

We consider a *randomly mating population* so that individuals mate with each other indiscriminately, regardless of their genotype.

We assume that the population exists in a *one dimensional habitat*, so that we only consider diffusion in one spatial dimension. This is not unreasonable as a first
approximation since the population could exist along a shoreline, river, mountain ridge or valley.

We assume that the population moves randomly. This leads to a population density that obeys *Fickian diffusion*. Provided that long-range migration is rare and allele frequencies vary slowly in space and time, this is believed to be a good approximation [61]. The use of Fickian diffusion for selection-migration problems has often been the subject of dispute, however justification for its use has been given by many authors (for example, see [15, 25]). We have not explored other types of diffusion because we have been primarily interested in the effects of different source terms.

We assume that an individual’s genotype has no influence on an individual’s mobility, allowing us to use a uniform diffusion coefficient. The ability to re-scale variables allows us to assume without loss of generality that this diffusion coefficient is one. Setting the diffusion coefficient constant means that the environment must be homogeneous.

We also assume that all genotypes have the same death rate and that any differences in fitness and survival rates between the different phenotypes is attributed to variations in *reproductive success rates* alone. Using a different technique, Aronson and Weinberger [6] have shown that assuming a common, relatively large birth rate and small differences between the death rates, the same class of gene dispersion equations is obtained.
2.1.1 Using difference equations

In this section, we impose the above assumptions on a spatially homogeneous population with discrete breeding cycles. We use difference equations to find a reaction-diffusion equation that describes changes in a particular gene frequency.

Consider the case in which there are two particular alleles at the locus in question, labelled $A$ (the dominant allele) and $a$ (the recessive allele), giving rise to three different genotypes $AA$, $Aa$ and $aa$. We are interested in how the frequency of the recessive allele $a$ changes. In the classical Mendel binary scheme, the physical characteristic associated with the dominant allele will be equally apparent in individuals possessing two copies of the gene ($AA$) and those possessing one copy of the gene ($Aa$). We assume that these two genotypes have a survival rate $r_0$. The recessive characteristic will only be expressed by those individuals possessing two copies of the recessive gene, (those with genotype $aa$). We will assume that these individuals have a survival rate $r_2$.

Following the notation of Fulford, et al [31], at the beginning of the $k^{th}$ generation, we denote the total population as $N^*_k$. The populations of each of the three genotypes are written as $N^*_k(AA)$, $N^*_k(Aa)$ and $N^*_k(aa)$, while corresponding symbols without asterisks refer to the populations in the $k^{th}$ generation at sexual maturity. $G_k(AA)$, $G_k(Aa)$ and $G_k(aa)$ are the genotype frequencies in the $k^{th}$ generation, so that, for example, $G_k(AA) = N_k(AA)/N_k$. We denote the gene frequencies in the
gene pool at the $k^{th}$ generation by $P_k(A)$ and $P_k(a)$.

By definition,

$$N_{k+1}^*(AA) = G_{k+1}^*(AA)N_{k+1}^*, \tag{2.1}$$

By the assumption of random mating, the expected value of $G_{k+1}^*(AA)$ is $[P_k(A)]^2$.

For a large population, (2.1) reduces to

$$N_{k+1}^*(AA) = [P_k(A)]^2 N_{k+1}^*.$$  

Similarly, we can write

$$N_{k+1}^*(Aa) = 2P_k(A)P_k(a)N_{k+1}^*, \quad N_{k+1}^*(aa) = [P_k(a)]^2 N_{k+1}^*.$$  

By definition,

$$P_{k+1}(a) = \frac{\text{number of } a \text{ alleles}}{\text{total number of alleles in gene pool}} = \frac{N_{k+1}(Aa) + 2N_{k+1}(aa)}{2N_{k+1}(AA) + 2N_{k+1}(Aa) + 2N_{k+1}(aa)}. \tag{2.2}$$

Substituting

$$N_{k+1}(AA) = r_0 N_{k+1}^*(AA), \quad N_{k+1}(Aa) = r_0 N_{k+1}^*(Aa),$$

$$N_{k+1}(aa) = r_2 N_{k+1}^*(aa) \quad \text{and} \quad P_k(A) = 1 - P_k(a),$$

we obtain

$$P_{k+1}(a) = \frac{\left(\frac{r_2}{r_0} - 1\right) P_k^2(a) + P_k(a)}{1 + \left(\frac{r_2}{r_0} - 1\right) P_k^2(a)}, \tag{2.3}$$

where $r_2/r_0$ is the relative fitness of the two phenotypes.
Chapter 2: Formulation of the local deterministic model for gene propagation

Fisher considered the case in which the recessive allele \( a \), was an advantageous mutant. If the \( a \) allele is advantageous, then individuals expressing the phenotype associated with this allele (i.e. individuals with genotype \( aa \)) will have a greater survival rate, so that \( r_2 > r_0 \). These beneficial mutations most commonly only result in a small advantage, so that \( \frac{r_2}{r_0} - 1 \) is usually small, i.e. \( 0 < \frac{r_2}{r_0} - 1 \ll 1 \). This means that (2.3) implies

\[
P_{k+1}(a) - P_k(a) = \left( \frac{r_2}{r_0} - 1 \right) P_k^2(a)(1 - P_k(a)) + O \left( \frac{r_2}{r_0} - 1 \right)^2. \tag{2.4}\]

Note that this growth term is cubic in \( P_k(a) \) as opposed to Fisher’s quadratic logistic growth term.

If we generalise the above arguments to the case in which there is no dominance of the \( A \) allele so that all three genotypes have different survival rates, \( r_0, r_1 \) and \( r_2 \) (where the subscript refers to the number of \( a \) alleles present), we obtain

\[
P_{k+1}(a) = \frac{\frac{r_1}{r_0} P_k(a) + \left( \frac{r_2}{r_0} - \frac{r_1}{r_0} \right) P_k^2(a)}{1 + 2 \left( \frac{r_1}{r_0} - 1 \right) P_k(a) + \left( 1 - 2 \frac{r_1}{r_0} + \frac{r_2}{r_0} \right) P_k^2(a)}. \]

Again, since beneficial mutations usually result in only small advantages, \( 0 < \frac{r_1}{r_0} - 1 = O \left( \frac{r_2}{r_0} - 1 \right) \ll 1 \), which implies

\[
P_{k+1}(a) - P_k(a) = P_k(a)(1 - P_k(a)) \left[ \frac{r_1}{r_0} - 1 + \left( 1 - 2 \frac{r_1}{r_2} + \frac{r_2}{r_0} \right) P_k(a) \right]
+ O \left( \frac{r_2}{r_0} - 1 \right)^2. \tag{2.5}\]

If \( \Delta t \) is the time between successive generations, then (2.4) and (2.5) can be
written respectively as

\[
\frac{P_{k+1}(a) - P_k(a)}{\Delta t} = \left( \frac{r_2}{r_0} - 1 \right) P_k^2(a)(1 - P_k(a)), \quad \text{and} \quad (2.6)
\]

\[
\frac{P_{k+1}(a) - P_k(a)}{\Delta t} = P_k(a)(1 - P_k(a)) \left[ \frac{r_1}{r_0} - 1 + P_k(a) \left( 1 - 2 \frac{r_1}{r_2} + \frac{r_2}{r_0} \right) \right]. \quad (2.7)
\]

Since relative differences in selective advantages are small, the discrete model may be conveniently approximated by an interpolating continuous model with

\[
P_{k+1}(a) = P([k + 1] \Delta t, a)
\]

\[
= P_k(a) + \Delta t \frac{\partial}{\partial t} P(t, a) + O(\Delta t^2)
\]

at \( t = k \Delta t \). In the continuum model, we adopt a time scale over which \( P \) may change significantly. Then \( \Delta t \), the time between generations, is small compared to 1. The finite difference quotient in (2.6) and (2.7) may then be viewed as the Euler approximant of the time derivative.

Assuming Fickian diffusion with equal mobility for each genotype, rewriting \( P(t, a) \) as \( p(t) \) and allowing spatial variation, we obtain the following equations

\[
\frac{\partial p}{\partial t} = \frac{\partial^2 p}{\partial x^2} + \left( \frac{r_2}{r_0} - 1 \right) p^2(1 - p), \quad (2.8)
\]

\[
\frac{\partial p}{\partial t} = \frac{\partial^2 p}{\partial x^2} + p(1 - p) \left[ \frac{r_1}{r_0} - 1 + p \left( 1 - 2 \frac{r_1}{r_2} + \frac{r_2}{r_0} \right) \right]. \quad (2.9)
\]

For simplicity, we have assumed that mobility does not enlarge an individual’s habitat so much that one’s available pool of mating partners has a genetic composition greatly different from that of one’s local neighbourhood. Otherwise the local source terms would be integrals, as in [76].
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Equation (2.8) describes how the frequency of a recessive gene changes. Equation (2.9) describes how the frequency of a particular allele changes, regardless of whether or not the allele is dominant or recessive.

2.1.2 Using continuous genotype differential equations

For a diploid population having two available alleles at the locus in question ($A_1$ and $A_2$), there are three possible genotypes; $A_1A_1$, $A_1A_2$ and $A_2A_2$, where $A_1$ is the allele that we are concerned with. We can write three equations describing the change in the genotype frequencies $\rho_{11}(x, t)$, $\rho_{12}(x, t)$ and $\rho_{22}(x, t)$,

$$
\begin{align*}
\frac{\partial \rho_{11}}{\partial t} &= \frac{\partial^2 \rho_{11}}{\partial x^2} - \mu \rho_{11} + \gamma_{11} p^2 \rho, \\
\frac{\partial \rho_{12}}{\partial t} &= \frac{\partial^2 \rho_{12}}{\partial x^2} - \mu \rho_{12} + \gamma_{12} p(1 - p) \rho, \\
\frac{\partial \rho_{22}}{\partial t} &= \frac{\partial^2 \rho_{22}}{\partial x^2} - \mu \rho_{22} + \gamma_{22} (1 - p)^2 \rho,
\end{align*}
$$

(2.10)

where $\gamma_{ij}$ is the reproductive success rate of the genotype $A_iA_j$, $\mu$ is the common death rate (see the discussion in Section 2.1 concerning the common death rate and different reproductive success rates), $\rho(x, t)$ is the total population density, $\rho(x, t) = \rho_{11}(x, t) + \rho_{12}(x, t) + \rho_{22}(x, t)$, and $p(x, t)$ is the frequency of allele $A_1$. The frequency of allele $A_2$ is given by $(1 - p(x, t))$. The frequency of allele $A_1$ is

$$
p = \frac{2\rho_{11} + \rho_{12}}{2\rho}.
$$

(2.11)

Differentiating (2.11) with respect to $t$ we find that the three genotype equations (2.10) remarkably collapse into a single equation that describes the change in fre-
quency of the new mutant gene

\[
\frac{\partial p}{\partial t} = \frac{\partial^2 p}{\partial x^2} + \frac{2 \partial p}{\rho \partial x} \frac{\partial p}{\partial x} + p(1 - p) (g_1 - g_2 p),
\]  
(2.12)

where \( g_1 = \gamma_{12} - \gamma_{22} \) and \( g_2 = -\gamma_{11} + 2\gamma_{12} - \gamma_{22} \). This equation is a reaction-diffusion-convection equation with cubic nonlinearities. Equation (2.12) with \( \frac{\partial p}{\partial x} = 0 \) (i.e. total population density constant in space) is sometimes known as the Fitzhugh-Nagumo equation. If \( \frac{\partial p}{\partial x} \neq 0 \), we have an additional convective term due to the migratory diffusive flux of the total population. Comparison of this equation with equation (2.9) shows that the two different methods do indeed produce the same class of equations. The second method has an extra convective term because we have assumed a spatially non-uniform total population density.

If we consider the case examined by Fisher, so that the allele in question is considered to be completely recessive, genotypes \( AA \) and \( Aa \) have the same phenotype and hence the same reproductive success rate. If we set alleles \( A \) and \( a \) to be represented by alleles \( A_2 \) and \( A_1 \) respectively, (so that the recessive allele, \( A_1 \) is the one being considered), this means that \( \gamma_{12} = \gamma_{22} \) and equation (2.12) reduces to

\[
\frac{\partial p}{\partial t} = \frac{\partial^2 p}{\partial x^2} + \frac{2 \partial p}{\rho \partial x} \frac{\partial p}{\partial x} + g p^2 (1 - p),
\]  
(2.13)

where \( g = \gamma_{11} - \gamma_{22} \). This is a reaction-diffusion-convection equation with cubic nonlinearities. Without the convection term it is known as Huxley’s equation, and it is often used for modelling the propagation of impulses along nerve axons. On comparing this equation with equation (2.8) we see that we again have the same
equation with an extra convective term.

2.2 Significance of cubic and quadratic source terms

As described in Chapter 1, although the cubic source term has been suggested as a possibility by other authors [6, 9, 61, 72], its significance has not been stressed. This is possibly because assuming spatially uniform total population density (so that $\partial \rho / \partial x = 0$) and an arithmetic progression of the reproductive success rates (so that $\gamma_{11} - \gamma_{12} = \gamma_{12} - \gamma_{22}$) in equation (2.12), does recover Fisher’s equation (1.1), but this constraint has no particular relevance to biology. This assumption is made by Skellam [72] in order to make comparisons with Fisher’s equation.

It is also interesting to note that applying the same modelling methods to two cohabiting strains of an asexual species distinguished by alternative characteristics $A$ and $a$, does indeed recover Fisher’s equation (1.1). The terms describing the increase due to births of each genotype now only depend on the number of individuals of the same genotype, not on the frequency of the alleles. The genotype equations become

$$\frac{\partial \rho_{11}}{\partial t} = \frac{\partial^2 \rho_{11}}{\partial x^2} - \mu \rho_{11} + \gamma_{11} \rho_{11},$$

$$\frac{\partial \rho_{22}}{\partial t} = \frac{\partial^2 \rho_{22}}{\partial x^2} - \mu \rho_{22} + \gamma_{22} \rho_{22},$$

and the frequency of the $A_1$ allele can be written as $p = \rho_{11}/\rho$. Differentiating this
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with respect to time and recognising that $\rho_{22}/\rho = 1 - p$, we find

$$\frac{\partial p}{\partial t} = \frac{\partial^2 p}{\partial x^2} + \frac{2 \partial p}{\rho \partial x} + \frac{\partial}{\partial x} \left( (\gamma_{11} - \gamma_{22})p(1 - p) \right),$$

suggesting that Fisher’s equation is appropriate for an asexually reproducing species. Note that in this case, the product source term $(\gamma_{11} - \gamma_{22})p(1 - p)$ is not due to heterosexual coupling.

The cubic source terms are robust for a number of different situations and modelling assumptions. We have extended the model to include the more complicated case of a total of three possible alleles at the locus in question. This results in a system of equations with much more complex source terms, however it is still cubic in the allele frequencies (Chapter 4). The model can also be extended to examine the effect of spatially dependent birth rates (Chapter 5).

2.3 Comparison between Fisher and Huxley equations

2.3.1 Analytical comparison

We have shown in the preceding sections that for a sexually reproducing population, the most appropriate reaction-diffusion equation to describe the change in frequency of a new advantageous, recessive allele is the Huxley equation (2.13), rather than the Fisher equation (1.1).
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To analytically compare the travelling wavefront solutions of the Huxley and Fisher equations, we assume spatially uniform total population density \((\partial \rho / \partial x = 0)\) and include a diffusion constant, \(k\). Since we wish to compare the solutions on the same set of axes, we must require that they have the same wave speed. We rewrite the equations in terms of the travelling wave coordinate, \(p(x, t) = P(z)\) where \(z = x - ct\) and \(c\) is the wave speed, so that for Fisher’s equation (1.1) \((p_t = kp_{xx} + mp(1 - p))\) we have

\[
kP'' + cP' + mP(1 - P) = 0, \tag{2.14}
\]

and for Huxley’s equation (2.13) \((p_t = kp_{xx} + gp^2(1 - p))\), we have

\[
kP'' + cP' + gP^2(1 - P) = 0, \tag{2.15}
\]

where the prime denotes differentiation with respect to the travelling wave coordinate, \(z\). Notice that the diffusion coefficient is the same for both equations since we are most interested in comparing the different source terms. We choose the boundary conditions as

\[P(-\infty) = 1, \quad P(\infty) = 0,\]

so that at the left hand end of the range, the population is fixed for allele \(A_1\) and at the right hand end of the range it is fixed for allele \(A_2\).

In order to compare the travelling wave solutions, we have chosen to use the asymptotic solutions (see Murray [54] for more detail). Choosing the small param-
eter to be \( \varepsilon = 1/c^2 \), we find the asymptotic solutions for \( 0 < \varepsilon \ll 1 \) for equations (2.14) and (2.15) respectively are

\[
P^\varepsilon(z) = \left( 1 + \exp\left(\frac{m}{c}z\right) \right)^{-1} + e^{-2mk} \exp\left(\frac{m}{c}z\right) \left(1 + \exp\left(\frac{m}{c}z\right)\right)^{-2} \ln \left[ \frac{4 \exp\left(\frac{m}{c}z\right)}{\left(1 + \exp\left(\frac{m}{c}z\right)\right)^2} \right] + O(e^{-4})
\]

and

\[
P(z) = P_0 + e^{-2kg} \left( P_0^2 - P_0^3 \right) \ln \left[ 8 \left( P_0^2 - P_0^3 \right) \right] + O(e^{-4})
\]

with \( P_0 \) given by

\[
P_0 = \left[ W \left( \exp\left(\frac{g}{c}z + 1\right) + 1 \right) \right]^{-1},
\]

where \( W \) is Lambert’s W-Function, defined by \( W(x) \exp(W(x)) = x \) (see Appendix A for more detail). Since the solutions are invariant to any shift in the origin of the coordinate system, we have chosen \( z = 0 \) to be the point where \( P = 1/2 \).

In order to make a proper comparison between these solutions, consideration must be given to the relationships between the various constants. We have chosen to use the well known minimum speed for Fisher’s equation, so that \( c = 2\sqrt{km} \).

Secondly, we suggest that both waves should have the same width. The width can be defined as the inverse of the steepness of the wave [54]. We define the steepness as the maximum of the magnitude of the gradient, \( P_z(z) \). This occurs at the point of inflexion of each of our curves, which is at \( z = 0 \). Calculating and equating \( P_z(0) \)
for solutions (2.16) and (2.17) gives us the following relationship:

\[ g = (4\sqrt{6} - 8)m. \]

Figure 2.1 shows the graph of solutions (2.16) and (2.17) with \( k = 1 \) and \( m = 1 \), so that \( c = 2 \) and \( g = (4\sqrt{6} - 8) \approx 1.80 \). As expected, the solution for the Huxley equation has a much longer tail at the leading side of the graph. This is because of the cubic source term, which predicts lower temporal growth rates, represented in Figure 2.1 by lower slopes, at low values of \( p \).
2.3.2 Numerical comparison

In Figure 2.2, we display numerical solutions of the Fisher (1.1) and Huxley (2.13) equations (with spatially uniform total population density, $\partial p/\partial x = 0$). We use the same initial localized Gaussian clump of mutant alleles, contained within the region $0 \leq x \leq 2$ by zero flux boundary conditions, $p_x = 0$. This is a numerical method-of-lines solution obtained by using the program PDETWO of Melgaard & Sincovec [51]. We chose $m = 16g/27$ with $g = 1$ so that both source functions (i.e. $mp(1 - p)$ and $gp^2(1 - p)$) have the same maximum value.

The diffusion coefficient is small ($k = 0.005$) so that the differences in the source terms are highlighted in comparison to the diffusion effects. For both models, the mutant gene frequency can be seen to increase at the origin and then spread throughout the range. As expected, mutant takeover is greatly retarded in the Huxley model compared to the Fisher model.
Figure 2.2: Spread of an initial Gaussian clump $0.2 \exp(-4x^2)$ according to (a) Huxley’s equation with $g = 1$ and (b) Fisher’s equation with same maximum production rate. The diffusion constant is set at 0.005 for both cases.
Chapter 3

Solutions to the Huxley and Fitzhugh-Nagumo equations

In this chapter, we use nonclassical symmetry methods to look for solutions of equations (2.13) and (2.12). Equations of the type

$$ p_t = p_{xx} + Q(p), $$

where $Q(p)$ is a polynomial, have long been used to describe various physical and biological processes such as propagation of an electrical impulse along a nerve axon (see for example [69]), heating by microwave radiation [39], the theory of superconductivity [2], and genetic diffusion [44], as well as other problems arising in population dynamics. Due to the wide range of applications of these types of equations, their behaviour has been extensively studied (see for example Aronson and Wein-
berger [6] or Bramson [14]) and many types of solutions have been found. Here we
give a brief summary of some of the solutions to the Huxley and Fitzhugh-Nagumo
equations found by other authors.

Wang et al [78] found a solitary travelling wave solution to the generalised Huxley
equation \( p_t = p_{xx} + ap(1 - p^b)(p^b - c) \) by introducing nonlinear transformations.
We use similar transformations to find solutions to systems of reaction-diffusion
equations in Chapter 4.

Travelling wave solutions have been found by a number of authors, including
McKean [50], and Rinzel [65]. Others have found periodic solutions, for example
Carpenter [16] and Hastings [36].

Chen and Guo [17] found new solutions to the Fitzhugh-Nagumo equation (3.4)
by the Painlevé approach. Other analytic solutions are presented by Kudryashov
[46] and Kawahara and Tanaka [41].

3.1 Transformation of the convective term to zero

Before looking for solutions to equations (2.13) and (2.12) we transform the convec-
tive term to zero by changing to an accelerating reference frame. Setting
\[
\bar{x} = x + 2\eta(t) \quad ; \quad \bar{t} = t,
\]
and substituting into equations (2.13) and (2.12) we find that if we set
\[
\eta'(t) = \frac{1}{\rho} \frac{\partial \rho}{\partial x},
\]
the convective term is transformed to zero. This means that if the total population density takes the form

$$\rho(x, t) = \rho_0(t)e^{\eta(t)x},$$

we are able to transform the convective term to zero. This allows a restricted form of monotonic spatial variability in total population density at each time. The two common choices made by mathematicians for the form of the total population density, are such that it remains constant in space ($\partial \rho / \partial x = 0$), and constant in time ($\partial \rho / \partial t = 0$) [28]. Although the restricted form (3.2) for the total population density is probably unrealistic in practice, it still allows these two common choices: $\rho(x, t)$ constant in space (by choosing $\eta(t)$ constant); and $\rho(x, t)$ constant in time (by choosing $\eta(t)$ linear and $\rho_0(t)$ constant).

The gene frequency equations then become (after dropping the bars for convenience)

$$\frac{\partial p}{\partial t} = \frac{\partial^2 p}{\partial x^2} + gp^2(1 - p), \quad \text{and}$$

$$\frac{\partial p}{\partial t} = \frac{\partial^2 p}{\partial x^2} + p(1 - p)(g_1 - g_2p),$$

which are the Huxley and Fitzhugh-Nagumo equations respectively.

### 3.2 Nonclassical symmetry solutions

In this section, we find new genuine nonclassical symmetry solutions for the Huxley and Fitzhugh-Nagumo equations. Developed in the late nineteenth century by
Sophus Lie, the theory of continuous transformation groups has been extensively developed and generalised (for example, the reader is referred to books by Bluman and Kumei [13], Hill [38], Ibragimov [40] and Olver [57]). The method of symmetry analysis is an important tool for finding exact solutions to nonlinear PDEs. If a PDE is invariant under a point symmetry, the number of independent variables can be reduced by one and we can then look for solutions of the reduced equation.

We are interested in two particular equations of the form

\[ F(x, t, p, p_x, p_t, p_{xx}) = p_t - p_{xx} - Q(p) = 0, \tag{3.5} \]

where \( Q(p) = gp^2(1 - p) \) for the Huxley equation, and \( Q(p) = p(1 - p)(g_1 - g_2p) \) for the Fitzhugh-Nagumo equation. For classical Lie point symmetries, we seek a one-parameter group of transformations of the form

\[
\begin{align*}
x^* & = x + \epsilon X(x, t, p) + O(\epsilon^2), \\
t^* & = t + \epsilon T(x, t, p) + O(\epsilon^2), \\
p^* & = p + \epsilon P(x, t, p) + O(\epsilon^2),
\end{align*}
\]

that leave the governing equation (3.5) invariant. That is, we seek

\[
\Gamma^{(2)} F|_{F=0} = 0,
\]

where \( \Gamma^{(2)} \) is the second prolongation of the symmetry operator

\[
\Gamma = X \frac{\partial}{\partial x} + T \frac{\partial}{\partial t} + P \frac{\partial}{\partial p}.
\]
Requiring invariance of (3.5) then leads to an overdetermined linear system of equations for \( X(x, t, p) \), \( T(x, t, p) \) and \( P(x, t, p) \), the coefficients of the infinitesimal symmetry generating vector field, commonly called the \textit{infinitesimals}. Subsequent symmetries will allow successive reduction of order. (The method of finding and using classical point symmetries will be discussed in more detail in Chapter 5.)

The only symmetry group common to both equations (3.3) and (3.4) is the translation group, generated by

\[
\Gamma = a_1 \frac{\partial}{\partial x} + a_2 \frac{\partial}{\partial t}
\]

with \( a_1 \) and \( a_2 \) constant. This can easily be verified using a symmetry finding package such as Dimsym (see Chapter 5 for details). The group-invariant solutions are the steady states \((a_1 = 0)\), the spatially uniform solutions \((a_2 = 0)\) and the travelling wave solutions \((a_1 a_2 \neq 0)\). The travelling wave solution satisfies a nonlinear second order ODE for \( p(z) \) where \( z \) is the travelling wave variable \( z = x - a_2 t / a_1 \). Except for some special cases of wave speed [1], even the travelling wave solutions are difficult to obtain exactly. Neither the Fisher equation (1.1), the Huxley equation (3.3) nor the FitzHugh-Nagumo equation (3.4) possess additional classical symmetries.

We now investigate the possibility of \textit{nonclassical} symmetries. The nonclassical symmetry method was developed by Bluman and Cole [11] in 1969 and is related to the earlier conditional symmetry method of Ovsiannikov [58]. It seeks invariance of a system of partial differential equations made up of the given equations together
with the invariant surface condition (ISC)

\[ X_{px} + T_{pt} = P. \]  

(3.6)

Unlike the classical method, the nonclassical method leads to an overdetermined nonlinear system of equations for the infinitesimals \( X(x, t, p), T(x, t, p) \) and \( P(x, t, p) \). This system of equations is usually much more difficult to solve than for the classical case and in general, genuine nonclassical symmetries are rare. However, following the advent of Clarkson and Kruskal’s direct method [22], a number of new nonclassical solutions were constructed for practical nonlinear PDE’s [7, 23]. If we demand invariance of \( F = 0 \) subject to the constraint of the ISC, then this can sometimes lead to additional reductions that are not obtainable by the classical method. (The method of finding and using nonclassical symmetries will be discussed in more detail in Chapter 5.)

In the case of the Huxley equation with source term \( Q(p) = gp^2(1-p) \), without loss of generality we may set \( T(x, t, p) = 1 \), so that the determining relations become

\[
\begin{align*}
-P_{xx} + 3P gp^2 - 2P gp + P_t + 2X_xP - 2X_xgp^2(1-p) + P_p gp^2(1-p) &= 0 \\
X_{xx} + 2X_xP - 2P_{xp} - X_t - 2X_xX - 3X_p gp^2(1-p) &= 0 \\
2X_{xp} - 2X_p X - P_{pp} &= 0 \\
X_{pp} &= 0
\end{align*}
\]

Solving this system of equations for \( X(x, t, p) \) and \( P(x, t, p) \), we find that the in-
finitesimals must take the form:

\[ X(x, t, p) = \sqrt{\frac{g}{2}}(3p - 1), \quad T(x, t, p) = 1, \quad P(x, t, p) = \frac{3}{2}gp^2(1 - p). \]

The associated invariant surface condition (3.6) then becomes

\[ p_t + \sqrt{\frac{g}{2}}(3p - 1)p_x = \frac{3}{2}gp^2(1 - p). \]

Eliminating \( p_t \) using the governing equation (3.3), we have

\[ p_{xx} + \sqrt{\frac{g}{2}}(3p - 1)p_x - \frac{1}{2}gp^2(1 - p) = 0. \]

We can use the Hopf-Cole transformation, \( p = \sqrt{\frac{2}{g}}u_x \), to simplify this equation to

\[ u_{xxx} - \sqrt{\frac{g}{2}}u_{xx} = 0. \]

This equation is integrable, and we find the solution to be

\[ u = c_1(t) \exp\left(\sqrt{\frac{g}{2}}x\right) + c_2(t)x + c_3(t). \]

An expression for \( p(x, t) \) may be recovered by inverting the Hopf-Cole transformation to give

\[ p(x, t) = \frac{c_1(t) \exp\left(\sqrt{\frac{g}{2}}x\right) + \sqrt{\frac{2}{g}}c_2(t)}{c_1(t) \exp\left(\sqrt{\frac{g}{2}}x\right) + c_2(t)x + c_3(t)}, \]

where \( c_1(t) \), \( c_2(t) \) and \( c_3(t) \) are determined by requiring that this solution satisfies the invariant surface condition (3.6). The final form of the new solution to Huxley’s equation (3.3) is

\[ p(x, t) = \frac{\exp\left(\sqrt{\frac{g}{2}}x + \frac{g}{2}t\right) + \sqrt{\frac{g}{2}}c_1}{\exp\left(\sqrt{\frac{g}{2}}x + \frac{g}{2}t\right) + c_1x - \sqrt{2g}c_1t + c_2}, \quad (3.7) \]
where \( c_1 \) and \( c_2 \) are constants. We can find where the solution has a local minimum by solving \( \partial p/\partial x = 0 \). With \( c_1 = 1 \) and \( c_2 = 3 \), we find the local minimum to be at \( x = y(t) \), where

\[
y(t) = \sqrt{\frac{2}{g}} W \left( \sqrt{\frac{2}{g}} \exp \left[ 3 \sqrt{\frac{g}{2}} - 2 - \frac{3g}{2} t \right] \right) - 3 + 2 \sqrt{\frac{2}{g}} + t \sqrt{2g},
\]

where \( W \) is Lambert’s W-function. We now impose a Neumann zero-gradient boundary condition by choosing the accelerating reference frame (3.1) to follow this minimum so that \( 2 \dot{\eta}(t) = y(t) \).

In terms of the original coordinates, the governing gene transport equation is (2.13) with the particular choice \( \partial \ln \rho/\partial x = \eta'(t) = y'(t)/2 \). This equation has the solution

\[
p(x, t) = \frac{\exp \left( \sqrt{\frac{g}{2}} \bar{x} + \frac{g}{2} \bar{t} \right) + \sqrt{\frac{2}{g}}}{\exp \left( \sqrt{\frac{g}{2}} \bar{x} + \frac{g}{2} \bar{t} \right) + \bar{x} - t \sqrt{2g} + 3}
\]

with

\[
\bar{x} = x + y(t) \quad ; \quad \bar{t} = t.
\]

The solution with zero-gradient boundary condition is displayed in Figure 3.1.

The birth rates have been chosen so that the situation represented is that in which the allele under investigation (\( A_1 \)) is advantageous (\( \gamma_{11} = 0.7, \gamma_{22} = 0.2 \) so that \( g = 0.5 \)). This is the same situation as that examined by Fisher - a new advantageous, recessive mutant. At \( t = 0 \), the solution shows a population in which the right hand side of the range is fixed for the mutant allele. As time progresses, the new allele advances across the left hand side of the range, until it is fixed for the entire range.
Figure 3.1: Solution (3.8) at times $t = 0, 1, 2, 3$ to the Huxley equation with a convection term (2.13), subject to zero-gradient at $x = 0$.

We can use the same method to find a solution to the Fitzhugh-Nagumo equation (3.4), i.e. equation (3.5) with source term $Q(p) = p(1 - p)(g_1 - g_2 p)$. Setting $T(x, t, p) = 1$, the determining relations become

$$
\begin{align*}
-P_{xx} + P_t + 2g_2 Pp + 2g_1 Pp - 3g_2 Pp^2 - Pg_1 + 2X_x P \\
+ P_p(1 - p)(g_1 - g_2 p) - 2X_x p(1 - p)(g_1 - g_2 p) &= 0 \\
-2P_{xp} + 2X_p P - 2X_x X - X_t + X_{xx} - 3X_p p(1 - p)(g_1 - g_2 p) &= 0 \\
-2X_p X + 2X_{xp} - P_{pp} &= 0 \\
X_{pp} &= 0
\end{align*}
$$

Solving this equation for $X(x, t, p)$ and $P(x, t, p)$, we find that the infinitesimals
must take the form:

\[
X(x, t, p) = \sqrt{-\frac{g_2}{2}} \left( 3p - 1 - \frac{g_1}{g_2} \right), \quad T(x, t, p) = 1,
\]

\[
P(x, t, p) = \frac{3}{2} g_2 p (1 - p) \left( p - \frac{g_1}{g_2} \right),
\]

requiring that \(g_2 < 0\), so that \(\gamma_{11} - \gamma_{12} > \gamma_{12} - \gamma_{22}\).

The associated invariant surface condition (3.6) then becomes

\[
p_t + \sqrt{-\frac{g_2}{2}} \left( 3p - 1 - \frac{g_1}{g_2} \right) p_x = \frac{3}{2} g_2 p (p - 1) \left( p - \frac{g_1}{g_2} \right).
\]

Eliminating \(p_t\) using the governing equation (3.4), we have

\[
p_{xx} + \sqrt{-\frac{g_2}{2}} \left( 3p - 1 - \frac{g_1}{g_2} \right) p_x - \frac{1}{2} g_2 p (p - 1) \left( p - \frac{g_1}{g_2} \right) = 0.
\]

Via the Hopf-Cole transformation, \(p = \sqrt{\frac{g}{u_x}}\), this becomes

\[
u_{xxx} - \sqrt{-\frac{g_2}{2}} \left( 1 + \frac{g_1}{g_2} \right) u_{xx} - \frac{1}{2} g_1 u_x = 0,
\]

which has the solution

\[
u(x, t) = c_1(t) + c_2(t) \exp \left( \sqrt{-\frac{g_2}{2}} x \right) + c_3(t) \exp \left( \frac{-g_1}{\sqrt{-2g_2}} x \right).
\]

To find an expression for \(p(x, t)\) we invert the Hopf-Cole transformation to find

\[
p(x, t) = \frac{c_2(t) \exp \left( \sqrt{-\frac{g_2}{2}} x \right) + \frac{g_1}{g_2} c_3(t) \exp \left( \frac{-g_1}{\sqrt{-2g_2}} x \right)}{c_1(t) + c_2(t) \exp \left( \sqrt{-\frac{g_2}{2}} x \right) + c_3(t) \exp \left( \frac{-g_1}{\sqrt{-2g_2}} x \right)}
\]

where \(c_1(t), c_2(t)\) and \(c_3(t)\) are determined by requiring that this solution satisfies the invariant surface condition (3.6). The final form of the new solution to the
Fitzhugh-Nagumo equation (3.4) is
\[
p(x, t) = \frac{c_1 \exp \left( \sqrt{-\frac{g_1}{2}} x - \frac{g_2}{2} t \right) + c_2 \frac{g_1}{g_2} \exp \left( \frac{-g_1}{\sqrt{-2g_2}} x - \frac{g_1^2}{2g_2} t \right)}{\exp (-g_1 t) + c_1 \exp \left( \sqrt{-\frac{g_1}{2}} x - \frac{g_2}{2} t \right) + c_2 \exp \left( \frac{-g_1}{\sqrt{-2g_2}} x - \frac{g_1^2}{2g_2} t \right)},
\]
(3.9)
where \(c_1\) and \(c_2\) are constants.

We now impose Dirichlet boundary conditions so that the origin of the new coordinate system follows the point where \(p(x, t) = 0\). This implies that the accelerating reference frame (3.1) should be defined by
\[
\dot{x} = x + w(t) \quad ; \quad \dot{t} = t
\]
\[
w(t) = \frac{g_1 + g_2}{\sqrt{-2g_2}} - \frac{\sqrt{-2g_2}}{g_1 - g_2} \ln \left( \frac{-c_1 g_2}{c_2 g_1} \right)
\]
(3.10)
so that the new reference frame has constant velocity.

In terms of the original coordinates, the governing gene transport equation is (2.12) with \(\partial \ln \rho / \partial x = \eta'(t) = w'(t)/2\). This equation has the solution
\[
p(x, t) = \frac{c_1 \exp \left( \sqrt{-\frac{g_2}{2}} x \right) - c_2 \exp \left( \frac{-g_1}{\sqrt{-2g_2}} x \right)}{\left( -\frac{c_1 g_2}{c_2 g_1} \right)^{\frac{-g_2}{g_1 - g_2}} \exp \left( -\frac{3}{2} g_1 t \right) + c_1 \exp \left( \sqrt{-\frac{g_2}{2}} x \right) - c_2 \frac{g_2}{g_1} \exp \left( \frac{-g_1}{\sqrt{-2g_2}} x \right)}
\]
(3.11)
In the limit as \(t \to \infty\), the solution (3.11) reduces to
\[
p = \frac{1 - \exp \left( \frac{g_2 - g_1}{\sqrt{-2g_2}} x \right)}{1 - \frac{g_2}{g_1} \exp \left( \frac{g_2 - g_1}{\sqrt{-2g_2}} x \right)}.
\]
(3.12)
The solution (3.11) is shown in Figure 3.2 (with \(c_1 = c_2 = 1\)). The birth rates have been chosen so that individuals that are homozygous in the allele in question...
Figure 3.2: Solution (3.11) at times $t = 0, 5$ and as $t \to \infty$ to the Fitzhugh-Nagumo equation with a convection term (2.12), subject to Dirichlet boundary conditions.

$(A_1)$ have the greatest advantage, and those individuals that are homozygous in the second allele $(A_2)$ are the most disadvantaged ($\gamma_{11} = 0.9$, $\gamma_{12} = 0.3$, $\gamma_{22} = 0.1$ so that $g_1 = 0.2$ and $g_2 = -0.4$). At $t = 0$ the graph shows a population which is fixed for the allele in question at the right hand end of the range. The boundary condition $p(0, t) = 0$ means that the proportion of the allele in question remains fixed at zero at the left boundary. This could occur, for example, by continuous selective culling by pest controllers. As time progresses, the frequency can be seen to increase to the limiting steady state expressed above.

The solution (3.9) to the ordinary Fitzhugh-Nagumo equation (3.4), approaches a travelling wave as $t \to \infty$. As $x \to \infty$, $p(x, t) \to p_+ = 1$ and as $x \to -\infty$,
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$p(x,t) \rightarrow p_- = g_1/g_2$ so that the travelling wave joins the stable constant solutions $g_1/g_2$ and 1, and passes through the unstable constant solution $p(x,t) = 0$. Since both $p_+$ and $p_-$ are stable, this is referred to as a bistable situation [77]. There are well established results [77] for travelling wave solutions that state that in the bistable case for the particular situation in which there is exactly one constant solution in the interval $(p_+, p_-)$, then the wave exists and there is a unique value for the wavespeed, $c$. In this case, we can see from (3.10) that the solution (3.9) approaches a travelling wave with speed $c = (g_1 + g_2)/\sqrt{-2g_2}$.

Solutions (3.7) and (3.9) are the same as those found by Chen and Guo [17] using the Painlevé approach.

3.3 Stability of the nonclassical symmetry solutions

Stability discussions are important when modelling biological situations, or indeed any “real world” situation, be it in the field of biology, chemistry, physics or engineering. Solutions that are stable relative to small perturbations in the initial conditions are the most physically realistic. Although the stable solutions are the most interesting physically [4], unstable solutions are also interesting and worthwhile investigating, especially from a mathematical point of view. They often form “watersheds” or boundaries between basins of attraction [54], whereby the solution that
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evolves depends on the relation of the initial conditions to the unstable solution.

For this reason we investigate the stability of the constant solutions and the nonclassical symmetry solutions found in the previous section.

We use linear stability analysis to examine the stability of the constant solutions to the Huxley (3.3) and Fitzhugh-Nagumo (3.4) equations. We also use linear stability analysis and a maximum principle to determine the stability of the nonclassical symmetry solutions (3.7) and (3.9).

The Huxley equation (3.3) has two constant solutions, \( p(x, t) = 0 \) and \( 1 \). Linear stability analysis shows that \( p(x, t) = 0 \) is an unstable solution, whereas \( p(x, t) = 1 \) is a stable solution.

To determine the stability of solution (3.7) to the Huxley equation with \( g > 0 \), we perform a linear stability analysis. Let

\[ p(x, t) = P(x, t) + q(x, t) \]

where \( P(x, t) \) is the particular solution (3.7). \( q(x, t) \) is a perturbation resulting from a change in initial conditions and satisfies

\[ |q(x, \tau)| \leq M \quad \text{and} \quad q(x, t) \to 0 \quad \text{as} \quad x \to \pm \infty, \]

where \( \tau \) is yet to be determined. Substituting this into the Huxley equation (3.3) we obtain the following equation for \( q(x, t) \),

\[ q_t = q_{xx} + qg(2P - 3P^2). \]
We now define the operator

\[ Lq = q_t - q_{xx} - qf(x, t), \]

where \( f(x, t) = g(2P - 3P^2) \). It is possible to show that there is a number \( \tau \) such that for \( t > \tau \), \( f(x, t) < -\epsilon \) where \( \epsilon \) is a positive constant (see Appendix B).

Consider

\[ v(x, t) = -Me^{\lambda \tau} e^{-\lambda t} \pm q(x, t), \]

where \( \lambda \) is a positive constant, so that

\[ v(x, \tau) = -Me^{\lambda \tau} \pm q(x, \tau) \leq 0 \]

and

\[ v(x, t) \to -Me^{\lambda \tau} e^{-\lambda t} < 0 \quad \text{as} \quad x \to \pm \infty. \]

We can now write

\[
Lv = \lambda \varepsilon^\lambda e^{-\lambda t} + Me^{\lambda \tau} e^{-\lambda t} f(x, t) \\
= Me^{\lambda \tau} e^{-\lambda t} (\lambda + f(x, t)) \\
\leq 0 \quad \text{provided} \quad \lambda < \epsilon.
\]

Then by the maximum principle [63],

\[ v(x, t) \leq 0 \quad \text{for all} \quad x, t > \tau. \]
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Thus,

$$|q(x, t)| \leq Me^{\lambda t}e^{-\lambda t} \to 0 \quad \text{as} \quad t \to \infty,$$

so that the perturbation decays exponentially and the solution (3.7) is stable.

We can also use the program PDETWO [51] described in Chapter 2 to introduce a perturbation to the initial conditions. This numerical analysis also suggests that the solution (3.7) is stable.

The Fitzhugh-Nagumo equation has three constant solutions, $p(x, t) = 0, 1$ and $g_1/g_2$. Linear stability analysis shows that (with $g_1/g_2 < 0$) $g_1/g_2$ and 1 are stable, while 0 is unstable. As $x \to \infty$ in solution (3.9), $p(x, t) \to 1$ and as $x \to -\infty$, $p(x, t) \to g_1/g_2$, so that the solution joins the stable constant solutions $g_1/g_2$ and 1, and passes through the unstable constant solution $p = 0$.

To learn more about the solution (3.9) to the Fitzhugh-Nagumo equation with $g_1 > 0$, $g_2 < 0$, we again use linear stability analysis. Let

$$p(x, t) = P(x, t) + q(x, t)$$

where $P(x, t)$ is the particular solution (3.9), and $q(x, 0)$ is a perturbation in the initial conditions. Substituting this into the Fitzhugh-Nagumo equation (3.4) we obtain the following equation for $q(x, t)$,

$$q_t = q_{xx} + q \left( g_1 - 2(g_1 + g_2)P + 3g_2P^2 \right).$$
We now define the operator
\[
Lq = q_t - q_{xx} - q h(x, t),
\]
where \( h(x, t) = g_1 - 2(g_1 + g_2)P + 3g_2P^2 \). Recall \( g_1 > 0, g_2 < 0 \). It is possible to show that the function \( h(x, t) \) has a maximum in \( x \) for each \( t \) such that (see Appendix B)
\[
h_{\text{max}} = \frac{1}{3g_2} \left( 3g_1g_2 - (g_1 + g_2)^2 \right) > 0.
\]
Since the function \( h(x, t) \) has a maximum in \( x \) for each \( t \) that is greater than zero, the solution (3.9) is not likely to be asymptotically stable.

Once again, we can use the program PDE TWO [51] to introduce a perturbation in the initial conditions. This numerical analysis also suggests the solution (3.9) is unstable.
Chapter 4

Extending the model

To date there has been a great deal of interest in developing equations to describe the changes in frequency of alleles in a population that has two possible alleles at the locus in question (for example [6, 9, 27, 71, 72, 73]). In particular, some have studied the advance of a mutant advantageous gene through a population (for example [28, 61]). Very few authors have examined situations in which there are greater than two possible alleles at the locus in question (there is a limited number who have studied this situation using stochastic methods, for example [48]). In this chapter we are interested in the case in which there is a total of three possible alleles at the locus in question, resulting in six possible genotypes in the population. A system of reaction-diffusion-convection equations can be developed to describe this situation.

Many of the techniques used in the study of reaction-diffusion equations cannot
easily be extended to the study of systems of equations. It is only in recent times that new methods are becoming available that enable the features of a system of equations to be analysed. This is perhaps one of the reasons why only the most simple cases of gene invasion have been studied to date.

After developing the system of reaction-diffusion equations, we find a new exact travelling wave solution using the method of Rodrigo and Mimura [66]. We then examine the spread of a new advantageous allele. The model shows that for appropriate values of the reproductive success rates, the frequency of a new advantageous gene increases at the expense of the two original alleles and spreads throughout the range of the population.

Once again, we assume that all genotypes have a similar death rate and that any differences in fitness and survival rates between the different phenotypes are attributed to variations in reproductive success rates. We also assume genotype independent migration rates and, without loss of generality, set the diffusion coefficient to one.

4.1 Formulation of the model for three possible alleles at the locus in question

In order to find expressions describing the change in allelic frequencies, we first write equations describing the change in frequency of each of the genotypes. We denote
the three alleles by $A_1$, $A_2$, $A_3$, and the six possible genotypes by $A_1A_1$, $A_1A_2$, $A_1A_3$, $A_2A_2$, $A_2A_3$, $A_3A_3$. Denoting the frequency of individuals of genotype $A_iA_j$ by $\rho_{ij}(x,t)$, the six genotype equations are then written as

\[
\begin{align*}
\frac{\partial \rho_{11}}{\partial t} &= \frac{\partial^2 \rho_{11}}{\partial x^2} - \mu \rho_{11} + \gamma_{11} \rho_{11}^2 \\
\frac{\partial \rho_{12}}{\partial t} &= \frac{\partial^2 \rho_{12}}{\partial x^2} - \mu \rho_{12} + 2\gamma_{12} \rho_{12} \rho_{21} \\
\frac{\partial \rho_{13}}{\partial t} &= \frac{\partial^2 \rho_{13}}{\partial x^2} - \mu \rho_{13} + 2\gamma_{13} \rho_{11}(1 - \rho_{11} - \rho_{21}) \\
\frac{\partial \rho_{22}}{\partial t} &= \frac{\partial^2 \rho_{22}}{\partial x^2} - \mu \rho_{22} + \gamma_{22} \rho_{22}^2 \\
\frac{\partial \rho_{23}}{\partial t} &= \frac{\partial^2 \rho_{23}}{\partial x^2} - \mu \rho_{23} + 2\gamma_{23} \rho_{22}(1 - \rho_{11} - \rho_{21}) \\
\frac{\partial \rho_{33}}{\partial t} &= \frac{\partial^2 \rho_{33}}{\partial x^2} - \mu \rho_{33} + \gamma_{33}(1 - \rho_{11} - \rho_{21})^2 
\end{align*}
\]

where $\rho_i(x,t)$ is the frequency of allele $A_i$, which can be expressed as

\[
\begin{align*}
p_1 &= \frac{2\rho_{11} + \rho_{12} + \rho_{13}}{2\rho}, \quad p_2 = \frac{\rho_{12} + 2\rho_{22} + \rho_{23}}{2\rho} \quad \text{and} \quad p_3 = 1 - p_1 - p_2,
\end{align*}
\]

$\rho(x,t) = \rho_{11}(x,t) + \rho_{12}(x,t) + \rho_{13}(x,t) + \rho_{22}(x,t) + \rho_{23}(x,t) + \rho_{33}(x,t)$ is the total population density, $\mu$ is the common death rate, and $\gamma_{ij}$ is the reproductive success rate of individuals with genotype $A_iA_j$ (see the discussion in Section 2.1 concerning the common death rate and different reproductive success rates).

Remarkably, these six equations collapse into two independent equations describing the change in frequency of two of the alleles (see Appendix C for details). We
also include a trivial balance equation:

\[
\frac{\partial p_1}{\partial t} = \frac{\partial^2 p_1}{\partial x^2} + \frac{2 \partial \rho}{\partial x} \frac{\partial p_1}{\partial x} + \Phi(p_1, p_2),
\]

\[
\frac{\partial p_2}{\partial t} = \frac{\partial^2 p_2}{\partial x^2} + \frac{2 \partial \rho}{\partial x} \frac{\partial p_2}{\partial x} + \Psi(p_1, p_2),
\]

\[
p_3 = 1 - p_1 - p_2,
\]

with

\[
\Phi(p_1, p_2) = p_1(\gamma_{13} - \gamma_{33}) + p_1^2(\gamma_{11} - 3\gamma_{13} + 2\gamma_{33}) + p_1^3(-\gamma_{11} + 2\gamma_{13} - \gamma_{33}) + p_1 p_2(\gamma_{12} - \gamma_{13} - 2\gamma_{23} + 2\gamma_{33}) + p_2^2(-2\gamma_{12} + 2\gamma_{13} + 2\gamma_{23} - 2\gamma_{33}) + p_1 p_2^2(-\gamma_{22} + 2\gamma_{23} - \gamma_{33}),
\]

and

\[
\Psi(p_1, p_2) = p_2(\gamma_{23} - \gamma_{33}) + p_2^2(\gamma_{22} - 3\gamma_{23} + 2\gamma_{33}) + p_2^3(-\gamma_{22} + 2\gamma_{23} - \gamma_{33}) + p_1 p_2(\gamma_{12} - 2\gamma_{13} - \gamma_{23} + 2\gamma_{33}) + p_1 p_2^2(-2\gamma_{12} + 2\gamma_{13} + 2\gamma_{23} - 2\gamma_{33}) + p_1^2 p_2(-\gamma_{11} + 2\gamma_{13} - \gamma_{33}).
\]

Equations (4.3) are a system of reaction-diffusion-convection equations with cubic nonlinearities. The convection terms are due to the migratory diffusive flux of the total population.

Thus far, we have made no assumptions about dominance, or the advantage afforded by possessing a particular allele. This system of reaction-diffusion-convection equations (4.3) can therefore be used to examine the advance of a recessive advantageous mutant (a similar, but more complicated, case to that of Fisher’s) or simply to look at changing gene frequencies in a population.
Chapter 4: Extending the model

Note that if we set $\gamma_{13} = \gamma_{12}$ and $\gamma_{23} = \gamma_{33}$, so that genotypes $A_1A_2$ and $A_1A_3$, and $A_2A_2$, $A_2A_3$ and $A_3A_3$ are indistinguishable, then equation (4.3) reduces to equation (2.12).

4.2 A travelling wave solution

In order to find travelling wave solutions to equations (4.3) we first transform the convective term to zero by changing to an accelerating reference frame, using the same method as that used in Chapter 3. Once again, we find that by setting

$$\bar{x} = x + 2\eta(t) \quad ; \quad \bar{t} = t,$$

where $\eta'(t) = \partial \ln \rho / \partial x$, the convective terms are transformed to zero. This means that if the total population density takes the form given by (3.2), the gene frequency equations become (after dropping the bars for convenience)

$$\frac{\partial p_1}{\partial t} = \frac{\partial^2 p_1}{\partial x^2} + \Phi(p_1, p_2),$$
$$\frac{\partial p_2}{\partial t} = \frac{\partial^2 p_2}{\partial x^2} + \Psi(p_1, p_2).$$

In order to remove the convective term, many authors assume the total population density to be constant in space. The restriction (3.2), while still admitting the common choice of population density being uniform in either space ($\partial \rho / \partial x = 0$ if $\eta(t)$ is constant), or time ($\partial \rho / \partial t = 0$ if $\rho_0(t)$ is constant and $\eta(t)$ is linear), allows a slightly more general form of the total population density.
To look for exact travelling wave solutions, we first rewrite equations (4.4) in terms of the travelling wave coordinate $z$, where $z = x - ct$, where $c$ is the wave speed. Setting $p_i(x,t) = \bar{p}_i(x - ct)$ in (4.4) and dropping the bars for convenience, we have

\[
\frac{d^2p_1}{dz^2} + c\frac{dp_1}{dz} + \Phi(p_1, p_2) = 0,
\]

\[
\frac{d^2p_2}{dz^2} + c\frac{dp_2}{dz} + \Psi(p_1, p_2) = 0.
\]

(4.5)

The system of equations (4.5) has seven constant solutions, $(p_1, p_2) = (0,0), (0,1), (0,\alpha), (1,0), (\beta,0), (r_1, r_2), (s_1, s_2)$, where $\beta, r_1, r_2, s_1, s_2$ are complicated expressions involving the $\gamma_{ij}$, and $\alpha$ is given below (see Appendix D for details). In order to find a solution to the system of equations, we choose the boundary conditions to be

\[
(p_1, p_2)(-\infty) = (1, 0),
\]

\[
(p_1, p_2)(\infty) = (0, \alpha),
\]

(4.6)

where

\[
\alpha = \frac{\gamma_{23} - \gamma_{33}}{-\gamma_{22} + 2\gamma_{23} - \gamma_{33}}, \quad \text{and we require} \quad 0 \leq \alpha \leq 1.
\]

This means that at $t = 0$, at the right hand end of the range, allele $A_1$ will not be present, allele $A_2$ will have frequency $\alpha$ and $A_3$ will have frequency $1 - \alpha$. The left hand end of the range will be fixed for allele $A_1$. Choosing these constant solutions as boundary conditions (over the other five constant solutions) ensures that each of the three alleles is present at some time and place. Solutions can also be found by choosing the other constant solutions as boundary conditions, however the solutions
obtained are very similar to each other. An example of these other solutions is given in Appendix E.

Following [66], we look for solutions that satisfy

$$\frac{dp_1}{dz} = F(p_1), \quad p_2 = G(p_1),$$

choosing the new independent variable to be $p_1$. We could also have chosen $p_2$ to be the independent variable and assumed that

$$\frac{dp_2}{dz} = F(p_2), \quad p_1 = G(p_2).$$

Once again, similar solutions are obtained (see Appendix E).

Applying this transformation to equations (4.5) gives

$$F \frac{dF}{dp_1} + cF + \Phi(p_1, G) = 0, \tag{4.8}$$
$$F \frac{dG}{dp_1} + F^2 \frac{d^2G}{dp_1^2} + cF \frac{dG}{dp_1} + \Psi(p_1, G) = 0.$$

We now assume that $F$ and $G$ are polynomials in $p_1$, i.e., let

$$F(p_1) = \sum_{n=0}^{\nu} a_n p_1^n, \quad G(p_1) = \sum_{n=0}^{\sigma} b_n p_1^n,$$

where $\nu$, $\sigma$, $a_n$ and $b_n$ are constants to be determined. Substituting this into equations (4.8) gives

$$\left( \sum_{n=0}^{\nu} a_n p_1^n \right) \left( \sum_{n=1}^{\nu} n a_n p_1^{n-1} \right) + c \sum_{n=0}^{\nu} a_n p_1^n + \Phi \left( p_1, \sum_{n=0}^{\sigma} b_n p_1^n \right) = 0,$$
$$\left( \sum_{n=0}^{\nu} a_n p_1^n \right) \left( \sum_{n=1}^{\nu} n b_n p_1^{n-1} \right) + \left( \sum_{n=0}^{\nu} a_n p_1^n \right)^2 \left( \sum_{n=2}^{\sigma} n(n-1) b_n p_1^{n-2} \right)$$
$$+ c \left( \sum_{n=0}^{\nu} a_n p_1^n \right) \left( \sum_{n=1}^{\nu} n b_n p_1^{n-1} \right) + \Psi \left( p_1, \sum_{n=0}^{\sigma} b_n p_1^n \right) = 0.$$
By balancing the exponents of the highest order derivative terms with the exponents of the highest order non-linear terms, we find that $\sigma = 1$ and $\nu = 2$. We can then write $F(p_1)$ and $G(p_1)$ as

$$F(p_1) = a_0 + a_1 p_1 + a_2 p_1^2,$$

$$G(p_1) = b_0 + b_1 p_1.$$

From the boundary conditions (4.6), we deduce that

$$a_0 = 0, \quad b_0 = \alpha,$$

$$a_1 = -a_2 = a, \quad b_1 = -\alpha,$$

so that

$$F(p_1) = a(p_1 - p_1^2),$$

$$G(p_1) = \alpha(1 - p_1).$$

Substituting these into equations (4.8) and equating coefficients of powers of $p_1$ to zero, we get seven equations for $a$ and $c$, which can be reduced to three independent equations:

\[
\begin{align*}
    a^2 + ca + (\gamma_{13} - \gamma_{33}) + \alpha(\gamma_{12} - \gamma_{13} - \gamma_{23} + \gamma_{33}) &= 0 \\
    2a^2 + (-\gamma_{11} + 2\gamma_{13} - \gamma_{33}) + \alpha(2\gamma_{12} - 2\gamma_{13} - \gamma_{23} + \gamma_{33}) &= 0 \\
    a^2 + ca + (-\gamma_{12} + 2\gamma_{13} + 2\gamma_{23} - 3\gamma_{33}) + \alpha(2\gamma_{12} - 2\gamma_{13} + 2\gamma_{22} - 5\gamma_{23} + 3\gamma_{33}) &= 0
\end{align*}
\]

Solving these equations, we obtain expressions for the constant $a$ and the wave speed $c$, provided that $\gamma_{12} = \gamma_{13}$ or $\gamma_{22} = \gamma_{23}$. For the purposes of this investigation, we are more interested in the first case since setting $\gamma_{22} = \gamma_{23}$ makes $\alpha = 1$, so that
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$p_1 = 0$, $p_2 = 1$ and $p_3 = 0$ at the right boundary (i.e. $p_3 = 0$ at both boundaries).

We therefore set

$$\gamma_{13} = \gamma_{12},$$

and $a$ and $c$ can be written as

$$a = -\frac{1}{\sqrt{2}} \sqrt{(\gamma_{11} - 2\gamma_{12} + \gamma_{33}) + \alpha(\gamma_{23} - \gamma_{33})},$$

$$c = \frac{1}{2a} \left[ (-\gamma_{11} + \gamma_{33}) + \alpha(\gamma_{23} - \gamma_{33}) \right],$$

with the restriction that $a$ is real. (Solving the three equations gives us two values for $a$, one positive, one negative. The negative value is chosen to satisfy the boundary conditions (4.6).)

Using (4.9), we integrate the first equation in (4.7) and substitute the result into the second to obtain

$$p_1(z) = \frac{A \exp az}{1 + A \exp az},$$

$$p_2(z) = \frac{\alpha}{1 + A \exp az},$$

where $A$ is a constant. Since the solution is invariant with respect to any shift in the coordinate system, we can choose $z = 0$ to be the point where $p_1 = 1/2$, so that a solution to the system of equations (4.5) with $\gamma_{12} = \gamma_{13}$ is

$$p_1(z) = \frac{\exp az}{1 + \exp az},$$

$$p_2(z) = \frac{\alpha}{1 + \exp az}. \tag{4.10}$$

The solution curves are shown in Figure 4.1. The birth rates have been chosen so that allele $A_1$ is advantageous ($\gamma_{11} = 0.5$, $\gamma_{12} = \gamma_{13} = 0.3$, $\gamma_{22} = 0.2$, $\gamma_{23} = 0.1$ and $\gamma_{33} = 0.25$). For these particular values, $\alpha = 3/5$, $a \approx -0.1732$ and $c \approx 0.9815.$
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The waves are moving to the right, so that the advantageous allele $A_1$ is shown to take over the range at the expense of the other two alleles, $A_2$ and $A_3$. This direction of wave travel is as expected since we have chosen the values of the $\gamma_{ij}$ so that $A_1$ is advantageous.

![Graph showing travelling wave solution](image)

Figure 4.1: Travelling wave solution (4.10) for the system of equations (4.5). The waves are moving to the right.

### 4.2.1 Direction of wave travel

It is important to determine the direction in which the wave is travelling since this will determine whether a new gene spreads throughout the population or recedes and is lost. A “Z” shaped wave for the frequency of allele $A_1$ (like the one in Figure 4.1) must be forward moving in order for the allele to spread through the population,
so that $c > 0$. This requires that

$$(-\gamma_{11} + \gamma_{33}) + \alpha(\gamma_{23} - \gamma_{33}) < 0.$$ 

This condition is easily satisfied by many different values of the $\gamma_{ij}$.

### 4.3 Stability

#### 4.3.1 Stability of the constant solutions

The system of equations (4.5) has seven constant solutions, $(p_1, p_2) = (0,0), (0,1), (0,\alpha), (1,0), (\beta,0), (r_1, r_2), (s_1, s_2)$, where $\alpha$ has already been defined and $\beta, r_1, r_2, s_1, s_2$ are complicated expressions involving the $\gamma_{ij}$ (see Appendix D for further details). The stability of these solutions can be found by considering the eigenvalue problem $F'(q)u = \lambda u$ where $F(p) = (\Phi(p_1, p_2), \Psi(p_1, p_2))$ and $q$ is a solution of $F(q) = 0$ [77]. We find that $(0,0)$ and $(0,1)$ are unstable and $(1,0)$ is stable. The eigenvalues for the other constant solutions depend in a complicated way on the $\gamma_{ij}$ and it is not easy to determine their sign. (See Appendix D for working.)

#### 4.3.2 Stability of the travelling wave solution

The problem of stability for travelling wave solutions to systems of equations is not straightforward, and cannot be immediately inferred from the scalar case [75]. The method usually used for the scalar case becomes so complicated for systems that it
can only be used in a limited number of cases.

Sattinger [67] introduced a method to investigate the stability of travelling wave solutions to systems of nonlinear parabolic equations which was further developed by Takase and Sleeman [75]. The method is based on investigating the spectrum of the linear operator which is obtained by linearising the governing equation as follows: let \( \mathbf{P}(z) = \mathbf{P}(x - ct) \) be the travelling wave solution and \( q(x, t) \) be a perturbation. Looking for solutions that are perturbations of the travelling wave solution, we substitute

\[
\mathbf{p}(x, t) = \mathbf{P}(x - ct) + q(x, t)
\]

into the governing system of equations. After transforming this equation to travelling wave coordinates we obtain the following equation for \( q \):

\[
q_t = Lq + R(q),
\]

where \( L \) is a second order linear differential operator and \( R \) is a first order nonlinear operator. We must then show that the essential spectrum of \( L \) is contained in the negative half-complex plane and that all the eigenvalues of \( L \) (except zero) have negative real parts.

For our system of equations (4.4) this is not an easy task. The eigenvalues of \( L \) contain expressions involving the difference between two or more of the reproductive success rates (\( \gamma_{ij} \)). In general we are unable to comment about whether or not these differences are positive or negative.
Chapter 4: Extending the model

The most recent and comprehensive investigation on stability of systems of reaction-diffusion equations is that by Volpert and Volpert [77]. The first step in determining the stability of a solution is to show that the system is locally monotone. The system (4.5) is defined as locally monotone if for any solution of the equation

\[ F_i(p) = 0, \]

we have

\[ \frac{\partial F_i(p)}{\partial p_k} \geq 0, \quad k \neq i \quad (4.11) \]

for all \( p \) in the neighbourhood of the solution [77]. Once again, expression (4.11) involves differences between the \( \gamma_{ij} \), so that for our particular system, we are unable to say whether or not this inequality (4.11) is satisfied in general, and are therefore unable to comment on the stability of our solution (4.10) for the system of equations.

One approach that could possibly enable us to discover more about the stability of the travelling wave solution, is to use the Evan’s function to solve the linear stability problem (see [3], [34] or [60]). However, this problem is beyond the scope of this thesis and will be further examined in the future.
4.4 Gene dispersion equation with any number of competing alleles

In this section, we extend the arguments of section 4.1 to describe the situation in which there is any number of pre-existing alleles and one new allele at the locus in question. Equation (2.12) can be shown to hold true using proof by induction. The assumption of partial dominance of the original alleles must be assumed from the beginning, so that all those genotypes possessing no copies of the new gene have reproductive success rate \( \gamma_{22} \), those genotypes possessing one copy of the new gene have reproductive success rate \( \gamma_{12} \) and those genotypes possessing two copies of the new gene have reproductive success rate \( \gamma_{11} \).

We then set up the proof as follows. First consider the case in which there is a total of \( n \) alleles ((\( n - 1 \) original alleles and one new allele, giving rise to \( \frac{1}{2}(n^2 + n) \) possible different genotypes). Let \( A_1 \) be the new gene.

Let \( p_1^{(n)}(x, t), \rho_{ij}^{(n)}(x, t) \) and \( \rho^{(n)}(x, t) \) represent the allele proportions, the genotype densities and the total population density for the case of \( n \) competing alleles. We can now write \( \frac{1}{2}(n^2 + n) \) genotype equations for the case in which there is a total of \( n \) alleles as follows:

\[
\frac{\partial p_{11}^{(n)}}{\partial t} = \frac{\partial^2 \rho_{11}^{(n)}}{\partial x^2} - \mu \rho_{11}^{(n)} + \gamma_{11} p_1^{(n)} \rho^{(n)}.
\]
for $j = 2, 3, \ldots, n$

$$\frac{\partial \rho_{ij}^{(n)}}{\partial t} = \frac{\partial^2 \rho_{ij}^{(n)}}{\partial x^2} - \mu \rho_{ij}^{(n)} + 2 \gamma_{12} p_1^{(n)} p_j^{(n)} \rho^{(n)}, \quad (4.12)$$

for $i = 2, 3, \ldots, n$, $j = i, i+1, \ldots, n$

$$\frac{\partial \rho_{ij}^{(n)}}{\partial t} = \frac{\partial^2 \rho_{ij}^{(n)}}{\partial x^2} - \mu \rho_{ij}^{(n)} + (2 - \delta_{ij}) \gamma_{22} p_i^{(n)} p_j^{(n)} \rho^{(n)},$$

with the total population density

$$\rho^{(n)} = \sum_{i=1}^{n} \sum_{j=i}^{n} \rho_{ij}.$$ 

The second summation for the third equation runs from $j = i$ to $j = n$ since an individual with genotype $A_i A_j$ is indistinguishable from an individual with genotype $A_j A_i$. The property that there are two possible ways that an individual can have the $A_i$ and the $A_j$ alleles (i.e. $A_i A_j$ or $A_j A_i$) except when $j = i$, is taken into account by the Kronecker delta in the genotype equations. For convenience we express the gene frequencies as

$$p_i^{(n)} = \frac{1}{2 \rho^{(n)}} \left[ \sum_{j=1}^{i} \rho_{ji} + \sum_{j=i}^{n} \rho_{ij} \right].$$

Since we will use proof by induction, we now consider the case in which there is a total of $n+1$ possible alleles at the locus in question. Let $p_i^{(n+1)}(x, t)$, $\rho_{ij}^{(n+1)}(x, t)$ and $\rho^{(n+1)}(x, t)$ represent the allele proportions, the genotype densities and the total population density for the case of $n+1$ competing alleles. Given the genotype densities $\rho_{ij}^{(n+1)}(x, t)$ at a particular time $t$, we may notionally extract those individuals
that have no copy of the \((n + 1)^{th}\) allele. Now temporarily consider reproduction among these individuals without considering the offspring from any of the parents that possess one or more copies of the \((n + 1)^{th}\) allele. This contribution to the new population evolves as if it were contained in a community with no \((n + 1)^{th}\) alleles. That is, it obeys equation (2.12) for \(p_i^{(n)}\), with \(\rho\) replaced by \(\rho^{(n)}\), interpreted here as the subpopulation of \(\rho^{(n+1)}\) that excludes individuals carrying the \((n + 1)^{th}\) allele. This means that the genotype frequencies are the same for the case in which there are \(n\) alleles and the case in which there are \((n + 1)\) alleles, however the \textit{total population density} increases, which means that the allele frequencies change since they are \textit{proportions}. We can then write

\[
\rho_{ij}^{(n)}(x, t) = \rho_{ij}^{(n+1)}(x, t) = \rho_{ij}(x, t), \quad \forall i, j \neq n + 1,
\]

\[
\rho^{(n)}(x, t) \neq \rho^{(n+1)}(x, t),
\]

\[
p_i^{(n)}(x, t) \neq p_i^{(n+1)}(x, t).
\]

Using \(n\) as the index for the sequence of inductive hypotheses, we assume that

\[
\frac{\partial p_1^{(n)}}{\partial t} = \frac{\partial^2 p_1^{(n)}}{\partial x^2} + \frac{2}{\rho^{(n)}} \frac{\partial \rho^{(n)}}{\partial x} \frac{\partial p_1^{(n)}}{\partial x} + p_1^{(n)}(1 - p_1^{(n)})([\gamma_{12} - \gamma_{22}] - p_1^{(n)}(-\gamma_{11} + 2\gamma_{12} - \gamma_{22})]
\]

\[(4.13)\]

holds true (equation (2.12)). Note that this has already been established for \(n = 2\) and \(n = 3\).

We then write \(\frac{1}{2}((n + 1)^2 + (n + 1))\) genotype equations for the case in which
there is a total of \((n+1)\) alleles:

\[
\frac{\partial \rho_{11}}{\partial t} = \frac{\partial^2 \rho_{11}}{\partial x^2} - \mu \rho_{11} + \gamma_{11} \rho_1^{(n+1)} \rho_{11}^{(n+1)},
\]

for \(j = 2, 3, \ldots, n + 1\)

\[
\frac{\partial \rho_{1j}}{\partial t} = \frac{\partial^2 \rho_{1j}}{\partial x^2} - \mu \rho_{1j} + 2 \gamma_{12} \rho_1^{(n+1)} \rho_j^{(n+1)} \rho_{1j}^{(n+1)},
\]

(4.14)

for \(i = 2, 3, \ldots, n + 1, j = i, i + 1, \ldots, n + 1\)

\[
\frac{\partial \rho_{ij}}{\partial t} = \frac{\partial^2 \rho_{ij}}{\partial x^2} - \mu \rho_{ij} + (2 - \delta_{ij}) \gamma_{22} \rho_i^{(n+1)} \rho_j^{(n+1)} \rho_{ij}^{(n+1)},
\]

with the total population density

\[
\rho^{(n+1)} = \sum_{i=1}^{n+1} \sum_{j=1}^{n+1} \rho_{ij},
\]

and allele frequency

\[
p_i^{(n+1)} = \frac{1}{2\rho^{(n+1)}} \left[ \sum_{j=1}^{i} \rho_{ji} + \sum_{j=1}^{n+1} \rho_{ij} \right].
\]

We can also write relationships between the two different cases:

\[
\rho^{(n+1)} = \rho^{(n)} + \sum_{i=1}^{n+1} \rho_i^{(n+1)},
\]

\[
p_i^{(n+1)} = \frac{2p_i^{(n)} \rho_i^{(n)} + \rho_i^{(n+1)}}{2\rho^{(n+1)}},
\]

and in particular

\[
p_1^{(n+1)} = \frac{2p_1^{(n)} \rho_1^{(n)} + \rho_{1(n+1)}}{2\rho^{(n+1)}}.
\]

(4.15)

Taking the time derivative of the above expression for \(p_1^{(n+1)}\), we can show that equation (2.12) holds true for the case of \((n+1)\) alleles, providing (4.13) is true.
Differentiating expression (4.15) with respect to \( t \), we obtain (after some working) the following expression

\[
\frac{\partial p_1^{(n+1)}}{\partial t} = \frac{\rho^{(n)}}{\rho^{(n+1)}} \left[ \frac{\partial^2 p_1^{(n)}}{\partial x^2} + \frac{2}{\rho^{(n)}} \frac{\partial \rho^{(n)}}{\partial x} \frac{\partial p_1^{(n)}}{\partial x} \right] + p_1^{(n)} \left(1 - p_1^{(n)}\right) \left[ (\gamma_{12} - \gamma_{22}) - p_1^{(n)}( -\gamma_{11} + 2\gamma_{12} - \gamma_{22}) \right] + \frac{p_1^{(n)}}{\rho^{(n+1)}} \frac{\partial \rho^{(n)}}{\partial t} + \frac{1}{2\rho^{(n+1)}} \frac{\partial \rho_1^{(n+1)}}{\partial t} - \frac{p_1^{(n+1)}}{\rho^{(n+1)2}} \frac{\partial \rho^{(n+1)}}{\partial t} - \frac{\rho_1^{(n+1)}}{2\rho^{(n+1)2}} \frac{\partial \rho^{(n+1)}}{\partial t}.
\]

(4.16)

Rearranging (4.15), and differentiating twice with respect to \( x \), it can be shown that

\[
\frac{\rho^{(n)}}{\rho^{(n+1)}} \left( \frac{\partial^2 p_1^{(n)}}{\partial x^2} + \frac{2}{\rho^{(n)}} \frac{\partial \rho^{(n)}}{\partial x} \frac{\partial p_1^{(n)}}{\partial x} \right) = \frac{\partial^2 p_1^{(n+1)}}{\partial x^2} + \frac{2}{\rho^{(n+1)}} \frac{\partial \rho^{(n+1)}}{\partial x} \frac{\partial p_1^{(n+1)}}{\partial x} - \frac{p_1^{(n)}}{\rho^{(n+1)}} \frac{\partial^2 \rho^{(n)}}{\partial x^2} + \frac{p_1^{(n+1)}}{\rho^{(n+1)}} \frac{\partial^2 \rho^{(n+1)}}{\partial x^2} - \frac{1}{2\rho^{(n+1)}} \frac{\partial^2 \rho_1^{(n+1)}}{\partial x^2}.
\]

Substituting this into (4.16) and using the fact that

\[
\frac{p_1^{(n)} \rho^{(n)}}{\rho^{(n+1)2}} + \frac{\rho_1^{(n+1)}}{2\rho^{(n+1)2}} = \frac{p_1^{(n+1)}}{\rho^{(n+1)}}
\]

(equation (4.15)) we obtain

\[
\frac{\partial p_1^{(n+1)}}{\partial t} = \frac{\partial^2 p_1^{(n+1)}}{\partial x^2} + 2\eta^{(n+1)} p_1^{(n+1)} \frac{\partial}{\partial x} + \frac{1}{\rho^{(n+1)}} \left[ p_1^{(n)} \frac{\partial \rho^{(n)}}{\partial t} - p_1^{(n)} \frac{\partial^2 \rho^{(n)}}{\partial x^2} - p_1^{(n+1)} \frac{\partial \rho^{(n+1)}}{\partial t} + p_1^{(n+1)} \frac{\partial^2 \rho^{(n+1)}}{\partial x^2} \right].
\]
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\[ + \frac{\rho^{(n)}}{\rho^{(n+1)}} \left[ p_{1}^{(n)}(1 - p_{1}^{(n)}) \left( (\gamma_{12} - \gamma_{22}) - p_{1}^{(n)}(-\gamma_{11} + 2\gamma_{12} - \gamma_{22}) \right) \right] \]
\[ + \frac{1}{2\rho^{(n+1)}} \left[ \frac{\partial p_{1(n+1)}}{\partial t} - \frac{\partial^2 p_{1(n+1)}}{\partial x^2} \right]. \quad (4.17) \]

Since \( \rho^{(n)} = \sum_{i=1}^{n} \sum_{j=1}^{n} \rho_{ij} \), we can replace \( \partial \rho^{(n)}/\partial t - \partial^2 \rho^{(n)}/\partial x^2 \) by the sum of all the expressions given for each of the different genotypes (4.12). Similarly for \( \partial \rho^{(n+1)}/\partial t - \partial^2 \rho^{(n+1)}/\partial x^2 \) (4.14). The resulting expression contains many terms involving the death rate \( \mu \) and we now examine them separately. The coefficients of \( -\mu \) are as follows:

\[ p_{1}^{(n)} \rho^{(n)} - p_{1}^{(n+1)} \rho^{(n+1)} + \frac{1}{2} \rho_{1(n+1)} \]
\[ = p_{1}^{(n)} \rho^{(n)} - \left[ p_{1}^{(n)} \rho^{(n)} + \frac{1}{2} \rho_{1(n+1)} \right] + \frac{1}{2} \rho_{1(n+1)} \]
\[ = 0. \]

So, after substituting the expressions for each of the genotypes ((4.12) and (4.14)) into (4.17) and eliminating all terms involving the death rate \( \mu \), we obtain

\[ \frac{\partial p_{1}^{(n+1)}}{\partial t} = \frac{\partial^2 p_{1}^{(n+1)}}{\partial x^2} + \frac{2}{\rho^{(n+1)}} \frac{\partial \rho^{(n+1)}}{\partial x} \frac{\partial p_{1}^{(n+1)}}{\partial x} \]
\[ + \frac{1}{\rho^{(n+1)}} \left[ \rho^{(n)} p_{1}^{(n)}(1 - p_{1}^{(n)}) \left( (\gamma_{12} - \gamma_{22}) - p_{1}^{(n)}(-\gamma_{11} + 2\gamma_{12} - \gamma_{22}) \right) \right] \]
\[ + p_{1}^{(n)} \rho^{(n)} \gamma_{11} p_{1}^{(n)} + 2\gamma_{12} p_{1}^{(n)} \sum_{i=2}^{n} p_{i}^{(n)} \]
\[ + \gamma_{22} p_{2}^{(n)} + 2\gamma_{22} p_{2}^{(n)} \sum_{i=3}^{n} p_{i}^{(n)} \]
\[ + \ldots \]
\[ + \gamma_{22} p_{n-1}^{(n)} + 2\gamma_{22} p_{n-1}^{(n)} p_{n}^{(n)} \]
+ \gamma_{22} p_n^{(n+1)2}

\left( \gamma_{11} p_1^{(n+1)2} + 2 \gamma_{12} p_1^{(n+1)} \sum_{i=2}^{n+1} p_i^{(n+1)}

+ \gamma_{22} p_2^{(n+1)2} + 2 \gamma_{22} p_2^{(n+1)} \sum_{i=3}^{n+1} p_i^{(n+1)}

+ \cdots

+ \gamma_{22} p_n^{(n+1)2} + 2 \gamma_{22} p_n^{(n+1)} p_{n+1}^{(n+1)}

+ \gamma_{22} p_{n+1}^{(n+1)2}

\right).

Now separate this expression into the coefficients of \( \gamma_{11}, \gamma_{12} \) and \( \gamma_{22} \),

$$
\frac{\partial p_1^{(n+1)}}{\partial t} = \frac{\partial^2 p_1^{(n+1)}}{\partial x^2} + \frac{2}{\rho^{(n+1)}} \frac{\partial \rho^{(n+1)}}{\partial x} \frac{\partial p_1^{(n+1)}}{\partial x}

+ \frac{\gamma_{11}}{\rho^{(n+1)}} \left[ \rho^{(n)} p_1^{(n+1)2} - \rho^{(n+1)} p_1^{(n+1)3} \right]

+ \frac{\gamma_{12}}{\rho^{(n+1)}} \left[ \rho^{(n)} p_1^{(n)} - 3 \rho^{(n)} p_1^{(n)2} + 2 \rho^{(n)} p_1^{(n)3} + 2 \rho^{(n)} p_1^{(n)2} \sum_{i=2}^{n+1} p_i^{(n)}

- 2 \rho^{(n+1)} p_1^{(n+1)2} \sum_{i=2}^{n+1} p_i^{(n+1)} + \rho^{(n+1)} p_1^{(n+1)} \sum_{i=2}^{n+1} p_i^{(n+1)} \right]

+ \frac{\gamma_{22}}{\rho^{(n+1)}} \left[ - \rho^{(n)} p_1^{(n)} + 2 \rho^{(n)} p_1^{(n)2} - \rho^{(n)} p_1^{(n)3}

+ \rho^{(n)} p_1^{(n)} p_2^{(n)} + 2 p_2^{(n)} \sum_{i=3}^{n+1} p_i^{(n)}

+ p_3^{(n)} + 2 p_3^{(n)} \sum_{i=4}^{n+1} p_i^{(n)}

+ \cdots

+ p_{n-1}^{(n)} + 2 p_{n-1}^{(n)} p_n^{(n)}

+ p_n^{(n)2} \right).$$
$-\rho^{(n+1)} p_1^{(n+1)} \left( p_2^{(n+1)2} + 2 p_2^{(n+1)} \sum_{i=3}^{n+1} p_i^{(n+1)} \right) + p_3^{(n+1)2} + 2 p_3^{(n+1)} \sum_{i=4}^{n+1} p_i^{(n+1)} + \ldots + p_n^{(n+1)2} + 2 p_n^{(n+1)} p_{n+1}^{(n+1)} + p_{n+1}^{(n+1)2} \right].$

By expanding the sums and using the fact that $p_i^{(n)} = 1 - \sum_{i=1}^{n-1} p_i^{(n)}$ and $p_{n+1}^{(n+1)} = 1 - \sum_{i=1}^{n} p_i^{(n+1)},$ we can show that

$$\frac{\partial p_1^{(n+1)}}{\partial t} = \frac{\partial^2 p_1^{(n+1)}}{\partial x^2} + \frac{2}{\rho^{(n+1)}} \frac{\partial \rho^{(n+1)}}{\partial x} \frac{\partial p_1^{(n+1)}}{\partial x} + \frac{711}{\rho^{(n+1)}} \left[ \rho^{(n)} p_1^{(n)2} - \rho^{(n+1)} p_1^{(n+1)3} \right] + \frac{712}{\rho^{(n+1)}} \left[ \rho^{(n)} p_1^{(n)2} - \rho^{(n+1)} p_1^{(n+1)3} - 2 \rho^{(n+1)} p_1^{(n+1)2} \right] + 2 \rho^{(n+1)} p_1^{(n+1)3} + \rho^{(n+1)} p_1^{(n+1)} p_{n+1}^{(n+1)} + \rho^{(n+1)} p_1^{(n+1)} \sum_{i=1}^{n} p_i^{(n+1)} \right] + \frac{722}{\rho^{(n+1)}} \left[ -\rho^{(n+1)} p_1^{(n+1)} + 2 \rho^{(n+1)} p_1^{(n+1)2} - \rho^{(n+1)} p_1^{(n+1)3} \right].$$

Now, since $\rho_{ij}^{(n)} = \rho_{ij}^{(n+1)} \forall i, j \neq (n + 1),$ we can deduce

$$p_i^{(n)} p_j^{(n)} \rho^{(n)} = p_i^{(n+1)} p_j^{(n+1)} \rho^{(n+1)}, \quad (4.18)$$

to obtain

$$\frac{\partial p_1^{(n+1)}}{\partial t} = \frac{\partial^2 p_1^{(n+1)}}{\partial x^2} + \frac{2}{\rho^{(n+1)}} \frac{\partial \rho^{(n+1)}}{\partial x} \frac{\partial p_1^{(n+1)}}{\partial x}.$$
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\[ + \gamma_{11} \left[ p_1^{(n+1)^2} - p_1^{(n+1)^3} \right] \]
\[ + \gamma_{12} \left[ p_1^{(n+1)} - 3p_1^{(n+1)^2} + 2p_1^{(n+1)^3} \right] \]
\[ + \gamma_{22} \left[ -p_1^{(n+1)} + 2p_1^{(n+1)^2} - p_1^{(n+1)^3} \right]. \]

Then

\[ \frac{\partial p_1^{(n+1)}}{\partial t} = \frac{\partial^2 p_1^{(n+1)}}{\partial x^2} + \frac{2}{\rho^{(n+1)}} \frac{\partial \rho^{(n+1)}}{\partial x} \frac{\partial p_1^{(n+1)}}{\partial x} \]
\[ + p_1^{(n+1)} (1 - p_1^{(n+1)}) ((\gamma_{12} - \gamma_{22}) - p_1^{(n+1)} (-\gamma_{11} + 2\gamma_{12} - \gamma_{22})). \]

And since this is true for \( n = 2 \) and \( n = 3 \), we have shown that it holds true for all \( n \geq 2 \), i.e. for any total number of alleles \( n \) at the locus in question.

A similar proof can also be constructed to show that the Huxley equation is appropriate for any number of pre-existing alleles for the case where all genotypes having one or no copies of the new allele express the original phenotype, and only those individuals homozygous in the new allele express the new phenotype.

Both of these results are essentially intuitive, since assuming that there are only three different reproductive success rates (or two different reproductive success rates in the case of Huxley’s equation) effectively splits the population into three (or two) different groups, each made up of a number of different genotypes. However, this proof shows rigorously that such a population behaves in the same manner as a much simpler population made up of only three (or two) different genotypes.
Chapter 5

Including explicit spatial dependence

In this chapter we extend the problem examined in Chapter 2 to include explicit spatial dependence in the source term. For the study of changing gene frequencies, this would represent spatially dependent birth rates. This problem is worthy of attention because it is a possibility that one particular genotype might have an advantage in one part of the range, while another genotype has the advantage in the remainder of the range. The variation in the advantage that each genotype enjoys could be a result of environmental change along the length of the range. In nature things are clearly much more complex than is described by the previous simple models. This is one possible extension of the ideas already examined. Aside from being an interesting problem for population genetics, the equations that are
formulated in this chapter are interesting in themselves.

Spatial variability in the viability of different genotypes has been examined by a number of authors including Fife and Peletier [26], Fisher [29], Nagylaki [55] and Slatkin [71]. The most commonly examined case is the step environment, however the effect of gradual environmental change has also been investigated (where the advantage of one genotype is proportional to $x$). General dependence of the reproductive success rates on the spatial coordinate has not been previously studied.

In this chapter, we are not concerned with what form of spatial dependence might be the most appropriate biologically. Rather, we are more interested in studying the equations themselves to discover what forms of spatial variability will enable us to find exact solutions to our equations. To do this, we use the methods of classical Lie point symmetry analysis and nonclassical symmetry analysis. Nonclassical symmetry analysis is chosen because it has previously been used successfully to find solutions to the equations developed to describe the situation in which the source term depends on the dependent variable only (Chapter 3). Given the success of this approach in solving spatially uniform nonlinear equations, there is some hope of extending it to the spatially heterogeneous case.
5.1 Formulation of the equations with spatially dependent reproductive success rates

We return to the case of a population in which there is a total of two possible alleles at the locus in question. We denote them as \( A_1 \) and \( A_2 \), so that the possible genotypes are \( A_1A_1, A_1A_2 \) and \( A_2A_2 \). We are interested in developing an equation describing the change in frequency of one of the alleles. Using the same method as that described in Section 2.1.2, we first write equations describing the change in genotype population densities, \( \rho_{ij}(x,t) \),

\[
\begin{align*}
\frac{\partial \rho_{11}}{\partial t} &= \frac{\partial^2 \rho_{11}}{\partial x^2} - \mu \rho_{11} + \gamma_{11}(x)p^2 \rho, \\
\frac{\partial \rho_{12}}{\partial t} &= \frac{\partial^2 \rho_{12}}{\partial x^2} - \mu \rho_{12} + 2\gamma_{12}(x)p(1-p)\rho, \\
\frac{\partial \rho_{22}}{\partial t} &= \frac{\partial^2 \rho_{22}}{\partial x^2} - \mu \rho_{22} + \gamma_{22}(x)(1-p)^2 \rho,
\end{align*}
\]

where \( p(x,t) \) is the frequency of allele \( A_1 \), \( (1 - p(x,t)) \) is the frequency of allele \( A_2 \) which can be expressed as

\[
p = \frac{2\rho_{11} + \rho_{12}}{2\rho}
\]

with \( \rho(x,t) = \rho_{11}(x,t) + \rho_{12}(x,t) + \rho_{22}(x,t) \) being the total population density. \( \mu \) is the common death rate, and \( \gamma_{ij}(x,t) \) is the reproductive success rate of individuals with genotype \( A_iA_j \). Again, we have assumed that any difference in survival rates between the different genotypes can be attributed to a difference in the reproductive success rates alone.
Differentiating the above expression for $p$ with respect to $t$, and noticing that

$$2 \frac{\partial^2 \rho_{11}}{\partial x^2} + \frac{\partial^2 \rho_{11}}{\partial x^2} = 2 \rho \frac{\partial^2 p}{\partial x^2} + 4 \frac{\partial p}{\partial x} \frac{\partial p}{\partial x} + 2 \frac{\partial^2 p}{\partial x^2},$$

we obtain the following expression for the change in frequency of the $A_1$ allele,

$$\frac{\partial p}{\partial t} = \frac{\partial^2 p}{\partial x^2} + \frac{2 \partial p}{\partial x} \frac{\partial p}{\partial x} + g_1(x)p(1-p)(p-g_2(x)) \quad (5.1)$$

where

$$g_1(x) = \gamma_{11}(x) - 2\gamma_{12}(x) + \gamma_{22}(x) \quad \text{and} \quad g_2(x) = \frac{-\gamma_{12}(x) + \gamma_{22}(x)}{\gamma_{11}(x) - 2\gamma_{12}(x) + \gamma_{22}(x)}.$$

We do not consider the special case where $\gamma_{11}(x) + \gamma_{22}(x) = 2\gamma_{12}(x)$ for which (5.1) is a spatially heterogeneous version of Fisher’s quadratic equation (with an additional convective term).

For the purpose of examining this equation, we assume that the total population density is constant across the range (so that $\partial \rho/\partial x = 0$). Again, we examine two different cases: the first when $\gamma_{12}(x) = \gamma_{22}(x)$ so that $g_2(x) = 0$,

$$\frac{\partial p}{\partial t} = \frac{\partial^2 p}{\partial x^2} + g(x)p^2(1-p), \quad (5.2)$$

where $g(x) = \gamma_{11}(x) - \gamma_{22}(x)$; the second when $\gamma_{12}(x) \neq \gamma_{22}(x)$,

$$\frac{\partial p}{\partial t} = \frac{\partial^2 p}{\partial x^2} + g_1(x)p(1-p)(p-g_2(x)). \quad (5.3)$$

When $g(x)$, $g_1(x)$ and $g_2(x)$ are constant, equations (5.2) and (5.3) reduce to the Huxley (3.3) and Fitzhugh-Nagumo equations (3.4) respectively. We know that for
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this case a number of solutions exist (see Chapter 3). We now wish to discover what
other forms \( g(x) \), \( g_1(x) \) and \( g_2(x) \) can take such that group invariant solutions to
equations (5.2) and (5.3) exist.

5.2 Classical Lie point symmetries

In this section we outline some of the ideas of the theory of Lie symmetry analysis
for differential equations. The details of the theory in this section are intended as
an overview only. For more details about classical Lie point symmetry analysis the
reader is referred to Bluman and Kumei [13], Hill [38], Ibragimov [40] or Olver [57].

This technique for finding exact solutions to differential equations was first inves-
tigated by Sophus Lie in the late nineteenth century. It is based on the invariance of
a differential equation under a continuous group of symmetries. The theory of classi-
cal symmetry analysis is concerned with point symmetries of a differential equation.
Point symmetries are a group of invertible transformations that map every solution
of the differential equation to another solution of the differential equation, or the
points \((x, p)\) to the points \((x^*, p^*)\). This is in contrast to contact transformations,
in which the transformed variables also depend on the first derivatives of \(p\) with
respect to the independent variables.

The classical method of finding point symmetry reductions for a given \(n^{th}\) order
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PDE with dependent variable $p$ and $k$ independent variables $\mathbf{x}(x_1, x_2, x_3, \ldots, x_k)$,

$$
\Delta(\mathbf{x}, p, \partial p, \partial^2 p, \ldots, \partial^n p) = 0
$$

(5.4)

is to find a one-parameter group of transformations

$$
x^*_i = f_i(\mathbf{x}, p, \epsilon), \quad p^* = g(\mathbf{x}, p, \epsilon),
$$

(5.5)

which leave the governing equation (5.4) invariant. The functions (5.5) are referred to as the \textit{global form} of the group. The group can also be expressed in its \textit{infinitesimal form}

$$
x^*_i = x_i + \epsilon X_i(\mathbf{x}, p) + O(\epsilon^2),
$$

$$
p^* = p + \epsilon P(\mathbf{x}, p) + O(\epsilon^2),
$$

(5.6)

by considering the expansion of (5.5) using the Taylor series expansion about the point $\epsilon = 0$. The coefficients $X_i(\mathbf{x}, p)$ and $P(\mathbf{x}, p)$ are often referred to as the \textit{infinitesimals}, and can be written as

$$
X_i(\mathbf{x}, p) = \left( \frac{\partial x^*_i}{\partial \epsilon} \right)_{\epsilon=0}, \quad P(\mathbf{x}, p) = \left( \frac{\partial p^*}{\partial \epsilon} \right)_{\epsilon=0}.
$$

Lie showed that the transformations $\mathbf{x}^*$ and $p^*$ form a group [38]. That is, the transformations together with a group operation (often multiplication) satisfy the following properties:

(i) \textit{identity} - the value $\epsilon = 0$ characterises the identity transformation.

(ii) \textit{inversion} - the parameter $-\epsilon$ characterises the inverse transformation.
(iii) closure - if two transformations are characterised by the parameters $\epsilon$ and $\delta$ respectively, then the product transformation will also be a member of the set of transformations, and will be characterised by the parameter $\epsilon + \delta$.

We define the group operator of a one-parameter transformation group as the operator

$$\Gamma = X_i \frac{\partial}{\partial x_i} + P \frac{\partial}{\partial p},$$

(5.7)

where we sum over the repeated index. $\Gamma$ is also sometimes known as the group generator or the infinitesimal generator. An $l$-parameter transformation group has $l$ associated group operators which we will denote by $\Gamma_1, \Gamma_2, \ldots, \Gamma_l$.

5.2.1 Classical Lie point symmetries as applied to second order 1+1 dimensional PDEs

In this thesis we are primarily concerned with finding symmetries of 1+1 dimensional second order PDEs of the form

$$\Delta = p_t - p_{xx} - Q(x, t, p) = 0.$$  (5.8)

If a PDE is invariant under a point symmetry, we may transform the equation under the invariants to reduce the number of variables by one, so that we can now look for solutions to a second order ODE. If this reduced equation is invariant under a one-parameter group of transformations, we may simplify it further to obtain a
first order ODE. In this manner we may write the equation in its simplest form and attempt to construct solutions to this simpler equation. Once a solution has been found, we may invert the transformations to recover the solution to our PDE (5.8).

For these particular 1+1 dimensional PDEs (5.8), a one-parameter group of transformations may be written as

\[
\begin{align*}
    x^* &= x + \epsilon X(x, t, p) + O(\epsilon^2) \\
    t^* &= t + \epsilon T(x, t, p) + O(\epsilon^2) \\
    p^* &= p + \epsilon P(x, t, p) + O(\epsilon^2)
\end{align*}
\]  

(5.9)

with the group generator

\[
\Gamma = X \frac{\partial}{\partial x} + T \frac{\partial}{\partial t} + P \frac{\partial}{\partial p}.
\]  

(5.10)

An example of a one-parameter Lie group of transformations is the stretching group,

\[
\begin{align*}
    x^* &= e^\epsilon x, & t^* &= e^{2\epsilon} t, & p^* &= p.
\end{align*}
\]  

(5.11)

We can find the infinitesimals by calculating

\[
\begin{align*}
    X(x, t, p) &= \left( \frac{\partial x^*}{\partial \epsilon} \right)_{\epsilon=0} = x, \\
    T(x, t, p) &= \left( \frac{\partial t^*}{\partial \epsilon} \right)_{\epsilon=0} = 2t, \\
    P(x, t, p) &= \left( \frac{\partial p^*}{\partial \epsilon} \right)_{\epsilon=0} = 0,
\end{align*}
\]

so that the group generator is

\[
\Gamma = x \frac{\partial}{\partial x} + 2t \frac{\partial}{\partial t}.
\]
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Requiring invariance of our governing equation (5.8) requires that the following be satisfied:

$$\Delta = p_t^* - p_{x^*x}^* - Q(x^*, t^*, p^*) = 0, \quad (5.12)$$

so that we must find expressions for $p_t^*$ and $p_{x^*x}^*$. We define the Jacobian of the transformation from $(x, y)$ to $(u, v)$ as

$$J = \frac{\partial(x, y)}{\partial(u, v)} = \begin{vmatrix} x_u & x_v \\ y_u & y_v \end{vmatrix} = \frac{\partial x}{\partial u} \frac{\partial y}{\partial v} - \frac{\partial x}{\partial v} \frac{\partial y}{\partial u}.$$ 

Using this definition and the infinitesimal form of the group, we can write expressions for $p_t^*$ and $p_{x^*x}^*$ in terms of the infinitesimals, the original variables and their derivatives as follows,

$$\frac{\partial p^*}{\partial t^*} = p_t + \epsilon \left[ \frac{\partial P}{\partial t} + \left( \frac{\partial P}{\partial p} - \frac{\partial T}{\partial t} \right) p_t - \frac{\partial X}{\partial t} p_x - \frac{\partial X}{\partial p} p_x p_t - \frac{\partial T}{\partial p} (p_t) \right] + O(\epsilon^2),$$

$$\frac{\partial^2 p^*}{\partial x^2} = p_{xx} + \epsilon \left[ \frac{\partial^2 P}{\partial x^2} + \left( 2 \frac{\partial^2 P}{\partial x \partial p} - \frac{\partial^2 X}{\partial x^2} \right) p_x - \frac{\partial^2 T}{\partial x^2} p_t + \left( \frac{\partial P}{\partial p} - 2 \frac{\partial X}{\partial x} \right) p_{xx} \right.$$

$$\left. - 2 \frac{\partial T}{\partial x} p_{xt} + \left( 2 \frac{\partial^2 X}{\partial x \partial p} - 2 \frac{\partial X}{\partial x} \right) p_{xx} \right) (p_x)^2 - 2 \frac{\partial^2 T}{\partial x \partial p} p_x p_t - \frac{\partial^2 X}{\partial p^2} (p_x)^3$$

$$\left. - \frac{\partial^2 T}{\partial p^2} (p_x)^2 p_t - 3 \frac{\partial X}{\partial p} p_x p_{xx} - \frac{\partial T}{\partial p} p_{xx}^2 - 2 \frac{\partial T}{\partial p} p_{xx} p_{xt} \right] + O(\epsilon^2).$$

In order to express this more concisely, we define the prolongation or extension of the symmetry generating operator. For second order PDEs we require knowledge of the second prolongation of $\Gamma$, defined as [24]

$$\Gamma^{(2)} = X \frac{\partial}{\partial x} + T \frac{\partial}{\partial t} + P \frac{\partial}{\partial p} + P_x \frac{\partial}{\partial p_x} + P_{[t]} \frac{\partial}{\partial p_t} + P_{[xx]} \frac{\partial}{\partial p_{xx}} + P_{[tt]} \frac{\partial}{\partial p_{tt}} + P_{[xt]} \frac{\partial}{\partial p_{xt}}.$$
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where

\[ P_{[i]} = D_i(P) - D_i(X)p_x - D_i(T)p_t, \quad \text{and} \]

\[ P_{[i_1i_2]} = D_{i_2}(P_{[i_1]}) - D_{i_2}(X)p_{i_1x} - D_{i_2}(T)p_{i_1t} \]

where the subscripts \( i \) represent either \( x \) or \( t \), and \( D_{x_i} \) represents the total derivative,

\[ D_{x_i} = \frac{D}{Dx_i} = \frac{\partial}{\partial x_i} + p_{x_i} \frac{\partial}{\partial p_x} + p_{xx_i} \frac{\partial}{\partial p_x^2} + p_{txi} \frac{\partial}{\partial p_t} + p_{xxx_i} \frac{\partial}{\partial p_x^3}. \]

The requirement that the governing equation be invariant (5.12) can now be written as

\[ \Gamma^{(2)} \Delta|_{\Delta=0} = 0. \]

As a result of this requirement, we obtain a set of overdetermined linear PDEs for the infinitesimals. These determining equations may be solved to find \( X(x, t, p) \), \( T(x, t, p) \) and \( P(x, t, p) \), and hence the group generators (5.10).

In order to transform the PDE (5.8) to a reduced ODE, we must find the invariants of the group. The invariants can be taken as the constants of integration which arise when the characteristic equation

\[ \frac{dx}{X(x, t, p)} = \frac{dt}{T(x, t, p)} = \frac{dp}{P(x, t, p)} \]

is solved.

For example, the stretching group (5.11) has one independent invariant. The characteristic equation for the stretching group is

\[ \frac{dp}{0} = \frac{dx}{x} = \frac{dt}{2t}. \]
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Upon integrating the last two expressions, we find that \( x = A\sqrt{t} \), where \( A \) is the constant of integration. Hence our invariant could be

\[
\phi = xt^{-1/2}
\]  

(5.13)

This invariant often arises in symmetry analysis and is known as Boltzmann’s similarity variable. Any function of \( \phi \) would also be an invariant. Integrating the first and last expressions, we find that our other invariant is \( u(\phi) = p(x,t) \).

The symmetries of a differential equation can be determined using a specific computational algorithm (known as Lie’s classical method or Lie’s algorithm). As a result of this, many computer packages have been developed to find the symmetries of a differential equation (for example SPDE [68]). The current analysis was performed using the symmetry finding package Dimsym [70] under REDUCE [37]. Dimsym is a program that is primarily used for finding Lie point symmetries. When supplied with a differential equation, Dimsym finds the determining equations and attempts to solve them.

Dimsym will report in two ways. The first is if when attempting to solve the determining equations, an operation is performed which involves division by an expression that contains an unknown function. Dimsym makes the assumption that the expression is not equal to zero. By considering the case when the expression is equal to zero we may ensure that all cases have been examined. The second arises when in splitting the determining equations, Dimsym makes the assumption
that a number of expressions are linearly independent. If these expressions include any unknown functions, this assumption excludes some specific cases. By assuming that the expressions are not linearly independent, we may obtain a differential equation for the arbitrary function. Forms of the arbitrary function that satisfy this differential equation must then be considered separately.

By considering all the assumptions made by Dimsym as it attempts to solve the determining equations, a full classification of the differential equation in question may be made. An example of the output generated by Dimsym can be found in Appendix F.

In the following sections we perform an analysis of equations (5.2) and (5.3), looking in particular for classical Lie point symmetries. We do not perform a complete classification of the equations. We do not consider any special cases flagged by Dimsym that reduce the equations (5.2) and (5.3) to the heat equation which has been thoroughly analysed (see for example Galaktionov, et al [32]).

5.2.2 Results for \( p_t = p_{xx} + g(x)p^2(1 - p) \)

Dimsym reports that when \( g(x) \) is arbitrary, equation (5.2) has only one classical point symmetry - translations in time:

\[
\Gamma_1 = \frac{\partial}{\partial t}.
\]
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Dimsym also reports that it has assumed the following expressions are linearly independent

$$x \frac{\partial g(x)}{\partial x}, \frac{\partial g(x)}{\partial x}, x^2g(x), xg(x), g(x).$$

This means that for any $g(x)$ that satisfies the ODE

$$a_1x\frac{\partial g(x)}{\partial x} + a_2\frac{\partial g(x)}{\partial x} + a_3x^2g(x) + a_4xg(x) + a_5g(x) = 0 \quad (5.14)$$

(where the $a_i$ are constants) equation (5.2) may admit an additional symmetry generating operator. We can solve this ODE explicitly to obtain

for $a_1 \neq 0$, set $a_1 = 1$, \quad $g(x) = c_5 \exp(c_1 x^2) \exp(c_2 x)(x + c_4)^c$, \quad (5.15)

for $a_1 = 0$, set $a_2 = 1$, \quad $g(x) = c_9 \exp(c_6 x^3) \exp(c_7 x^2) \exp(c_8 x)$, \quad (5.16)

where the constants $a_i$ have been renamed. These specific forms for $g(x)$ may now be investigated to determine whether or not they yield extra symmetries.

Setting $g(x)$ to take the form indicated by (5.15), Dimsym reports a large number of special cases that require further investigation. Since we have not investigated all of these cases, we cannot claim to have completed a full classification of equation (5.2), however we can still examine any special cases that result in equation (5.2) possessing an extra symmetry. One of these special cases is when $c_1 = c_2 = 0$ and $c_3 = -2$. Rather than examine the case where $c_4$ and $c_5$ are arbitrary, we consider the case where

$$g(x) = \frac{c}{x^2}$$
where $c$ is a constant, since these forms of $g(x)$ can be related by a simple change of variable. When $g(x)$ takes this form, equation (5.2) becomes

\[
\frac{\partial p}{\partial t} = \frac{\partial^2 p}{\partial x^2} + \frac{c}{x^2} p^2 (1 - p) \tag{5.17}
\]

which admits an additional classical point symmetry,

\[
\Gamma_1 = \frac{\partial}{\partial t} \quad \text{and} \quad \Gamma_2 = x \frac{\partial}{\partial x} + 2t \frac{\partial}{\partial t}.
\]

The characteristic equation corresponding to $\Gamma_2$ is

\[
\frac{dp}{0} = \frac{dx}{x} = \frac{dt}{2t}
\]

so that we obtain the invariants and hence the functional form,

\[
p(x, t) = u(\phi), \quad \text{where} \quad \phi = x t^{-1/2}.
\]

Using the functional form in equation (5.2), we obtain the ODE

\[
u'' + \frac{1}{2} \phi u' + \frac{c}{\phi^2} u^2 (1 - u) = 0. \tag{5.18}
\]

Exact solutions to this ODE cannot be found. An attempt could be made to find numerical solutions using a computer algebra package (for example MAPLE or MATLAB). However, in this thesis we are primarily interested in finding exact solutions, so we leave this as an open problem to be re-examined in the future.
5.2.3 Results for $p_t = p_{xx} + g_1(x)p(1-p)(p-g_2(x))$

Dimsym reports that when $g_1(x)$ and $g_2(x)$ are arbitrary, equation (5.3) has only one classical point symmetry - translations in time:

$$\Gamma_1 = \frac{\partial}{\partial t}.$$ 

Dimsym also reports that it has assumed that the following expressions are linearly independent

$$x \frac{\partial g_1(x)}{\partial x}, \frac{\partial g_1(x)}{\partial x}, x^2 g_1(x), x g_1(x), g_1(x).$$

This means that any $g_1(x)$ that satisfies the ODE

$$a_1 x \frac{\partial g_1(x)}{\partial x} + a_2 \frac{\partial g_1(x)}{\partial x} + a_3 x^2 g_1(x) + a_4 x g_1(x) + a_5 g_1(x) = 0$$

(where the $a_i$ are constants) may lead to equation (5.3) possessing an additional symmetry generating operator. Noticing that this equation is the same as the ODE for $g(x)$ in the previous section (5.14), we find two expressions for $g_1(x)$ identical to (5.15) and (5.16). These specific forms for $g_1(x)$ may now be investigated to determine whether or not they yield extra symmetries. If we set $g_1(x)$ to take the form indicated by (5.15), Dimsym reports that there are many specific values of the constants $c_i$ and forms of $g_2(x)$ that may lead to special cases. We cannot claim to have completed a full classification of equation (5.3) since we have not investigated all of these cases. However for two particular forms of $g_1(x)$ and $g_2(x)$, equation (5.3) possesses an extra symmetry. We now examine these two cases.
The first interesting case is when

\[ g_1(x) = \frac{c}{x^2}, \quad g_2(x) = 1, \]

(where \( c \) is a constant) \(^1\) so that equation (5.3) becomes

\[
\frac{\partial p}{\partial t} = \frac{\partial^2 p}{\partial x^2} + \frac{c}{x^2} p(1 - p)(p - 1) \\
= \frac{\partial^2 p}{\partial x^2} - \frac{c}{x^2} p(1 - p)^2. \tag{5.19}
\]

Under the transformation \( p^* = 1 - p \), equation (5.19) is identically equal to equation (5.17), which has been already been investigated.

The second interesting case is when

\[ g_1(x) = \frac{c}{x^2}, \quad g_2(x) = -1, \]

so that equation (5.3) becomes

\[
\frac{\partial p}{\partial t} = \frac{\partial^2 p}{\partial x^2} + \frac{c}{x^2} p(1 - p)(p + 1). \tag{5.20}
\]

This equation admits an additional classical point symmetry,

\[ \Gamma_1 = \frac{\partial}{\partial t} \quad \text{and} \quad \Gamma_2 = x \frac{\partial}{\partial x} + 2t \frac{\partial}{\partial t}. \]

The characteristic equation corresponding to \( \Gamma_2 \) is

\[
\frac{dp}{0} = \frac{dx}{x} = \frac{dt}{2t}.
\]

\(^1g_1(x)\) could take the more complicated form, \( c_5(x + c_4)^{-2} \), but this is an equivalent problem and can be transformed easily to the one under consideration.
so that we obtain the invariants and hence the functional form,

\[ p(x, t) = u(\phi), \quad \text{where } \phi = xt^{-1/2}. \]

Using the functional form in equation (5.3), we obtain the ODE

\[ u'' + \frac{1}{2} \frac{\phi u'}{\phi^2} + \frac{c}{\phi^2} u(1 - u)(u + 1) = 0. \]

Exact solutions to this ODE cannot be found. An attempt could be made to find numerical solutions using a computer algebra package (for example MAPLE or MATLAB). In this thesis we are primarily interested in finding exact solutions, so we leave this as an open problem to be re-examined in the future.

### 5.3 Nonclassical symmetry analysis

So far in this chapter, we have used the method of classical symmetry analysis to look for a one-parameter group of point transformations that leaves the governing equation invariant. Lie’s method of classical symmetry analysis was generalised in 1969 by Bluman and Cole [11]. They named this method the nonclassical method, and it is related to the earlier conditional symmetry method of Ovsiannikov [58].

In this method, we augment our governing equation (5.8) by the invariant surface condition (ISC)

\[ X(x, t, p) \frac{\partial p}{\partial x} + T(x, t, p) \frac{\partial p}{\partial t} = P(x, t, p). \quad (5.21) \]
Requiring invariance of the governing equation subject to the constraint of the ISC leads to *nonlinear* determining equations for the infinitesimals. In terms of the second prolongation $\Gamma^{(2)}$, the nonclassical symmetry determining relations are

$$\Gamma^{(2)} E \mid_{F=0,ISC} = 0. \quad (5.22)$$

The set of solutions for the infinitesimals will also contain all those found by the classical method and so in general this will be a larger set. We will be interested in *strictly nonclassical symmetries*, namely those particular solutions which are not equivalent to any classical symmetry. The determining equations (5.22) are more difficult to solve than those found for the classical case, so that strictly nonclassical symmetries are rare. However, following Clarkson and Kruskal’s direct method [22] we can attempt to construct new nonclassical symmetry solutions.

After using the ISC to eliminate $p_t$ and its derivatives from the determining equations, then subsequently using the governing equation to eliminate $p_{xx}$ and higher order derivatives, (5.22) reduces to a polynomial equation in $p_x$. Setting the coefficients of this polynomial to zero, we obtain the determining relations for the coefficients $X(x, t, p)$, $T(x, t, p)$ and $P(x, t, p)$ of the infinitesimal symmetry generating operator $\Gamma$.

Once we have determined the form of the infinitesimals, we can either use the ISC to reduce the governing equation to an ODE, or transform the governing equation to an ODE using the new set of variables.
Once again, we do not consider any special cases that set \( g(x) = 0 \) or \( g_1(x) = 0 \) since this reduces each of the equations to the heat equation. We also do not consider the case when \( g(x) \) or \( g_1(x) \) and \( g_2(x) \) are constants since this case has already been examined in Chapter 3.

In order to look for nonclassical symmetries possessed by the governing equation, we use an interactive computer algebra package. The results presented in the following sections have been obtained using MAPLE (an example of the Maple output is shown in Appendix F).

### 5.3.1 Results for \( p_t = p_{xx} + g(x)p^2(1 - p) \)

We now apply the nonclassical symmetry method to equation (5.3). For the case where \( T \neq 0 \) in equation (5.21), we can set \( T(x,t,p) = 1 \) without loss of generality. This gives rise to the following determining equations,

\[
\begin{align*}
P_t - P_{xx} + 2X_xP - 2Pg(x)p + 3Pp(x)p^2 \\
- Xg'(x)p^2(1 - p) + P_p g(x)p^2(1 - p) - 2X_xg(x)p^2(1 - p) &= 0 \\
-2P_{xp} - X_t + X_{xx} + 2X_pP - 2X_xX - 3X_pg(x)p^2(1 - p) &= 0 \\
2X_{xp} - P_{pp} - 2X_pX &= 0 \\
X_{pp} &= 0.
\end{align*}
\]

From equation (5.23)\(_4\), we can say that \( X(x,t,p) \) must take the form

\[ X(x,t,p) = f_1(x,t)p + f_2(x,t). \]
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Substituting this into equation (5.23)_3, we obtain an equation which can be solved to give

\[ P(x, t, p) = -\frac{1}{3} f_1(x, t)^2 p^3 + \frac{\partial f_1(x, t)}{\partial x} p^2 - f_1(x, t)f_2(x, t)p^2 + f_3(x, t)p + f_4(x, t). \]

Substituting this into equations (5.23)_1 and (5.23)_2, we can now equate coefficients of powers of \( p \) to zero to obtain nine nonlinear PDEs in \( f_1(x, t) \), \( f_2(x, t) \), \( f_3(x, t) \), \( f_4(x, t) \) and \( g(x) \). From one of these equations we can deduce that \( f_1(x, t) \) must take one of the following forms:

\[ f_1(x, t) = 0, \quad f_1(x, t) = \pm 3\sqrt{\frac{g(x)}{2}}. \quad (5.24) \]

We must now investigate each of these situations.

Setting \( f_1(x, t) = \pm 3\sqrt{g(x)/2} \), enables us to simplify the other eight equations only marginally. A solution to these equations may exist, however in general it is not easy to find and we proceed to the remaining form that \( f_1(x, t) \) may take.

Setting \( f_1(x, t) = 0 \), we prescribe that the infinitesimals must take the form

\[ X(x, t, p) = f_2(x, t), \quad T(x, t, p) = 1, \]
\[ P(x, t, p) = f_3(x, t)p + f_4(x, t), \]

and we are left with five PDEs in \( f_2(x, t) \), \( f_3(x, t) \), \( f_4(x, t) \) and \( g(x) \). From one of these equations, we deduce that \( f_3(x, t) = -3f_4(x, t) \), and from another we find that

\[ f_4(x, t) = \frac{1}{6g(x)} \left[ f_2(x, t) \frac{dg(x)}{dx} + 2\frac{\partial f_2(x, t)}{\partial x} g(x) \right]. \]
From the remaining three equations we deduce that

$$f_2(x, t) = \frac{f_5(t)}{\sqrt{g(x)}},$$

so that $f_3(x, t) = f_4(x, t) = 0$. We are now left with the following

$$4 f_5'(t) g(x)^2 - 3 f_5(t) (g'(x))^2 + 2 f_5(t) g(x) g''(x) - 4 f_5(t)^2 g'(x) \sqrt{g(x)} = 0. \quad (5.25)$$

We can show that there are a limited number of solutions to this equation for $f_5(t)$ and $g(x)$. Let

$$g = G^{-2}, \quad \text{so that} \quad g' = -2G^{-3}G', \quad \text{and} \quad g'' = 6G^{-4}(G')^2 - 2G^{-3}G''.$$ 

Substituting this into equation (5.25) and rearranging, we find that

$$f_5'(t)G(x) - f_5(t)G''(x) + 2f_5^2(t)G(x)G'(x) = 0. \quad (5.26)$$

Provided $f_5(t) \neq 0$, we can divide by $f_5(t)$ and differentiate with respect to $t$ to obtain

$$\frac{1}{f_5(t)} \frac{d}{dt} \left( \frac{f_5'(t)}{f_5(t)} \right) = -2G'(x) = 2\eta$$

where $2\eta$ is the separation constant. Integrating the second two expressions, we obtain

$$G(x) = -\eta x + c_1 \quad \text{so that} \quad g(x) = \frac{1}{(-\eta x + c_1)^2}$$

where $c_1$ is a constant. Substituting this into (5.26), we can integrate to find the expression for $f_5(t)$:

$$f_5(t) = \frac{-1}{2\eta t + c_2}$$
where \( c_2 \) is a constant. In Section 5.2.2, this form of \( g(x) \) was found to result in equation (5.2) admitting classical symmetries. Indeed, when the infinitesimals take the form

\[
X(x, t, p) = \frac{f_5(t)}{\sqrt{g(x)}} = \frac{-\eta x + c_1}{-2\eta t + c_2}, \quad T(x, t, p) = 1, \quad P(x, t, p) = 0
\]

we find that the same reduced equation (5.18) is obtained.

If \( \eta = 0 \) we find that \( G(x) \) and therefore \( g(x) \) is a constant. In this case, we find that \( f_5(t) \) is also a constant. Since we are looking for a form of \( g(x) \) that depends explicitly on \( x \) we are not interested in this case.

Returning to equation (5.26), we may follow the same line of reasoning, but this time we take the derivative with respect to \( x \), after first dividing by \( G(x) \) (provided \( G(x) \neq 0 \)). After rearranging, we obtain

\[
\frac{1}{G''(x)} \frac{d}{dx} \left( \frac{G''(x)}{G(x)} \right) = 2f_5(t) = 2\omega
\]

where \( 2\omega \neq 0 \) is the separation constant. Solving the second two expressions, we find that \( f_5(t) = \omega \). Substituting this into (5.26) we arrive at the following equation for \( G(x) \):

\[
G''(x) - 2\omega G(x)G'(x) = 0.
\]

Transforming back to the variable \( g(x) \) we find we have the following differential equation for \( g(x) \):

\[
2g(x)g''(x) - 3(g'(x))^2 - 4\omega \sqrt{g(x)}g'(x) = 0.
\]
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We now solve this equation for $g(x)$ to determine the possible forms that $g(x)$ may take in order that equation (5.2) possesses a nonclassical symmetry. Indeed, the only strictly nonclassical symmetries are found when $f_5(t)$ is a constant and $g(x)$ satisfies the above differential equation. By setting $u = dg/dx$ we obtain

$$u \left( 2g \frac{du}{dg} - 3u - 4\omega \sqrt{g} \right) = 0.$$ 

If $u = dg/dx = 0$, $g(x)$ is a constant. Since this case has already been examined in Chapter 3, we assume $u \neq 0$ so that the expression in the brackets is equal to zero. Integrating this, we obtain

$$u = \frac{dg}{dx} = -2\omega \sqrt{g} + c_1 g^{3/2}.$$ 

If $c_1 = 0$, the above equation can be integrated directly to find $g(x) = \omega^2 (-x + c_2)^2$. If $c_1 \neq 0$ we use the transformation $v = \sqrt{g}$ to obtain

$$\int \frac{2}{-2\omega + c_1 v^2} dv = dx.$$ 

Solving this equation and transforming back to the variable $g$, we find that depending on the choice of $\omega$ and the first constant of integration $c_1$, $g(x)$ may take the following forms,

$$c_1 = 0, \quad g(x) = \omega^2 (-x + c_2)^2, \quad (5.27)$$

$$c_1 \omega > 0, \quad g(x) = \frac{2\omega}{c_1} \tanh \left( -c_1 \sqrt{-\omega} x + c_2 \right), \quad (5.28)$$

$$c_1 \omega < 0, \quad g(x) = -\frac{2\omega}{c_1} \tan \left( c_1 \sqrt{-\omega} x + c_2 \right). \quad (5.29)$$
Chapter 5: Including explicit spatial dependence

We now consider each of the above forms of $g(x)$ separately. Since a full classical classification of equation (5.2) has not been completed, we must first check if these forms for $g(x)$ enable equation (5.2) to admit classical symmetries. This can easily be done using Dimsym, and we are able to verify that each of the following symmetries is indeed strictly nonclassical.

(i) $p_t = p_{xx} + g(x)p^2(1 - p)$ with $g(x) = \omega^2(-x + c_2)^2$.

This equation admits the strictly nonclassical symmetry

$$\Gamma = \frac{1}{(-x + c_2)} \frac{\partial}{\partial x} + \frac{\partial}{\partial t},$$

with the corresponding characteristic equation

$$(-x + c_2)dx = \frac{dt}{\Gamma} = \frac{dp}{0}.$$

We now find the invariants and hence the functional form to be

$$p(x, t) = u(\phi), \quad \text{where } \phi = \frac{1}{2}(-x + c_2)^2 + t.$$

Using this functional form we find the above equation reduces to

$$u'' + \omega^2 u^2(1 - u) = 0.$$ 

By using the transformation $v = du/d\phi$, we can integrate this once to obtain

$$\left(\frac{du}{d\phi}\right)^2 = v^2 = 2\omega^2 \left(\frac{1}{4}u^4 - \frac{1}{3}u^3 + c_3\right),$$
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where \( c_3 \) is a constant. This equation is separable, and upon integration we find

\[
\int \frac{du}{\sqrt{\frac{1}{4}u^4 - \frac{1}{3}u^3 + c_3}} = \sqrt{2} \omega \phi + c_4.
\]

Changing back to our original variables \( p(x, t) \) we have

\[
\int \frac{dp}{\sqrt{\frac{1}{4}p^4 - \frac{1}{3}p^3 + c_3}} = \sqrt{2} \omega \left( \frac{1}{2}(-x + c_2)^2 + t \right) + c_4. \tag{5.30}
\]

(This form of the solution can also be obtained using Polyanin and Zaitsev [62], equation 2.9.2.4.)

If \( c_3 = 0 \), we can write the integral as

\[
\int \frac{dp}{\sqrt{\frac{1}{4}p^4 - \frac{1}{3}p^3}} = \int \frac{dp}{y},
\]

where \( y^2 = \frac{1}{4}p^4 - \frac{1}{3}p^3 \). Using the transformation

\[
p = \frac{1}{q}, \quad y = \frac{Y}{q^2},
\]

we can write the integral as

\[
\int \frac{dp}{y} = -\int \frac{dq}{Y} = -\int \frac{dq}{\sqrt{\frac{1}{4} - \frac{1}{3}q}},
\]

which can be integrated directly to find

\[
\int \frac{dp}{\sqrt{\frac{1}{4}p^4 - \frac{1}{3}p^3}} = -\int \frac{dq}{\sqrt{\frac{1}{4} - \frac{1}{3}q}} = 6 \sqrt{\frac{1}{4} - \frac{1}{3}q} = 6 \sqrt{\frac{1}{4} - \frac{11}{3}p}. 
\]
Using this in equation (5.30) and rearranging, we find that

\[
p(x, t) = \left[ \frac{3}{4} - 3 \left[ \frac{\sqrt{2} \omega}{6} \left( \frac{1}{2} (-x + c_2)^2 + t \right) + \frac{c_4}{6} \right]^2 \right]^{-1}
\]

(5.31)
is a solution to equation (5.2) when \( g(x) \) takes the form given by (5.27).

If \( c_3 \neq 0 \), the integral in equation (5.30) can be written as

\[
\int \frac{dp}{\sqrt{\frac{1}{4} p^4 - \frac{1}{3} p^3 + c_3}} = \int \frac{dp}{y},
\]

where \( y^2 = \frac{1}{4} p^4 - \frac{1}{3} p^3 + c_3 \). If \( c_3 \) is a real zero of \( y^2 \), then this integral may be expressed in terms of elliptic functions (see Bateman [8] or Spanier and Oldham [74]). We find that either \( c_3 = 0 \) or \( c_3 \approx -1.24 \). Since we have already examined the case when \( c_3 = 0 \), we now turn our attention to \( c_3 \approx -1.24 \).

Using the transformation

\[
p = c_3 + \frac{1}{q}, \quad y = \frac{Y}{q^2},
\]

we find that we can write the integral in equation (5.30) as

\[
\int \frac{dp}{\sqrt{\frac{1}{4} p^4 - \frac{1}{3} p^3 + c_3}} = \int \frac{dp}{y} = - \int \frac{dq}{Y} = \frac{-1}{\sqrt{c_3^2 - c_3^3}} \int \frac{dq}{\sqrt{-q^4 + a_2 q^2 + a_1 q + a_0}},
\]

where

\[
a_2 = \frac{\frac{3}{2} c_3^2 - c_3}{c_3^2 - c_3^3} \approx 1.03, \quad a_1 = \frac{c_3 - \frac{1}{3}}{c_3^2 - c_3^3} \approx 0.35, \quad a_0 = \frac{\frac{1}{4} c_3}{c_3^2 - c_3^3} \approx 0.072.
\]
Chapter 5: Including explicit spatial dependence

The function \(-q^3 + a_2 q^2 + a_1 q + a_0\) has one real zero, \(r \approx 1.33\). By using Section 62:14 of Spanier and Oldham [74], we find we can write

\[
\int \frac{dq}{\sqrt{-q^3 + a_2 q^2 + a_1 q + a_0}} = hF \left( k; 2 \arctan(h \sqrt{r - q}) \right)
\]

where \(F\) is an incomplete elliptic integral of the first kind and

\[
h^2 = \frac{1}{\sqrt{3r^2 + 2a_2 r + a_1}} \approx 0.346, \quad k^2 = \frac{2 + (3r + a_2)h^2}{4} \approx 0.933.
\]

Substituting this into (5.30) we can write

\[
\frac{-1}{\sqrt{c_3^2 - c_3^3}} hF \left( k; 2 \arctan(h \sqrt{r - q}) \right) = \sqrt{2} \omega \left( \frac{1}{2}(-x + c_2)^2 + t \right) + c_1.
\]

Now, if \(F(k : \phi) = z\), we can write \(\tan \phi = \text{sc}(k ; z)\) where \(\text{sc}(k ; z)\) is a Jacobian elliptic function. Using the double angle formula for \(\tan 2\theta\),

\[
\tan \left( 2 \arctan(h \sqrt{r - q}) \right) = \frac{2h \sqrt{r - q}}{1 - h^2(r - q)},
\]

so that

\[
\frac{2h \sqrt{r - q}}{1 - h^2(r - q)} = \text{sc} \left( k; \frac{-\sqrt{c_3^2 - c_3^3}}{h} \left[ \sqrt{2} \omega \left( \frac{1}{2}(-x + c_2)^2 + t \right) + c_4 \right] \right).
\]

Since \(q = 1/(p - c_3)\), we find that

\[
\frac{2h \sqrt{r - \frac{1}{p - c_3}}}{1 - h^2 \left( r - \frac{1}{p - c_3} \right)} = \text{sc} \left( k; \frac{-\sqrt{c_3^2 - c_3^3}}{h} \left[ \sqrt{2} \omega \left( \frac{1}{2}(-x + c_2)^2 + t \right) + c_4 \right] \right) \quad (5.32)
\]

(where \(c_3 \approx -1.24\) is a real zero of \(y^2\)) is a solution to equation (5.2) when \(g(x)\) takes the form given by (5.27).
(ii) \( p_t = p_{xx} + g(x)p^2(1 - p) \) with \( g(x) = \frac{2\omega}{c_1} \tanh^2 \left( -c_1 \sqrt{\frac{\omega}{2c_1}} x + c_2 \right), \ c_1 \omega > 0. \)

This equation admits the strictly nonclassical symmetry

\[
\Gamma = \frac{\omega}{\sqrt{\frac{2\omega}{c_1} \tanh \left( -c_1 \sqrt{\frac{\omega}{2c_1}} x + c_2 \right)}} \frac{\partial}{\partial x} + \frac{\partial}{\partial t},
\]

with the corresponding characteristic equation

\[
\frac{1}{\omega} \sqrt{\frac{2\omega}{c_1}} \tanh \left( -c_1 \sqrt{\frac{\omega}{2c_1}} x + c_2 \right) dx = \frac{dt}{1} = \frac{dp}{0}.
\]

Upon integration, we find the infinitesimals and the functional form to be

\[
u(\phi) = p(x,t), \quad \text{where } \phi = \ln \left[ \cosh \left( -c_1 \sqrt{\frac{\omega}{2c_1}} x + c_2 \right) \right] + \frac{c_1 \omega}{2} t.
\]

Using this functional form we find that the above equation can be reduced to

\[
u'' - \nu' = -\frac{4}{c_1^2} u^2(1 - u).
\]

Noticing that the independent variable \( \phi \) does not explicitly appear in this equation, we use the transformation \( v = du/d\phi \) to find

\[
\frac{dv}{du} - v = -\frac{4}{c_1^2} u^2(1 - u), \quad (5.33)
\]

which is an Abel equation of the second kind [62].

If \( c_1 = \sqrt{2} \) (so that \( \omega > 0 \) since \( c_1 \omega > 0 \) for this case), we find the particular solution [62]

\[
v(u) = u - u^2.
\]
By inverting each of the transformations, we find that

$$u(\phi) = \frac{c_3 e^{\phi}}{1 + c_3 e^{\phi}}$$

where $c_3$ is a constant. Since $p(x, t) = u(\phi)$, we find that a solution to equation (5.2) with $g(x)$ given by (5.28) with $c_1 = \sqrt{2}$ is

$$p(x, t) = \frac{c_3 \exp \left( \frac{\omega}{\sqrt{2}} t \right) \cosh \left( -\frac{\sqrt{\omega}}{\sqrt{2}} x + c_2 \right)}{1 + c_3 \exp \left( \frac{\omega}{\sqrt{2}} t \right) \cosh \left( -\frac{\sqrt{\omega}}{\sqrt{2}} x + c_2 \right)},$$

(5.34)

where $\omega > 0$, $c_2$ and $c_3$ are constants. We could equally well have chosen $c_1 = -\sqrt{2}$, however due to the restriction that $c_1 \omega > 0$ and the fact that $\cosh(-\theta) = \cosh(\theta)$, this leads to the same final solution.

A second particular solution can be found if $c_1 = 2\sqrt{2}$ (so that $\omega > 0$ since $c_1 \omega > 0$ for this case). Equation (5.33) now has the solution

$$v(u) = \frac{1}{2} u^2,$$

which cannot be found in Polyanin and Zaitsev [62]. By inverting the transformations we find

$$u(\phi) = \frac{-2}{\phi + c_3}$$

where $c_3$ is a constant. Since $p(x, t) = u(\phi)$ we find that a solution to equation (5.2) with $g(x)$ given by (5.28) with $c_1 = 2\sqrt{2}$ is

$$p(x, t) = -2 \left[ \ln \left( \cosh \left( -\sqrt{2}\sqrt{\omega} x + c_2 \right) \right) + \sqrt{2} \omega t + c_3 \right]^{-1},$$

(5.35)
where $\omega > 0$, $c_2$ and $c_3$ are constants\(^2\).

(iii) $p_t = p_{xx} + g(x)p^2(1 - p)$ with $g(x) = -\frac{2\omega}{c_1^2}\tan^2 \left( c_1 \sqrt{-\omega 2c_1 x + c_2} \right)$, $c_1 \omega < 0$.

This equation admits the strictly nonclassical symmetry

$$
\Gamma = \frac{\omega}{\sqrt{-\omega} \tan \left( c_1 \sqrt{-\omega 2c_1 x + c_2} \right)} \frac{\partial}{\partial x} + \frac{\partial}{\partial t}.
$$

The corresponding characteristic equation can be written as

$$
\frac{1}{\omega} \sqrt{-\omega} \tan \left( c_1 \sqrt{-\omega 2c_1 x + c_2} \right) dx = \frac{dt}{1} = \frac{dp}{0}.
$$

Upon integration, we find the infinitesimals and the functional form to be

$$
u(\phi) = p(x, t), \text{ where } \phi = \ln \left( \sec \left( c_1 \sqrt{-\omega 2c_1 x + c_2} \right) \right) - \frac{c_1 \omega}{2} t.
$$

Using this functional form, the above equation can be reduced to

$$
u'' + \nu' = -\frac{4}{c_1^2} u^2(1 - u).
$$

Noticing that the independent variable does not appear explicitly in this equation, we use the transformation $v = du/d\phi$ to get

$$
v \frac{dv}{du} + v = -\frac{4}{c_1^2} u^2(1 - u), \quad (5.36)
$$

which under the transformation $v \rightarrow -v$ is the same as equation (5.36), an Abel equation of the second kind [62].

\(^{2}\)Once again, we could equally well have chosen $c_1 = -2\sqrt{2}$, however the same solution is obtained.
Chapter 5: Including explicit spatial dependence

Once again, if \( c_1 = \sqrt{2} \) (so that \( \omega < 0 \), since \( c_1 \omega < 0 \) for this case), this equation has the particular solution [62]

\[
v(u) = -u + u^2.
\]

Inverting the transformations, we find

\[
u(\phi) = \frac{1}{1 + c_3 e^\phi}
\]

where \( c_3 \) is a constant. Since \( p(x, t) = (\phi) \), we find that a solution to equation (5.2) with \( g(x) \) given by (5.29) with \( c_1 = \sqrt{2} \) is

\[
p(x, t) = \left[ 1 + c_3 \exp\left( -\frac{\omega}{\sqrt{2}} t \right) \sec\left( \sqrt{\frac{\omega}{2}} x + c_2 \right) \right]^{-1}, \tag{5.37}
\]

where \( \omega < 0 \), \( c_2 \) and \( c_3 \) are constants. We could equally well have chosen \( c_1 = -\sqrt{2} \), however due to the restriction that \( c_1 \omega < 0 \) and the fact that \( \sec(-\theta) = \sec(\theta) \), the same final solution is obtained.

A second particular solution can be found if \( c_1 = 2\sqrt{2} \) (so that \( \omega < 0 \) since \( c_1 \omega < 0 \) for this case). Equation (5.36) has the particular solution

\[
v(u) = -\frac{1}{2} u^2,
\]

which cannot be found in Polyanin and Zaitsev [62]. Inverting the transformations, we find

\[
u(\phi) = \frac{2}{\phi + c_3}.
\]
where \( c_3 \) is a constant. Since \( p(x, t) = u(\phi) \) we find that the solution to equation (5.2) with \( g(x) \) given by (5.29) with \( c_1 = 2\sqrt{2} \) is

\[
p(x, t) = 2 \left[ \ln \left( \sec \left( \sqrt{2} \sqrt{-\omega x + c_2} \right) \right) - \sqrt{2} \omega t + c_3 \right]^{-1}, \tag{5.38}
\]

where \( \omega < 0 \), \( c_2 \) and \( c_3 \) are constants.\(^3\)

In this section, we have found three different forms of \( g(x) \) that enable equation (5.2) to admit additional symmetries (apart from translations in time), (5.27), (5.28) and (5.29). For each of these forms of \( g(x) \) we have found two new exact solutions (5.31) and (5.32), (5.34) and (5.35), and (5.37) and (5.38).

Since we have not considered the case where \( f_1(x, t) = \pm 3\sqrt{g(x)/2} \) (5.24), we cannot claim to have completed a nonclassical classification of equation (5.2).

### 5.3.2 Results for \( p_t = p_{xx} + g_1(x)p(1 - p)(p - g_2(x)) \)

We now apply the nonclassical symmetry method to equation (5.3). Once again, we can set \( T(x, t, p) = 1 \) without loss of generality to find the determining relations as

\(^3\)Once again, we could have chosen \( c_1 = -2\sqrt{2} \) however the same final solution is obtained.
follows:

\[
\begin{align*}
    P_t - P_{xx} + X g_1' p g_2 - X g_1' p^2 g_2 + X g_1 p g_0' - X g_1 p^2 g_2 - X g_1 p^2 g_2' \\
    -2 P g_1 p g_2 - X g_1' p^2 + X g_1' p^3 - 2 P g_1 p + P g_1 g_2 + 3 P g_1 p^2 \\
    +2X_x P - P g_1 p(1 - p)(p - g_2) - 2X_x g_1 p(1 - p)(p - g_2) = 0 \\
    -2P_{xp} - X_t + X_{xx} + 2X_p P - 2X_x X - 3X_p g_1 p(1 - p)(p - g_2) = 0 \\
    2X_{xp} - P_{pp} - 2X_p X = 0 \\
    X_{pp} = 0.
\end{align*}
\] (5.39)

Once again we can deduce the form of $X(x, t, p)$ and $P(x, t, p)$ to be

\[
X(x, t, p) = f_1(x, t) p + f_2(x, t) \quad \text{and} \quad P(x, t, p) = -\frac{1}{3} f_1(x, t) p^3 + \frac{\partial f_1(x, t)}{\partial x} p^2 - f_1(x, t) f_2(x, t) p^2 + f_3(x, t) p + f_4(x, t),
\]

so that from equations (5.39)$_1$ and (5.39)$_2$ we can equate the coefficients of powers of $p$ to zero to obtain nine nonlinear PDEs for $f_1(x, t)$, $f_2(x, t)$, $f_3(x, t)$, $f_4(x, t)$ and $g(x)$. However, in this case, the PDEs are much more complicated and a solution cannot easily be found. We therefore leave this as an open problem to be reexamined in the future.

### 5.3.3 Some comments on the biological relevance of the solutions

From a biological point of view, case (ii) (where $g(x)$ takes the form given by (5.28)) is probably the most interesting. A graph of $g(x) = \gamma_{11} - \gamma_{22}$ (5.28) is shown in
Figure 5.1. This form of $g(x)$ could represent a population in which genotype $A_1A_1$ has a greater advantage at the edges of the range than in the centre of the range — a type of barrier problem. The first solution that we found (5.34) is shown in Figure 5.2. The solution shows that initially, the $A_1$ alleles are common at the edges of the range, but much less common towards the centre. This is as we would expect. Over time, the $A_1$ alleles take over the entire range.

The other forms of $g(x)$ ((5.27), (5.29)) are not bounded, and the other solutions ((5.31), (5.32), (5.35), (5.37), (5.38)) each contain singularities and so it is most likely that these are not biologically significant.
Figure 5.1: Spatial variability of the difference between reproductive success rates (5.28).

Figure 5.2: Nonclassical symmetry solution (5.34) for the allele frequency with spatially dependent birthrates.
Chapter 6

Symmetry analysis of related systems of equations

In the previous chapters, we have developed a number of equations to describe various related problems in population genetics and we have found classical and nonclassical symmetry solutions to a number of them. In Chapter 4 we developed a system of equations to describe the change in allele frequencies in a population in which there are a total of three possible alleles at the locus in question. So far, we have not performed any symmetry analysis on this system. In looking for classical point symmetries of the system of equations (4.4), we find that the only symmetries admitted by the system are translations in space and time,

$$\Gamma_1 = \frac{\partial}{\partial x}, \quad \Gamma_2 = \frac{\partial}{\partial t}.$$
Using Dimsym, we can show that no additional symmetries are admitted unless the
equations are greatly simplified by setting many of the parameters \( \gamma_{ij} \) equal.

We have therefore chosen to use classical symmetry analysis to investigate the
following related system of equations:

\[
\begin{align*}
    p_t &= p_{xx} + R_1 p^m q^n, \\
    q_t &= q_{xx} + R_2 p^r q^s,
\end{align*}
\]

(6.1)

where \( R_1, R_2, m, n, r \) and \( s \) are constants.

\section*{6.1 Symmetry analysis for systems of equations}

Knowledge of a classical symmetry admitted by a system of equations has the same
consequences as that for single equations [57]. In this Chapter we are interested in a
system of two 1+1 dimensional second order PDEs. Finding a one parameter group
of transformations will enable us to rewrite the system of PDEs as a system of two
second order ODEs. If this reduced system of equations possesses a further sym-
metry, the order of the system may be reduced further. For a detailed explanation
of the application of symmetry methods to systems of PDEs, the reader is referred
to Bluman and Anco [10], Bluman and Cole [12], Bluman and Kumei [13] or Olver
[57].

Once again, we can use Dimsym under REDUCE to analyse the system of equa-
tions.
6.2 Symmetry analysis of power law

A complete classification of the system of equations

\[ \lambda_1 p_t = \Delta p + F(p, q), \]
\[ \lambda_2 q_t = \Delta q + G(p, q), \]

where \( \lambda_1 \) and \( \lambda_2 \) are constants, \( \Delta \) is the Laplacian and \( F \) and \( G \) are arbitrary smooth functions, was recently completed by Cherniha and King \[18, 19, 20, 21\]. They provide a list of the symmetries admitted by the above system of equations for various functions \( F \) and \( G \), however the number of reductions provided is limited.

In this Chapter we examine the symmetries admitted by the above system of equations when \( F \) and \( G \) follow a power law so that we have (6.1). In particular, we examine the following two systems of equations:

\[ p_t = p_{xx} + R_1 p^m q^n, \]  
\[ q_t = q_{xx} + p^{m-1} q^{n+1}, \]  
(6.2)

where \( m \neq 0, 1 \), \( n \neq 0, -1 \), and

\[ p_t = p_{xx} + R_1 p \left( \frac{p}{q} \right)^m, \]  
\[ q_t = q_{xx} + R_2 q \left( \frac{p}{q} \right)^m, \]  
(6.3)

where \( m \neq 0 \).

The system of equations (6.2) is chosen because in this case we are free to choose values for both \( m \) and \( n \). This system is most like the system of equations formulated in Chapter 4 since \( m \) and \( n \) can be chosen so that the source terms have no
singularities. The system of equations (6.3) is chosen because by setting \( n = -m + 1 \) in equations (6.2) (and relabelling the power so that \( m - 1 \rightarrow m \)) we find that the system of equations admits an extra symmetry.

Using Dimsym, we find that equations (6.2) admit the following classical Lie point symmetries:

\[
\Gamma_1 = \frac{\partial}{\partial x}, \quad \Gamma_2 = \frac{\partial}{\partial t}, \quad \Gamma_3 = 2p \frac{\partial}{\partial p} + (1 - m)x \frac{\partial}{\partial x} + 2(1 - m)t \frac{\partial}{\partial t}, \quad \Gamma_4 = 2q \frac{\partial}{\partial q} - nx \frac{\partial}{\partial x} - 2nt \frac{\partial}{\partial t}. \quad (6.4)
\]

Dimsym also reports that the system of equations (6.3) admits the classical Lie point symmetries:

\[
\Gamma_1 = \frac{\partial}{\partial x}, \quad \Gamma_2 = \frac{\partial}{\partial t}, \quad \Gamma_3 = p \frac{\partial}{\partial p} + q \frac{\partial}{\partial q},
\Gamma_4 = xp \frac{\partial}{\partial p} + xq \frac{\partial}{\partial q} - 2t \frac{\partial}{\partial x}, \quad \Gamma_5 = \frac{1}{m} q \frac{\partial}{\partial q} + \frac{1}{2} x \frac{\partial}{\partial x} + t \frac{\partial}{\partial t}. \quad (6.5)
\]

### 6.3 Optimal systems and reductions

If our governing equation or system of equations admits an \( n \)-parameter group of transformations, a reduction is possible by any symmetry which is an arbitrary linear combination of the generators

\[
\Gamma = a_1 \Gamma_1 + a_2 \Gamma_2 + \ldots + a_n \Gamma_n, \quad a_1, a_2, \ldots, a_n \in \mathbb{R}. \quad (6.6)
\]

To ensure that a minimal set of reductions is investigated, we find the optimal system of the subgroup such that every subalgebra is equivalent to an element of the optimal system [24, 57]. Taking the general element (6.6), we simplify it as much
as possible by acting on it with carefully chosen Lie group elements in the adjoint representation. Alternatively, the optimal system can be determined by comparison of the Lie algebra with standard classifications that have been previously evaluated.

In this thesis, we use the former method.

We first provide a simple example. Consider the Lie algebra spanned by

\[ \Gamma_1 = \frac{\partial}{\partial x}, \quad \Gamma_2 = \frac{\partial}{\partial t}, \quad \Gamma_3 = x \frac{\partial}{\partial x} + 2t \frac{\partial}{\partial t}. \]

We must first construct the commutator table. The commutator (or Lie bracket) of two operators \( \Gamma_1 \) and \( \Gamma_2 \) is defined as

\[ [\Gamma_1, \Gamma_2] = \Gamma_1 \Gamma_2 - \Gamma_2 \Gamma_1, \]

so that the commutator table is

<table>
<thead>
<tr>
<th></th>
<th>( \Gamma_1 )</th>
<th>( \Gamma_2 )</th>
<th>( \Gamma_3 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \Gamma_1 )</td>
<td>0</td>
<td>0</td>
<td>( \Gamma_1 )</td>
</tr>
<tr>
<td>( \Gamma_2 )</td>
<td>0</td>
<td>0</td>
<td>2( \Gamma_2 )</td>
</tr>
<tr>
<td>( \Gamma_3 )</td>
<td>( -\Gamma_1 )</td>
<td>( -2\Gamma_2 )</td>
<td>0</td>
</tr>
</tbody>
</table>

where the \( ij^{th} \) entry is the commutator \([\Gamma_i, \Gamma_j]\).

In the adjoint representation, group elements act on the Lie algebra or infinitesimal generator of the group as follows:

\[
\text{Ad}(\exp(\epsilon \Gamma_i))\Gamma_j = e^{\epsilon \Gamma_i} \Gamma_j e^{-\epsilon \Gamma_i} = \Gamma_j - \epsilon [\Gamma_i, \Gamma_j] + \frac{1}{2} \epsilon^2 [\Gamma_i, [\Gamma_i, \Gamma_j]] - \ldots, \tag{6.7}
\]
where \([\Gamma_i, \Gamma_j]\) is the previously defined commutator of the two operators \(\Gamma_i\) and \(\Gamma_j\).

Using this definition together with the commutator table, we compute each of the elements of the adjoint table. For example,

\[
\text{Ad}(\exp(\epsilon \Gamma_2))\Gamma_3 = \Gamma_3 - \epsilon \Gamma_2, \\
\text{Ad}(\exp(\epsilon \Gamma_3))\Gamma_2 = \Gamma_2 - \epsilon \Gamma_3, \\
\text{Ad}(\exp(\epsilon \Gamma_3))\Gamma_1 = \Gamma_1 - \epsilon \Gamma_2.
\]

so that the adjoint table can be written as

<table>
<thead>
<tr>
<th>(\text{Ad})</th>
<th>(\Gamma_1)</th>
<th>(\Gamma_2)</th>
<th>(\Gamma_3)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(\Gamma_1)</td>
<td>(\Gamma_2)</td>
<td>(\Gamma_3 - \epsilon \Gamma_1)</td>
<td></td>
</tr>
<tr>
<td>(\Gamma_2)</td>
<td>(\Gamma_1 - \epsilon \Gamma_2)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(\Gamma_3)</td>
<td>(\epsilon \Gamma_1)</td>
<td>(\epsilon \Gamma_2)</td>
<td>(\Gamma_3)</td>
</tr>
</tbody>
</table>

To find the optimal system, we begin with the nonzero vector (6.6) with \(n = 3\),

\[\Gamma = a_1 \Gamma_1 + a_2 \Gamma_2 + a_3 \Gamma_3.\]

Suppose that \(a_3 \neq 0\). We can rescale \(\Gamma\) so that \(a_3 = 1\). Acting on this with \(\text{Ad}(\exp(c_1 \Gamma_1))\) we obtain

\[\Gamma' = \text{Ad}(\exp(c_1 \Gamma_1))\Gamma = (a_1 - c_1) \Gamma_1 + a_2 \Gamma_2 + \Gamma_3 = a_2 \Gamma_2 + \Gamma_3,\]
where the coefficient of $\Gamma_1$ has been eliminated by choosing $c_1 = a_1$. Acting on $\Gamma^I$ with $\text{Ad}(\exp(c_2\Gamma_2))$ we obtain

$$
\Gamma^{II} = \text{Ad}(\exp(c_2\Gamma_2))\Gamma^I = (a_2 - 2c_2)\Gamma_2 + \Gamma_3
$$

$$
= \Gamma_3,
$$

where the coefficient of $\Gamma_2$ has been eliminated by choosing $c_2 = a_2/2$. Therefore, any one-dimensional subalgebra spanned by $\Gamma$ with $a_3 \neq 0$ is equivalent to $\Gamma_3$. Any remaining one-dimensional sub-algebras are spanned by $\Gamma$ with $a_3 = 0$. If $a_1 \neq 0$ we can rescale $\Gamma$ so that $a_1 = 1$. Acting on this with $\text{Ad}(\exp(c_3\Gamma_3))$ we obtain

$$
\Gamma^I = \text{Ad}(\exp(c_3\Gamma_3))\Gamma = e^{c_3}\Gamma_1 + a_2e^{2c_3}\Gamma_2,
$$

which is a scalar multiple of

$$
\Gamma^{II} = \Gamma_1 + a_2e^{c_3}\Gamma_2.
$$

So, depending on the sign of $a_2$ we can choose $c_3$ so that the coefficient of $\Gamma_2$ is +1, -1, or 0. Therefore, any one-dimensional subalgebra spanned by $\Gamma$ with $a_3 = 0$, $a_1 \neq 0$ is equivalent to either $\Gamma_1 + \Gamma_2$, $\Gamma_1 - \Gamma_2$ or $\Gamma_1$. Any remaining one-dimensional subalgebras are spanned by $\Gamma$ with $a_3 = a_1 = 0$, so that the final element of the optimal system is $\Gamma_2$.

Thus, the optimal system is given by

$$
\left\{ \Gamma_1, \Gamma_2, \Gamma_1 \pm \Gamma_2, \Gamma_3, \right\}.
$$
Reduction of the governing equations by each element of the optimal system would enable us to obtain a complete set of reductions.

Using this method, we can ensure that a minimal complete set of symmetries of our systems of equations (6.2) and (6.3) is investigated. It must also be remembered that an optimal system is not unique, as the elements depend on the choice of the coefficients $a_i$.

### 6.3.1 Optimal system and reductions for the system of equations (6.2)

The commutator table for the Lie algebra spanned by (6.4) is

<table>
<thead>
<tr>
<th></th>
<th>$\Gamma_1$</th>
<th>$\Gamma_2$</th>
<th>$\Gamma_3$</th>
<th>$\Gamma_4$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\Gamma_1$</td>
<td>0</td>
<td>0</td>
<td>$-(m-1)\Gamma_1$</td>
<td>$-n\Gamma_1$</td>
</tr>
<tr>
<td>$\Gamma_2$</td>
<td>0</td>
<td>0</td>
<td>$-2(m-1)\Gamma_2$</td>
<td>$-2n\Gamma_2$</td>
</tr>
<tr>
<td>$\Gamma_3$</td>
<td>$(m-1)\Gamma_1$</td>
<td>$2(m-1)\Gamma_2$</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>$\Gamma_4$</td>
<td>$n\Gamma_1$</td>
<td>$2n\Gamma_2$</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

To compute the adjoint representation, we use (6.7) together with the commutator table. For example,

\[
\text{Ad}(\exp(\epsilon\Gamma_1))\Gamma_3 = \Gamma_3 - \epsilon[\Gamma_1, \Gamma_3] + \frac{1}{2} \epsilon^2 [\Gamma_1, [\Gamma_1, \Gamma_3]] - \ldots
\]

\[
= \Gamma_3 + \epsilon(m - 1)\Gamma_1,
\]

\[
\text{Ad}(\exp(\epsilon\Gamma_3))\Gamma_1 = \Gamma_1 - \epsilon[\Gamma_3, \Gamma_1] + \frac{1}{2} \epsilon^2 [\Gamma_3, [\Gamma_3, \Gamma_1]] - \ldots
\]
\[ \begin{align*}
\Gamma_1 & = \Gamma_1 - \epsilon(m - 1)\Gamma_1 + \frac{1}{2}\epsilon^2(m - 1)^2\Gamma_1 - \ldots \\
& = e^{-\epsilon(m-1)}\Gamma_1, \\
\end{align*} \]

etc, so that the adjoint table is given by

<table>
<thead>
<tr>
<th>Ad</th>
<th>(\Gamma_1)</th>
<th>(\Gamma_2)</th>
<th>(\Gamma_3)</th>
<th>(\Gamma_4)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(\Gamma_1)</td>
<td>(\Gamma_1)</td>
<td>(\Gamma_2)</td>
<td>(\Gamma_3 + \epsilon(m - 1)\Gamma_1)</td>
<td>(\Gamma_4 + \epsilon n\Gamma_1)</td>
</tr>
<tr>
<td>(\Gamma_2)</td>
<td>(\Gamma_1)</td>
<td>(\Gamma_2)</td>
<td>(\Gamma_3 + 2\epsilon(m - 1)\Gamma_2)</td>
<td>(\Gamma_4 + 2\epsilon n\Gamma_2)</td>
</tr>
<tr>
<td>(\Gamma_3)</td>
<td>(e^{-\epsilon(m-1)}\Gamma_1)</td>
<td>(e^{-2\epsilon(m-1)}\Gamma_2)</td>
<td>(\Gamma_3)</td>
<td>(\Gamma_4)</td>
</tr>
<tr>
<td>(\Gamma_4)</td>
<td>(e^{-\epsilon n\Gamma_1})</td>
<td>(e^{-2\epsilon n\Gamma_2})</td>
<td>(\Gamma_3)</td>
<td>(\Gamma_4)</td>
</tr>
</tbody>
</table>

To find the optimal system, we begin with the nonzero vector (6.6) where \(n = 4\)

\[ \Gamma = a_1\Gamma_1 + a_2\Gamma_2 + a_3\Gamma_3 + a_4\Gamma_4 \quad (6.8) \]

and simplify the \(a_i\) as much as possible by careful applications of adjoint maps to \(\Gamma\). Assuming that \(a_4 \neq 0\) we can rescale \(\Gamma\) so that \(a_4 = 1\). Acting on this with \(\text{Ad}(\exp(c_1\Gamma_1))\) we obtain

\[ \Gamma^I = \text{Ad}(\exp(c_1\Gamma_1))\Gamma = (a_1 + c_1a_3(m - 1) + c_1n)\Gamma_1 + a_2\Gamma_2 + a_3\Gamma_3 + \Gamma_4 \]

\[ = a_2\Gamma_2 + a_3\Gamma_3 + a_4\Gamma_4, \]

where the coefficient of \(\Gamma_1\) is eliminated by choosing

\[ c_1 = \frac{-a_1}{a_3(m - 1) + n} \quad \text{provided} \quad a_3 \neq \frac{-n}{m - 1}. \]

The case \(a_3 = -n/(m - 1)\) must be examined later (recall \(m \neq 1\)). Acting on \(\Gamma^I\)
with $\text{Ad}(\exp(c_2 \Gamma_2))$ we obtain

$$
\Gamma_{II} = \text{Ad}(\exp(c_2 \Gamma_2)) \Gamma_I = (a_2 + 2a_3 c_2 (m - 1) + 2c_2 n) \Gamma_2 + a_3 \Gamma_3 + \Gamma_4
$$

$$
= a_3 \Gamma_3 + \Gamma_4,
$$

where the coefficient of $\Gamma_2$ is eliminated by choosing

$$
c_2 = \frac{-a_2}{2(a_3 (m - 1) + n)} \quad \text{provided} \quad a_3 \neq \frac{-n}{m - 1}.
$$

We will consider the case $a_3 = -n/(m - 1)$ later. Therefore, every one-dimensional sub-algebra spanned by (6.8) with $a_4 \neq 0$ is equivalent to the sub-algebra spanned by $c \Gamma_3 + \Gamma_4$, where $c$ is a constant. Any remaining one-dimensional sub-algebras are spanned by (6.8) with $a_4 = 0$. Assuming that $a_3 \neq 0$ we rescale so that $a_3 = 1$.

Acting on this with $\text{Ad}(\exp(c_3 \Gamma_1))$ we obtain

$$
\Gamma^I = \text{Ad}(\exp(c_3 \Gamma_1)) \Gamma^I = (a_1 + c_3 (m - 1)) \Gamma_1 + a_2 \Gamma_2 + \Gamma_3
$$

$$
= a_2 \Gamma_2 + \Gamma_3,
$$

where the coefficient of $\Gamma_1$ is eliminated by choosing

$$
c_3 = \frac{-a_1}{m - 1}.
$$

Acting on $\Gamma^I$ with $\text{Ad}(\exp(c_4 \Gamma_2))$ we obtain

$$
\Gamma_{II} = \text{Ad}(\exp(c_4 \Gamma_2)) \Gamma^I = (a_2 + 2c_4 (m - 1)) \Gamma_2 + \Gamma_3
$$

$$
= \Gamma_3,
$$
where the coefficient of $\Gamma_2$ is eliminated by choosing

$$c_4 = \frac{-a_2}{2(m-1)}.$$ 

Any sub-algebra spanned by (6.8) with $a_4 = 0$, $a_3 \neq 0$ is equivalent to the sub-algebra spanned by $\Gamma_3$. Any remaining one-dimensional subalgebras are spanned by (6.8) with $a_3 = a_4 = 0$. Assuming that $a_1 \neq 0$, we rescale so that $a_1 = 1$. Acting on this with $\text{Ad}(\exp(c_5\Gamma_4))$, we obtain

$$\Gamma^I = \text{Ad}(\exp(c_5\Gamma_4))\Gamma = e^{-c_5 n}\Gamma_1 + a_2e^{-2c_5 n}\Gamma_2,$$

which is a scalar multiple of

$$\Gamma^{II} = \Gamma_1 + a_2e^{-c_5 n}\Gamma_2.$$ 

So, depending on the sign of $a_2$, we choose $c_5$ so that the coefficient of $\Gamma_2$ is $+1$, $-1$ or $0$. Therefore, any one-dimensional subalgebra spanned by (6.8) with $a_3 = a_4 = 0$, $a_1 \neq 0$ is equivalent to either $\Gamma_1 + \Gamma_2$, $\Gamma_1 - \Gamma_2$ or $\Gamma_1$. Any remaining one-dimensional subalgebras are spanned by (6.8) with $a_1 = a_3 = a_4 = 0$, so that the final element of the optimal system is $\Gamma_2$.

We must now consider the case when $a_3 = -n/(m-1)$, so that (6.8) can be written as

$$\Gamma = a_1\Gamma_1 + a_2\Gamma_2 - \frac{n}{m-1}\Gamma_3 + \Gamma_4.$$ 

Acting on this with $\text{Ad}(\exp(c_6\Gamma_4))$ we obtain

$$\Gamma^I = \text{Ad}(\exp(c_6\Gamma_4))\Gamma = a_1 e^{-c_6 n}\Gamma_1 + a_2e^{-2c_6 n}\Gamma_2 - \frac{n}{m-1}\Gamma_3 + \Gamma_4.$$
Chapter 6: Symmetry analysis of related systems of equations

If \( a_1 \neq 0 \), depending on the sign of \( a_1 \), we choose \( c_6 \) so that the coefficient of \( \Gamma_1 \) is +1 or -1, so that we have

\[
\pm \Gamma_1 + c \Gamma_2 - \frac{n}{m-1} \Gamma_3 + \Gamma_4,
\]

where \( c \) is a constant. If \( a_1 = 0 \), we can choose \( c_6 \) so that the coefficient of \( \Gamma_2 \) is +1, -1 or 0 so that we have

\[
\pm \Gamma_2 - \frac{n}{m-1} \Gamma_3 + \Gamma_4, \quad \frac{-n}{m-1} \Gamma_3 + \Gamma_4.
\]

Thus, the optimal system is given by

\[
\begin{align*}
\Gamma_1, \quad \Gamma_2, \quad \Gamma_1 \pm \Gamma_2, \quad \Gamma_3, \quad c \Gamma_3 + \Gamma_4, \\
\pm \Gamma_2 - \frac{n}{m-1} \Gamma_3 + \Gamma_4, \quad \pm \Gamma_1 + c \Gamma_2 - \frac{n}{m-1} \Gamma_3 + \Gamma_4
\end{align*}
\]

(6.9)

This optimal system can be used to construct a complete set of reduced equations. As an example, consider the 5th element of the optimal system with \( c = -n/(m-1) \), so that the symmetry is defined by

\[
\frac{-n}{m-1} \Gamma_3 + \Gamma_4 = \frac{-2n}{m-1} p \frac{\partial}{\partial p} + 2q \frac{\partial}{\partial q}.
\]

The corresponding characteristic equation is given by

\[
\frac{dp}{\frac{2n}{m-1}p} = \frac{dq}{2q} = \frac{dx}{0} = \frac{dt}{0}.
\]

Integrating the first two expressions, we obtain the invariant

\[
\phi = p(x, t) q(x, t)^r \quad \text{where} \quad r = \frac{n}{m-1}.
\]
Integrating the last two expressions, we obtain the functional forms

\[ x = u(\phi), \quad t = v(\phi). \]

The functional forms must now be substituted into the governing equations (6.2) where

\[ p_t = \frac{1}{t_p} \quad \text{where} \quad t_p = v'(\phi)q^r, \]

\[ p_{xx} = -\frac{1}{x_p^3}x_{pp} \quad \text{where} \quad x_p = u'(\phi)q^r \quad \text{and} \quad x_{pp} = u''(\phi)q^{2r}, \]

\[ q_t = \frac{1}{t_q} \quad \text{where} \quad t_q = v'(\phi)rpq^{r-1}, \]

\[ q_{xx} = -\frac{1}{x_q^3}x_{qq} \quad \text{where} \quad x_q = u'(\phi)rpq^{r-1} \]

and \[ x_{qq} = u''(\phi)r^2p^2q^{2r-2} + u'(\phi)r(r - 1)pq^{r-2}. \]

Substituting these expressions into the governing equation and simplifying, we obtain the following ODEs

\[ u'' + \frac{(u')^3}{v'} - R_1\phi^m(u')^3 = 0, \]

\[ r\phi u'' + \frac{r\phi(u')^3}{v'} + (r - 1)u' - R_2\phi^{m+1}(u')^3 = 0, \]

where the prime denotes differentiation with respect to \( \phi \).

Table 6.1 shows the complete set of reduced equations using the optimal system (6.9). The symmetries \( \Gamma_1 \) and \( \Gamma_2 \) represent translations in space and time respectively, and the reduced equations are not given for these cases.
### Reduced equations

\[
\Gamma_1 \pm \Gamma_2 = \frac{\partial}{\partial x} \pm \frac{\partial}{\partial t}
\]

\[
\Gamma_3 = 2p \frac{\partial}{\partial p} - (m - 1)x \frac{\partial}{\partial x} - 2(m - 1)t \frac{\partial}{\partial t}
\]

\[
c\Gamma_3 + \Gamma_4 = 2cp \frac{\partial}{\partial p} + 2q \frac{\partial}{\partial q} - (c(m - 1) + nx) \frac{\partial}{\partial x} - 2(c(m - 1) + nt) \frac{\partial}{\partial t}
\]

If \( c = -\frac{n}{m - 1} = -r \),

\[
\frac{-n}{m - 1} \Gamma_3 + \Gamma_4 = \frac{-2n}{m - 1}p \frac{\partial}{\partial p} + 2q \frac{\partial}{\partial q}
\]

\[
u'' + \frac{1}{2} \phi u' + \frac{1}{m - 1} u + R_1 u^m v^n = 0
\]

\[
\phi(x) = p(x,t), \quad \psi(x) = q(x,t)
\]

\[
u'' + \frac{1}{2} \phi v' + R_2 u^{m-1} v^{n+1} = 0
\]

with \( p(x,t) = u(\phi), q(x,t) = v(\phi), \phi = x \pm t \)

\[
u'' + \frac{1}{2} \phi u' + \frac{1}{m - 1} u + R_1 n u^m v^n = 0
\]

\[
v'' + \frac{1}{2} \phi v' + R_2 u^{m-1} v^{n+1} = 0
\]

with \( p(x,t) = u(\phi)^{1/(m-1)}, q(x,t) = v(\phi), \phi = xt^{-1/2} \)

\[
u'' + \frac{1}{2} \phi u' + \frac{c}{c(m - 1) + n} u + R_1 u^m v^n = 0
\]

\[
v'' + \frac{1}{2} \phi v' + \frac{1}{c(m - 1) + n} v + R_2 u^{m-1} v^{n+1} = 0
\]

with \( p(x,t) = u(\phi)^{-\frac{c}{c(m - 1) + n}}, q(x,t) = v(\phi) t^{-\frac{c}{c(m - 1) + n}}, \phi = xt^{-1/2} \), provided \( c \neq \frac{-n}{m - 1} \)

\[
u'' + \frac{(u')^3}{v'} - R_1 \phi \phi''(u')^3 = 0
\]

\[
r \phi u'' + \frac{r \phi(u')^3}{v'} + (r - 1) u' - R_2 r^2 \phi^{m+1}(u')^3 = 0
\]

with \( x = u(\phi), t = v(\phi), \phi = p(x,t)q(x,t)^r \)

continued on next page
continued from previous page

\[ \pm \Gamma_2 - \frac{n}{m-1} \Gamma_3 + \Gamma_4 = -\frac{2n}{m-1} p \frac{\partial}{\partial p} + 2q \frac{\partial}{\partial q} \pm \frac{\partial}{\partial t} \]

\[ \pm \Gamma_1 + c \Gamma_2 - \frac{n}{m-1} \Gamma_3 + \Gamma_4 = -\frac{2n}{m-1} p \frac{\partial}{\partial p} + 2q \frac{\partial}{\partial q} \pm \frac{\partial}{\partial x} + c \frac{\partial}{\partial t} \]

if \( c = 0 \)

\[ \pm \Gamma_1 - \frac{n}{m-1} \Gamma_3 + \Gamma_4 = -\frac{2n}{m-1} p \frac{\partial}{\partial p} + 2q \frac{\partial}{\partial q} \pm \frac{\partial}{\partial x} \]

\[ u'' \pm \frac{2n}{m-1} u + R_1 u^m v^n = 0 \]

\[ v'' \mp 2v + R_2 u^{m-1} v^{n+1} = 0 \]

with \( p(x, t) = u(\phi) \exp \left( \mp \frac{2n}{m-1} t \right) \),

\[ q(x, t) = v(\phi) \exp(\pm 2t), \phi = x \]

\[ c^2 u'' + u' + \frac{2n}{c(m-1)} u + R_1 u^m v^n = 0 \]

\[ c^2 v'' + v' - \frac{2}{c} v + R_2 u^{m-1} v^{n+1} = 0 \]

with \( p(x, t) = u(\phi) \exp \left( -\frac{2n}{c(m-1)} t \right) \),

\[ q(x, t) = v(\phi) \exp \left( \frac{2}{c} t \right), \phi = \pm cx - t, \text{ provided } c \neq 0 \]

\[ u' - \left( \frac{2n}{m-1} \right)^2 u - R_1 u^m v^n = 0 \]

\[ v' - 4v + R_2 u^{m-1} v^{n+1} = 0 \]

with \( p(x, t) = u(\phi) \exp \left( \pm \frac{2n}{m-1} x \right) \),

\[ q(x, t) = v(\phi) \exp(\pm 2x), \phi = t \]

Table 6.1: Reduced ODEs of the system of equations (6.2) by the optimal system (6.9)
6.3.2 Optimal system and reductions for the system of

equations (6.3)

The commutator table for the Lie algebra spanned by (6.5) is given by

\[
\begin{array}{cccccc}
\Gamma_1 & \Gamma_2 & \Gamma_3 & \Gamma_4 & \Gamma_5 \\
\hline
\Gamma_1 & 0 & 0 & 0 & \Gamma_3 & \frac{1}{2} \Gamma_1 \\
\Gamma_2 & 0 & 0 & 0 & -2 \Gamma_1 & \Gamma_2 \\
\Gamma_3 & 0 & 0 & 0 & 0 & 0 \\
\Gamma_4 & -\Gamma_3 & 2 \Gamma_1 & 0 & 0 & -\frac{1}{2} \Gamma_4 \\
\Gamma_5 & -\frac{1}{2} \Gamma_1 & -\Gamma_2 & 0 & \frac{1}{2} \Gamma_4 & 0 \\
\end{array}
\]

To compute the adjoint representation, we use (6.7) together with the commutator table. For example,

\[
\text{Ad}(\exp(\epsilon \Gamma_2)) \Gamma_5 = \Gamma_5 - \epsilon [\Gamma_2, \Gamma_5] + \frac{1}{2} \epsilon^2 [\Gamma_2, [\Gamma_2, \Gamma_5]] - \ldots
\]

\[
= \Gamma_5 - \epsilon \Gamma_2
\]

\[
\text{Ad}(\exp(\epsilon \Gamma_5)) \Gamma_2 = \Gamma_2 - \epsilon [\Gamma_5, \Gamma_2] + \frac{1}{2} \epsilon^2 [\Gamma_5, [\Gamma_5, \Gamma_2]] - \ldots
\]

\[
= \Gamma_2 + \epsilon \Gamma_2 + \frac{1}{2} \epsilon^2 \Gamma_2 - \ldots
\]

\[
= \epsilon \Gamma_3
\]

etc, so that the adjoint table is given by
Chapter 6: Symmetry analysis of related systems of equations

<table>
<thead>
<tr>
<th>Ad</th>
<th>$\Gamma_1$</th>
<th>$\Gamma_2$</th>
<th>$\Gamma_3$</th>
<th>$\Gamma_4$</th>
<th>$\Gamma_5$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\Gamma_1$</td>
<td>$\Gamma_1$</td>
<td>$\Gamma_2$</td>
<td>$\Gamma_3$</td>
<td>$\Gamma_4 - \epsilon \Gamma_3$</td>
<td>$\Gamma_5 - \frac{1}{2} \epsilon \Gamma_1$</td>
</tr>
<tr>
<td>$\Gamma_2$</td>
<td>$\Gamma_1$</td>
<td>$\Gamma_2$</td>
<td>$\Gamma_3$</td>
<td>$\Gamma_4 + 2 \epsilon \Gamma_1$</td>
<td>$\Gamma_5 - \epsilon \Gamma_2$</td>
</tr>
<tr>
<td>$\Gamma_3$</td>
<td>$\Gamma_1$</td>
<td>$\Gamma_2$</td>
<td>$\Gamma_3$</td>
<td>$\Gamma_4$</td>
<td>$\Gamma_5$</td>
</tr>
<tr>
<td>$\Gamma_4$</td>
<td>$\Gamma_1 + \epsilon \Gamma_3$</td>
<td>$\Gamma_2 - 2 \epsilon \Gamma_1 - \epsilon^2 \Gamma_3$</td>
<td>$\Gamma_3$</td>
<td>$\Gamma_4$</td>
<td>$\Gamma_5 + \frac{1}{2} \epsilon \Gamma_4$</td>
</tr>
<tr>
<td>$\Gamma_5$</td>
<td>$e^{\epsilon/2} \Gamma_1$</td>
<td>$e^\epsilon \Gamma_2$</td>
<td>$\Gamma_3$</td>
<td>$e^{-\epsilon/2} \Gamma_4$</td>
<td>$\Gamma_5$</td>
</tr>
</tbody>
</table>

In order to find the optimal system, we begin with (6.6) where $n = 5$,

$$\Gamma = a_1 \Gamma_1 + a_2 \Gamma_2 + a_3 \Gamma_3 + a_4 \Gamma_4 + a_5 \Gamma_5$$

and simplify the $a_i$ as much as possible by careful applications of adjoint maps to $\Gamma$.

Assuming $a_5 \neq 0$ we can set $a_5 = 1$. Acting on this with $\text{Ad}(\exp(c_1 \Gamma_2))$ we obtain

$$\Gamma^I = \text{Ad}(\exp(c_1 \Gamma_2)) = (a_1 + 2c_1 a_4) \Gamma_1 + (a_2 - c_1) \Gamma_2 + a_3 \Gamma_3 + a_4 \Gamma_4 + \Gamma_5$$

$$= (a_1 + 2a_2 a_4) \Gamma_1 + a_3 \Gamma_3 + a_4 \Gamma_4 + \Gamma_5,$$

where the coefficient of $\Gamma_2$ is eliminated by choosing $c_1 = a_2$. Acting on this with $\text{Ad}(\exp(c_2 \Gamma_1))$ we obtain

$$\Gamma^{II} = \text{Ad}(\exp(c_2 \Gamma_1)) = (a_1 + 2a_1 a_4 - \frac{1}{2} c_2) \Gamma_1 + (a_3 - c_2 a_4) \Gamma_3 + a_4 \Gamma_4 + \Gamma_5$$

$$= (a_3 - 2a_1 a_4 - 4a_2 a_4^2) \Gamma_3 + a_4 \Gamma_4 + \Gamma_5,$$

where the coefficient of $\Gamma_1$ is eliminated by choosing $c_2 = 2a_1 + 4a_2 a_4$. Acting on this with $\text{Ad}(\exp(c_3 \Gamma_4))$ we obtain

$$\Gamma^{III} = \text{Ad}(\exp(c_3 \Gamma_4)) = (a_3 - 2a_1 a_4 - 4a_2 a_4^2) \Gamma_3 + (a_4 + \frac{1}{2} c_3) \Gamma_4 + \Gamma_5$$
where the coefficient of $\Gamma_4$ is eliminated by choosing $c_3 = -2a_4$. Therefore, every one-dimensional subalgebra spanned by (6.10) with $a_5 \neq 0$ is equivalent to the subalgebra spanned by $c\Gamma_3 + \Gamma_5$. Any remaining subalgebras are spanned by the vector (6.10) with $a_5 = 0$. If $a_4 \neq 0$, we can rescale so that $a_4 = 1$. Acting on this with $\text{Ad}(\exp(c_4\Gamma_1))$ we obtain

$$\Gamma^I = \text{Ad}(\exp(c_4\Gamma_1)) = a_1\Gamma_1 + a_2\Gamma_2 + (a_3 - c_4)\Gamma_3 + \Gamma_4$$

$$= a_1\Gamma_1 + a_2\Gamma_2 + \Gamma_4,$$

where the coefficient of $\Gamma_3$ is eliminated by choosing $c_4 = a_3$. Acting on this with $\text{Ad}(\exp(c_5\Gamma_2))$ we obtain

$$\Gamma^{II} = \text{Ad}(\exp(c_5\Gamma_2)) = (a_1 + 2c_5)\Gamma_1 + a_2\Gamma_2 + \Gamma_4$$

$$= a_2\Gamma_2 + \Gamma_4,$$

where the coefficient of $\Gamma_1$ is eliminated by choosing $c_5 = -1/2 a_1$. Acting on this with $\text{Ad}(\exp(c_6\Gamma_3))$ we obtain

$$\Gamma^{III} = \text{Ad}(\exp(c_6\Gamma_3)) = a_2e^{c_6}\Gamma_2 + e^{-c_6/2}\Gamma_4,$$

which is a scalar multiple of

$$\Gamma^{IV} = a_2e^{3c_6/2}\Gamma_2 + \Gamma_4.$$
is equivalent to one spanned by $\Gamma_2 + \Gamma_4$, $-\Gamma_2 + \Gamma_4$ or $\Gamma_4$. Any remaining one-dimensional subalgebras are spanned by the vector (6.10) with $a_4 = a_5 = 0$. If $a_2 \neq 0$, we can rescale so that $a_2 = 1$. Acting on this with $\text{Ad}(\exp(c_7 \Gamma_4))$ we obtain

$$
\Gamma^I = \text{Ad}(\exp(c_7 \Gamma_4)) = (a_1 - 2c_7)\Gamma_1 + \Gamma_2 + (a_1 c_7 - c_7^2 + a_3)\Gamma_3
$$

$$
= \Gamma_2 + \left(\frac{1}{2}a_1^2 + a_3\right)\Gamma_3,
$$

where the coefficient of $\Gamma_1$ is eliminated by choosing $c_7 = 1/2 a_1$. Acting on this with $\text{Ad}(\exp(c_8 \Gamma_5))$ we obtain

$$
\Gamma^{II} = \text{Ad}(\exp(c_8 \Gamma_5)) = e^{c_8} \Gamma_2 + \left(\frac{1}{2}a_1^2 + a_3\right)\Gamma_3,
$$

which is a scalar multiple of

$$
\Gamma^{III} = \Gamma_2 + \left(\frac{1}{2}a_1^2 + a_3\right)e^{-c_8}\Gamma_3.
$$

So, depending on the sign of $(\frac{1}{2}a_1^2 + a_3)$, the coefficient of $\Gamma_3$ can be set to +1, -1 or 0. Therefore, every one-dimensional subalgebra spanned by (6.10) with $a_4 = a_5 = 0$, $a_2 \neq 0$ is equivalent to one spanned by $\Gamma_2 + \Gamma_3$, $\Gamma_2 - \Gamma_3$ or $\Gamma_2$. Any remaining one-dimensional subalgebras are spanned by the vector (6.10) with $a_2 = a_4 = a_5 = 0$. If $a_1 \neq 0$, we can rescale so that $a_1 = 1$. Acting on this with $\text{Ad}(\exp(c_9 \Gamma_5))$ we obtain

$$
\Gamma^I = \text{Ad}(\exp(c_9 \Gamma_5)) = e^{c_9/2} \Gamma_1 + a_3\Gamma_3,
$$

which is a scalar multiple of

$$
\Gamma^{II} = \Gamma_1 + a_3 e^{-c_9/2}\Gamma_3.
$$
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So, depending on the sign of $a_3$, the coefficient of $\Gamma_3$ can be set to $+1$, $-1$ or $0$. Therefore, every one-dimensional subalgebra spanned by (6.10) with $a_2 = a_4 = a_5 = 0$, $a_1 = 1$ is equivalent to one spanned by $\Gamma_1 + \Gamma_3$, $\Gamma_1 - \Gamma_3$ or $\Gamma_1$. Any remaining one-dimensional subalgebras are spanned by (6.10) with $a_1 = a_2 = a_4 = a_5 = 0$, so that the final element of the optimal system is $\Gamma_3$. Thus, the optimal system is given by

$$\left\{ \Gamma_1, \Gamma_1 \pm \Gamma_3, \Gamma_2, \Gamma_2 \pm \Gamma_3, \Gamma_3, \pm \Gamma_2 + \Gamma_4, \Gamma_4, c\Gamma_3 + \Gamma_5 \right\}. \quad (6.11)$$

This optimal system can be used to construct a complete set of reduced equations. As an example, consider the symmetry given by

$$\Gamma_2 + \Gamma_4 = xp \frac{\partial}{\partial p} + xq \frac{\partial}{\partial q} - 2t \frac{\partial}{\partial x} + \frac{\partial}{\partial t},$$

with the corresponding characteristic equation

$$\frac{dp}{xp} = \frac{dq}{xq} = \frac{dx}{-2t} = \frac{dt}{1}.$$

Integrating the last two expressions we obtain the invariant

$$\phi = x + t^2.$$

Integrating the first and last, and second and last expressions, we obtain the functional forms

$$p(x, t) = u(\phi) \exp \left( xt + \frac{2}{3} t^3 \right), \quad \text{and} \quad q(x, t) = v(\phi) \exp \left( xt + \frac{2}{3} t^3 \right),$$
respectively. Substituting the expressions for $p_t$, $p_{xx}$, $q_t$ and $q_{xx}$ into equations (6.2) we obtain the system of ODEs

\[
\frac{d^2 u}{d\phi^2} - \phi u + R_1 u \left( \frac{u}{v} \right)^m = 0
\]

\[
\frac{d^2 v}{d\phi^2} - \phi v + R_2 v \left( \frac{u}{v} \right)^m = 0.
\]

Table 6.2 shows the reduced systems of ODEs for each of the generators in the optimal system (6.11). The symmetries $\Gamma_1$ and $\Gamma_2$ generate translations in space and time respectively, and the reduced equations are not given for these cases.

<table>
<thead>
<tr>
<th>Reduced equations</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\Gamma_1 \pm \Gamma_3 = \pm \frac{\partial}{\partial p} \pm \frac{q}{\partial q}$ + $\frac{\partial}{\partial x}$</td>
</tr>
<tr>
<td>$u' - u - R_1 u \left( \frac{u}{v} \right)^m = 0$</td>
</tr>
<tr>
<td>$v' - v - R_2 v \left( \frac{u}{v} \right)^m = 0$</td>
</tr>
<tr>
<td>with $p(x,t) = u(\phi)e^{\pm x}$, $q(x,t) = v(\phi)e^{\pm x}$, $\phi = t$</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Reduced equations</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\Gamma_2 \pm \Gamma_3 = \pm \frac{\partial}{\partial p} \pm \frac{q}{\partial q}$ + $\frac{\partial}{\partial t}$</td>
</tr>
<tr>
<td>$u'' \mp u + R_1 u \left( \frac{u}{v} \right)^m = 0$</td>
</tr>
<tr>
<td>$v'' \mp v + R_2 v \left( \frac{u}{v} \right)^m = 0$</td>
</tr>
<tr>
<td>with $p(x,t) = u(\phi)e^{\pm t}$, $q(x,t) = v(\phi)e^{\pm t}$, $\phi = x$</td>
</tr>
</tbody>
</table>

continued on next page
\[ \Gamma_3 = p \frac{\partial}{\partial p} + q \frac{\partial}{\partial q} \]
\[ \Gamma_4 = x p \frac{\partial}{\partial p} + x q \frac{\partial}{\partial q} - 2t \frac{\partial}{\partial x} \]
\[ \pm \Gamma_2 + \Gamma_4 = x p \frac{\partial}{\partial p} + x q \frac{\partial}{\partial q} - 2t \frac{\partial}{\partial x} \pm \frac{\partial}{\partial t} \]
\[ \pm \Gamma_2 + \Gamma_4 = c p \frac{\partial}{\partial p} + \left( c + \frac{1}{m} \right) q \frac{\partial}{\partial q} + \frac{1}{2} x^2 \frac{\partial}{\partial x} + t \frac{\partial}{\partial t} \]
\[ u'' + \frac{(u')^3}{v'} - R_1 \phi^{m+1}(u')^3 = 0 \]
\[ \phi u'' + \frac{\phi(u')^3}{v'} + 2u' + R_2 \phi^{m+2}(u')^3 = 0 \]
with \( x = u(\phi), \ t = v(\phi), \ \phi = \frac{p(x, t)}{q(x, t)} \)
\[ u' + \frac{1}{2\phi} u - R_1 u \left( \frac{u}{v} \right)^m = 0 \]
\[ v' + \frac{1}{2\phi} v - R_2 v \left( \frac{u}{v} \right)^m = 0 \]
with \( p(x, t) = u(\phi)e^{-x^2/4t}, \ q(x, t) = v(\phi)e^{-x^2/4t}, \ \phi = t \)
\[ u'' \mp \phi u + R_1 u \left( \frac{u}{v} \right)^m = 0 \]
\[ v'' \mp \phi v + R_2 v \left( \frac{u}{v} \right)^m = 0 \]
with \( p(x, t) = u(\phi)e^{xt^2/3t^3}, \ q(x, t) = v(\phi)e^{xt^2/3t^3}, \ \phi = x \pm t^2 \)
\[ u'' + \frac{1}{2} \phi u' - cu + R_1 u \left( \frac{u}{v} \right)^m = 0 \]
\[ v'' + \frac{1}{2} \phi v' - \left( c + \frac{1}{m} \right) v + R_2 v \left( \frac{u}{v} \right)^m = 0 \]
with \( p(x, t) = u(\phi)t^c, \ q(x, t) = v(\phi)t^{-c-1/m}, \ \phi = xt^{-1/2} \)

Table 6.2: Reduced ODEs of the system of equations (6.3) by the optimal system (6.11)
6.4 Further reduction of one system of ODEs

In this section we examine one of the reduced systems of equations in more detail.

Consider the symmetry of equations (6.3) given by
\[
\Gamma_2 - c\Gamma_4 = -cxp \frac{\partial}{\partial p} - cxq \frac{\partial}{\partial q} + 2ct \frac{\partial}{\partial x} + \frac{\partial}{\partial t},
\]
where \(c\) is a constant (the fourth symmetry of the optimal system in Table 6.2 with an added constant). This symmetry has the corresponding characteristic equation
\[
\frac{dp}{-cxp} = \frac{dq}{-cxq} = \frac{dx}{2ct} = \frac{dt}{1}.
\]
Integrating the last two expressions, we obtain the invariant
\[
\phi = x - ct^2.
\]
Integrating the first and last, and second and last equations respectively, we obtain the functional forms
\[
p(x,t) = u(\phi) \exp \left( \frac{2}{3} c^2 t^3 - cxt \right), \quad \text{and} \quad q(x,t) = v(\phi) \exp \left( \frac{2}{3} c^2 t^3 - cxt \right). \quad (6.12)
\]
Substituting the expressions for \(p_t, p_{xx}, q_t\) and \(q_{xx}\) into equations (6.3) we obtain
\[
\begin{align*}
u'' + c\phi u + R_1 u \left( \frac{u}{v} \right)^m &= 0 \\
v'' + c\phi v + R_2 v \left( \frac{u}{v} \right)^m &= 0
\end{align*} \quad (6.13)
\]
where the prime denotes differentiation with respect to \(\phi\).

This system of equations is found to be invariant under the one-parameter symmetry group
\[
\Lambda = u \frac{\partial}{\partial u} + v \frac{\partial}{\partial v},
\]
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suggesting that the system of equations can be further reduced. The system (6.13) of two second order ODEs can be re-written as a system of four first order ODEs. Setting \( w = u' \) and \( z = v' \), we can write

\[
\begin{align*}
    u' &= w \\
    v' &= z \\
    w' &= -c\phi u - R_1 u \left( \frac{u}{v} \right)^m \\
    z' &= -c\phi v - R_2 v \left( \frac{u}{v} \right)^m.
\end{align*}
\]

(6.14)

This system of equations possesses the symmetry given by the first prolongation of the symmetry possessed by the corresponding system of two second order ODEs,

\[
\Lambda^I = \Lambda^{(1)} = 0 \frac{\partial}{\partial \phi} + u \frac{\partial}{\partial u} + v \frac{\partial}{\partial v} + w \frac{\partial}{\partial w} + z \frac{\partial}{\partial z}.
\]

We can now find a change of variables that will reduce the system of four first order ODEs to a system of three first order ODEs together with a quadrature.

In order to find the change of variables, we specify that we require

\[
\Lambda^{II} = 0 \frac{\partial}{\partial \sigma} + 1 \frac{\partial}{\partial y_1} + 0 \frac{\partial}{\partial y_2} + 0 \frac{\partial}{\partial y_3} + 0 \frac{\partial}{\partial y_4}
\]

so that the new variable \( y_1 \) will be found by a quadrature. This means that we will obtain a reduced system of four first order ODEs, three of which will be in terms of \( y_2, y_3, y_4 \) and \( \sigma \) only, and one which will give us \( y_1 \) in terms of one of the other
dependent variables. We now find that

\[
\Lambda^1(\sigma) = \left[ \frac{\partial}{\partial \phi} + u \frac{\partial}{\partial u} + v \frac{\partial}{\partial v} + w \frac{\partial}{\partial w} + z \frac{\partial}{\partial z} \right] \sigma = 0
\]

\[
\Lambda^1(y_1) = \left[ \frac{\partial}{\partial \phi} + u \frac{\partial}{\partial u} + v \frac{\partial}{\partial v} + w \frac{\partial}{\partial w} + z \frac{\partial}{\partial z} \right] y_1 = 1
\]

\[
\Lambda^1(y_2) = \left[ \frac{\partial}{\partial \phi} + u \frac{\partial}{\partial u} + v \frac{\partial}{\partial v} + w \frac{\partial}{\partial w} + z \frac{\partial}{\partial z} \right] y_2 = 0
\]

\[
\Lambda^1(y_3) = \left[ \frac{\partial}{\partial \phi} + u \frac{\partial}{\partial u} + v \frac{\partial}{\partial v} + w \frac{\partial}{\partial w} + z \frac{\partial}{\partial z} \right] y_3 = 0
\]

\[
\Lambda^1(y_4) = \left[ \frac{\partial}{\partial \phi} + u \frac{\partial}{\partial u} + v \frac{\partial}{\partial v} + w \frac{\partial}{\partial w} + z \frac{\partial}{\partial z} \right] y_4 = 0.
\]

These have the characteristic equations and corresponding functional forms

\[
\frac{d\phi}{\sigma} = \frac{du}{u} = \frac{dv}{v} = \frac{dw}{w} = \frac{dz}{z} = \frac{dy_1}{y_1}
\]

so that \(\sigma = f_1(\phi) + f_2\left(\frac{u}{v}\right) + f_3\left(\frac{w}{z}\right) + f_4\left(\frac{w}{u}\right)\),

\[
\frac{d\phi}{\sigma} = \frac{du}{u} = \frac{dv}{v} = \frac{dw}{w} = \frac{dz}{z} = \frac{dy_2}{y_2}
\]

so that \(y_1 = \ln u + g_1(\phi) + g_2\left(\frac{u}{v}\right) + g_3\left(\frac{w}{z}\right) + g_4\left(\frac{w}{u}\right)\),

\[
\frac{d\phi}{\sigma} = \frac{du}{u} = \frac{dv}{v} = \frac{dw}{w} = \frac{dz}{z} = \frac{dy_3}{y_3}
\]

so that \(y_2 = h_1(\phi) + h_2\left(\frac{u}{v}\right) + h_3\left(\frac{w}{z}\right) + h_4\left(\frac{w}{u}\right)\),

\[
\frac{d\phi}{\sigma} = \frac{du}{u} = \frac{dv}{v} = \frac{dw}{w} = \frac{dz}{z} = \frac{dy_4}{y_4}
\]

so that \(y_3 = k_1(\phi) + k_2\left(\frac{u}{v}\right) + k_3\left(\frac{w}{z}\right) + k_4\left(\frac{w}{u}\right)\),

\[
\frac{d\phi}{\sigma} = \frac{du}{u} = \frac{dv}{v} = \frac{dw}{w} = \frac{dz}{z} = \frac{dy_4}{y_4}
\]

so that \(y_4 = l_1(\phi) + l_2\left(\frac{u}{v}\right) + l_3\left(\frac{w}{z}\right) + l_4\left(\frac{w}{u}\right)\).

From these equations, we choose

\[
\sigma = \phi, \quad y_1 = \ln u, \quad y_2 = \frac{u}{v}, \quad y_3 = \frac{w}{z}, \quad y_4 = \frac{w}{u}.
\]
By finding expressions for $dy_i/d\sigma$, we find the new system of equations to be

$$
\frac{dy_2}{d\sigma} = y_2y_4 \left( 1 - \frac{y_2}{y_3} \right)
$$

$$
\frac{dy_3}{d\sigma} = \frac{y_3}{y_4} \left[ c\sigma \left( \frac{y_3}{y_2} - 1 \right) + (y_2)^m \left( \frac{y_3}{y_2} R_2 - R_1 \right) \right]
$$

$$
\frac{dy_4}{d\sigma} = -c\sigma - R_1 y_2^m - y_4^2
$$

(6.17)

together with the quadrature

$$
\frac{dy_1}{d\sigma} = y_4.
$$

(6.18)

Notice that $y_1$ does not appear in the first three equations. If we can solve equations (6.17) for $y_2$, $y_3$ and $y_4$ (which does not appear to be easy in this case), then $y_1$ can be found by integrating (6.18). We can then transform back to our original variables using (6.16) and (6.12).
Chapter 7

Summary and Outlook

In this thesis, we have developed and analysed a number of different equations important in the modelling of population genetics. The different equations have described various situations and provided extensions to the commonly used theories.

We have reinforced the validity of using reaction-diffusion equations with cubic source terms to describe changes in the frequency of alleles in a gene pool. Although the cubic source term had been previously derived by other authors [6, 9, 56, 61, 72], its significance had not been highlighted. Similarly, the difference between the Huxley equation and traditionally used Fisher-Kolmogorov equation (with quadratic source term) had not been examined. We have made analytical and numerical comparisons to show that the cubic source term can lead to the delayed spread of an advantageous allele.

The Huxley and Fitzhugh-Nagumo equations have been quite thoroughly anal-
ysed by previous authors, as these equations have long been used to describe various other physical and biological processes. However, using the method of nonclassical symmetry analysis, we found exact solutions to these equations. Although the same solutions had already been found using the Painlevé approach [17], use of a different method of analysis provides additional insight to the problem.

In Chapter 4, we developed a system of equations to describe the change in frequency of two alleles in a population in which there are three possible alleles for the locus in question. To date, very few studies exist that examine the case in which there are greater than two possible alleles at the locus under consideration. Existing models of this type use stochastic methods (for example [48]), and we are unaware of any other deterministic models describing this situation. Using a method recently proposed by Rodrigo and Mimura [66] we introduced a nonlinear transformation to find new exact travelling wave solutions to the system of equations.

In Chapter 5, we extended the existing models to include the case of spatially dependent reproductive success rates. General dependence of the reproductive success rates on the spatial coordinate has not been previously investigated. The importance of models of this kind has been acknowledged [55], however only the simplest cases have been examined. Our aim in this Chapter was more mathematically driven – to discover what forms of spatial variability would enable us to find exact solutions to our equations. By using the methods of classical and nonclassical symmetry analysis, we were able to find a number of forms of spatial dependence that allowed us
to discover new exact solutions. We feel that one of the nontrivial forms of spatial
dependence examined in this thesis is biologically significant (5.28), and the explicit
solution that we obtained (5.34) reflects the type of gene frequency changes that
might be expected.

As stated in Chapter 5, a complete classification of the equations which explicitly
include spatial dependence (equations (5.2) and (5.3)) using Lie point symmetry
analysis is yet to be completed. We have also left the search for strictly nonclassical
symmetries of equation (5.3) as an open question.

The study of spatially dependent selectivity is a new and interesting problem,
and this topic provides great scope for future investigations. For example, studies
of the relevant steady state equations may yield information about the long time
behaviour of populations.

Finally, we have demonstrated the benefits of systematic symmetry analysis by
studying two related systems of reaction-diffusion equations. The symmetries of the
systems of equations (6.2) and (6.3) were found by Cherniha and King [18, 19, 20, 21],
however they only provide a limited number of reductions. In Chapter 6 we find the
optimal system for each of the systems of PDEs and provide a complete minimal set
of reduced ODEs. We also showed that if a symmetry is possessed by the reduced
system of ODEs, we may reduce it further in order.

There are countless possible extensions and improvements that could be made
to existing population models. As mathematical techniques and our knowledge
of biological systems and population genetics improves, models can become more
detailed and more accurate in their predictions.
Appendix A

Asymptotic travelling wave solutions for the Fisher and Huxley equations

A.1 Asymptotic travelling wave solution to the Fisher equation

Before we look for asymptotic travelling wave solutions to the Fisher equation, we nondimensionalise equation (2.14). Under the transformation

\[ \tilde{z} = \sqrt{\frac{m}{k}} z, \]
equation (2.14) becomes

\[ P_{\xi \xi} + \bar{c} P_\xi + P(1 - P) = 0, \quad (A.1) \]

where \( \bar{c} = c/\sqrt{k} \).

To find the asymptotic travelling wave solutions, we use a standard singular perturbation technique, which is the same as that used by Murray [54]. We introduce a change of variable in the vicinity of the front in such a way that we can find the solution as a Taylor expansion in a small parameter, \( \varepsilon \). We set the front at \( z = 0 \) by choosing \( P(0) = 1/2 \). Under the transformation

\[ P(z) = u(\xi), \quad \xi = \frac{z}{\bar{c}} = \sqrt{\varepsilon z}, \]

equation (A.1), and the boundary conditions on \( P \) become

\[ \varepsilon \frac{d^2 u}{d\xi^2} + \frac{du}{d\xi} + u(1 - u) = 0 \quad (A.2) \]

\[ u(-\infty) = 1, \quad u(\infty) = 0. \]

We now look for solutions of (A.2) that are a perturbation series in \( \varepsilon \). Let

\[ u(\xi; \varepsilon) = u_0(\xi) + \varepsilon u_1(\xi) + \varepsilon^2 u_2(\xi) + \ldots \quad (A.3) \]

The boundary conditions at \( \pm\infty \) and our choice that \( P(0) = 1/2 \) (which requires that \( u(0) = 1/2 \) for all \( \xi \)) give us the following conditions

\[ u_0(-\infty) = 1, \quad u_0(\infty) = 0, \quad u_0(0) = \frac{1}{2} \]

\[ u_i(\pm\infty) = 0, \quad u_i(0) = 0, \quad \text{for } i = 1, 2, \ldots \]
Substituting equation (A.3) into equation (A.2) and equating powers of $\varepsilon$ we get

$$O(1): \quad \frac{du_0}{d\xi} = -u_0(1 - u_0) \quad \Rightarrow \quad u_0(\xi) = (1 + e^{\xi})^{-1}$$

$$O(\varepsilon): \quad \frac{du_1}{d\xi} + u_1(1 - 2u_0) = -\frac{d^2u_0}{d\xi^2} \quad \Rightarrow \quad u_1(\xi) = \frac{e^{\xi}}{(1 + e^{\xi})^2} \ln \left[ \frac{4e^{\xi}}{(1 + e^{\xi})^2} \right]$$

where the constants of integration have been chosen so that the condition $u(0) = 1/2$ is satisfied.

In terms of the variables $P$ and $\tilde{\varepsilon}$ we write

$$P(\tilde{\varepsilon}; \tilde{c}) = (1 + e^{\tilde{\varepsilon}/\tilde{c}})^{-1} + \frac{1}{\tilde{c}^2} \frac{e^{\tilde{\varepsilon}/\tilde{c}}}{(1 + e^{\tilde{\varepsilon}/\tilde{c}})^2} \ln \left[ \frac{4e^{\tilde{\varepsilon}/\tilde{c}}}{(1 + e^{\tilde{\varepsilon}/\tilde{c}})^2} \right] + O(\tilde{c}^{-4}).$$

Changing back to our original variables, $z = \sqrt{k/m\tilde{\varepsilon}}$ and $c = \sqrt{km\tilde{c}}$ we find that the asymptotic travelling wave solution to equation (2.14) is

$$P(z) = (1 + e^{mz/c})^{-1} + \frac{mk}{c^2} \frac{e^{mz/c}}{1 + e^{mz/c})^2} \ln \left[ \frac{4e^{mz/c}}{(1 + e^{mz/c})^2} \right] + O(c^{-4}).$$

### A.2 Asymptotic travelling wave solution to the Huxley equation

We now follow the same process as above for the Huxley equation. Under the transformation

$$\tilde{z} = \sqrt{\frac{g}{k}} z,$$

equation (2.15) becomes

$$P_{\tilde{z}\tilde{z}} + \tilde{c}P_{\tilde{z}} + P^2(1 - P) = 0, \quad (A.4)$$
Appendix A

where \( \bar{c} = c/\sqrt{kg} \).

Applying the transformation

\[
P(z) = v(\xi), \quad \xi = \frac{z}{c} = \sqrt{\bar{c}z}
\]

to equation (A.4) and the boundary conditions, we get

\[
\varepsilon \frac{d^2v}{d\xi^2} + \frac{dv}{d\xi} + v^2(1 - v) = 0 \tag{A.5}
\]

\( v(-\infty) = 1, \quad v(\infty) = 0. \)

We now look for solutions of (A.5) that are a perturbation series in \( \varepsilon \). Let

\[
v(\xi; \varepsilon) = v_0(\xi) + \varepsilon v_1(\xi) + \varepsilon^2 v_2(\xi) + \ldots \tag{A.6}
\]

The boundary conditions at \( \pm \infty \) and our choice that \( P(0) = 1/2 \) (which requires that \( v(0) = 1/2 \) for all \( \xi \)) give us the following conditions

\[
\begin{align*}
v_0(-\infty) &= 1, & v_0(\infty) &= 0, & v_0(0) &= \frac{1}{2} \\
v_i(\pm \infty) &= 0, & v_i(0) &= 0, & \text{for } i &= 1, 2, \ldots
\end{align*}
\]

Substituting equation (A.6) into equation (A.5) and equating powers of \( \varepsilon \) we get

\[
O(1) : \quad \frac{dv_0}{d\xi} = -v_0^2(1 - v_0) \quad \Rightarrow \quad \xi = -2 + \frac{1}{v_0} + \ln \left( \frac{1 - v_0}{v_0} \right) \\
\text{or} \quad v_0(\xi) = \frac{1}{W(e^{\xi+1}) + 1}
\]

where \( W \) is Lambert’s W-function, defined by \( W(x) \exp(W(x)) = x \).

\[
O(\varepsilon) : \quad \frac{dv_1}{d\xi} + v_0 v_1 (2 - 3v_0) = -\frac{d^2v_0}{d\xi^2} \quad \Rightarrow \quad v_1(\xi) = \left( v_0^2 - v_0^3 \right) \ln \left[ 8(v_0^2 - v_0^3) \right].
\]
Again, the constants of integration have been chosen so that the condition $v(0) = 1/2$ is satisfied.

In terms of the variables $P$ and $\tilde{z}$ we write

$$P(\tilde{z}; \tilde{c}) = P_0(\tilde{z}) + \frac{1}{\tilde{c}^2} (P_0^2(\tilde{z}) - P_0^3(\tilde{z})) \ln \left[ 8(P_0^2(\tilde{z}) - P_0^3(\tilde{z})) \right] + O(\tilde{c}^{-4})$$

where

$$P_0(\tilde{z}) = \frac{1}{W\left( \exp \left( \frac{\tilde{z}}{\tilde{c}} + 1 \right) \right) + 1}.$$ 

Changing back to our original variables, $z = \sqrt{k/g\tilde{z}}$ and $c = \sqrt{k/g\tilde{c}}$ we find that the asymptotic travelling wave solution to equation (2.15) is

$$P(z) = P_0(z) + \frac{gk}{\tilde{c}^2} (P_0^2(z) - P_0^3(z)) \ln \left[ 8(P_0^2(z) - P_0^3(z)) \right] + O(c^{-4}),$$

where

$$P_0(z) = \frac{1}{W\left( \exp \left( \frac{gz}{c} + 1 \right) \right) + 1}.$$
Appendix B

Calculations for the stability of the nonclassical symmetry solutions for the Huxley and Fitzhugh-Nagumo equations

B.1 Huxley equation

In this Appendix we show that there is a number $\tau$ such that $f(x, t) = g(2P - 3P^2) < -\epsilon$, $\epsilon > 0$ for all $x$ and $t > \tau$, where $P(x, t)$ is the particular solution (3.7) to the Huxley equation (3.3).
Setting \( \epsilon = g^2/2 \), we must show that

\[
g(2P - 3P^2) + \frac{g^2}{2} < 0
\]

or \( f^*(x,t) = 2P - 3P^2 + \frac{g}{2} < 0 \).

The function \( f^*(x,t) \) has stationary points at \( P_x = 0 \) and \( P = 1/3 \). Since \( P > 1/3 \) for \( t > \tau \), we are only interested in the case where \( P_x = 0 \). \( P_x = 0 \) when

\[
x = x^* = \sqrt[2]{g} W \left[ \sqrt[2]{g} \exp \left( 3 \sqrt[2]{g} - 2 - \frac{3}{2} g t \right) \right] - 3 + 2 \sqrt[2]{g} + t \sqrt[2]{g},
\]

where \( W \) is Lambert’s W function.

When \( x = x^* \), \( f^*(x,t) \) can be expressed as a function of \( t \) only. It can be shown that \( f^*(t) \) becomes negative after a certain \( t = \tau \), and \( \tau \) can be found by setting \( f^*(t) = 0 \) and solving for \( t \), so that

\[
t = \tau = \frac{1}{3g} \left[ 3 \sqrt[2]{g} - 2 - 2 \ln \left( \frac{1}{2g} \left( \sqrt[4]{4 + 6g - 2} - g \right) \right) \right.
\]

\[
- \ln 2 - \ln g - \frac{1}{g} \left( 2 \sqrt[4]{4 + 6g - 4} \right) \Bigg].
\]

### B.2 Fitzhugh-Nagumo equation

In this Appendix, we show that the function \( h(x,t) = g_1 - 2(g_1 + g_2)P + 3g_2P^2 \) (where \( P(x,t) \) is the particular solution (3.9) to the Fitzhugh-Nagumo equation (3.4) and \( g_1 > 0 \), \( g_2 < 0 \)) has a maximum in \( x \) for each \( t \) such that

\[
0 < h_{\text{max}} < -\frac{(g_1 - g_2)^2}{3g_2}.
\]
The maximum of $h(x, t)$ can be found by setting $h_x(x, t) = 0$ so that

$$2P_x (3g_2 P - 2(g_1 + g_2)) = 0,$$

and either

$$P_x = 0 \quad \text{or} \quad P = \frac{2(g_1 + g_2)}{3g_2}.$$

Since $P(x, t)$ is monotonically increasing, $P_x \neq 0$, so we must investigate the possibility that $P = 2(g_1 + g_2)/3g_2$. As $x \to -\infty$, $P \to g_1/g_2$ and as $x \to \infty$, $P \to 1$, so that if

$$g_1/g_2 < 2(g_1 + g_2)/3g_2 < 1,$$

then $P$ must take this value for some $x$. We must show that $2(g_1 + g_2)/3g_2 > g_1/g_2$:

$$\frac{2(g_1 + g_2)}{3g_2} - \frac{g_1}{g_2} = \frac{1}{3g_2}(2g_1 + 2g_2 - 3g_1) = \frac{1}{3g_2}(2g_2 - g_1) > 0 \quad \text{since} \ g_1 > 0, \ g_2 < 0,$$

and that $2(g_1 + g_2)/3g_2 < 1$:

$$\frac{2(g_1 + g_2)}{3g_2} - 1 = \frac{1}{3g_2}(2g_1 + 2g_2 - 3g_2) = \frac{1}{3g_2}(2g_1 - g_2) < 0 \quad \text{since} \ g_1 > 0, \ g_2 < 0.$$

Therefore, $P$ must take the value $2(g_1 + g_2)/3g_2$ for some $x$.

At $P = 2(g_1 + g_2)/3g_2$, $h(x, t)$ has a maximum $h_{\max}$,

$$h_{\max} = \frac{1}{3g_2} \left( 3g_1 g_2 - (g_1 + g_2)^2 \right) > 0 \quad \text{since} \ g_1 > 0, \ g_2 < 0.$$
Appendix C

Reduction of a system of six genotype equations to a system of two reaction-diffusion equations

In this appendix, we show how the six genotype equations (4.1) can be reduced to two reaction-diffusion-convection equations (4.3) describing the change in frequency of two of the alleles. Differentiating equation (4.2) with respect to $t$ and substituting the expressions for $\partial \rho_{ij}/\partial t$ we obtain

\[
\frac{\partial \rho_1}{\partial t} = \frac{1}{4\rho^2} \left[ 2\rho \left( 2 \frac{\partial^2 \rho_{11}}{\partial x^2} + \frac{\partial^2 \rho_{12}}{\partial x^2} + \frac{\partial^2 \rho_{13}}{\partial x^2} - 2\mu \rho_{11} - \mu \rho_{12} - \mu \rho_{13} 
+ 2\gamma_{11} \rho_1^2 \rho + 2\gamma_{12} \rho_1 \rho_2 \rho + 2\gamma_{13} \rho_1 (1 - \rho_1 - \rho_2) \rho \right) 
- 4\rho_1 \rho \left( \frac{\partial^2 \rho_{11}}{\partial x^2} + \frac{\partial^2 \rho_{12}}{\partial x^2} + \frac{\partial^2 \rho_{13}}{\partial x^2} + \frac{\partial^2 \rho_{22}}{\partial x^2} + \frac{\partial^2 \rho_{23}}{\partial x^2} + \frac{\partial^2 \rho_{33}}{\partial x^2} \right) \right]
\]
Appendix C

\[-\mu \rho_{11} - \mu \rho_{12} - \mu \rho_{13} - \mu \rho_{22} - \mu \rho_{23} - \mu \rho_{33}\]

\[+\gamma_{11} p_1^2 \rho + 2\gamma_{12} p_1 p_2 \rho + 2\gamma_{13} p_1 (1 - p_1 - p_2) \rho + \gamma_{22} p_2^2 \rho\]

\[+ 2\gamma_{23} p_2 (1 - p_1 - p_2) \rho + \gamma_{33} (1 - p_1 - p_2)^2 \rho\]}

Rearranging (4.2) \(_1\) and differentiating twice with respect to \(x\), we notice that

\[2 \frac{\partial^2 \rho_{11}}{\partial x^2} + \frac{\partial^2 \rho_{12}}{\partial x^2} + \frac{\partial^2 \rho_{13}}{\partial x^2} = 2 \frac{\partial^2 \rho_1}{\partial x^2} \rho + 4 \frac{\partial p_1}{\partial x} \frac{\partial \rho}{\partial x} + 2 p_1 \frac{\partial^2 \rho}{\partial x^2},\]

and from the definition of \(\rho\) we can write

\[\frac{\partial^2 \rho_{11}}{\partial x^2} + \frac{\partial^2 \rho_{12}}{\partial x^2} + \frac{\partial^2 \rho_{13}}{\partial x^2} + \frac{\partial^2 \rho_{22}}{\partial x^2} + \frac{\partial^2 \rho_{23}}{\partial x^2} + \frac{\partial^2 \rho_{33}}{\partial x^2} = \frac{\partial^2 \rho}{\partial x^2} .\]

Substituting these two expressions into the above equation and rearranging, we find

\[\frac{\partial p_1}{\partial t} = \frac{\partial^2 p_1}{\partial x^2} + \frac{2 \partial \rho}{\partial x} \frac{\partial p_1}{\partial x} + p_1 (\gamma_{13} - \gamma_{33}) + p_1^2 (\gamma_{11} - 3 \gamma_{13} + 2 \gamma_{33})\]

\[+ p_1^3 (-\gamma_{11} + 2 \gamma_{13} - \gamma_{33}) + p_1 p_2 (\gamma_{12} - \gamma_{13} - 2 \gamma_{23} + 2 \gamma_{33})\]

\[+ p_1^2 p_2 (-2 \gamma_{12} + 2 \gamma_{13} + 2 \gamma_{23} - 2 \gamma_{33}) + p_1 p_2^2 (-\gamma_{22} + 2 \gamma_{23} - \gamma_{33}) ,\]

equation (4.3) \(_1\).

The same procedure can be repeated to find the expression for \(\frac{\partial p_2}{\partial t}\) to be

\[\frac{\partial p_2}{\partial t} = \frac{\partial^2 p_2}{\partial x^2} + \frac{2 \partial \rho}{\partial x} \frac{\partial p_2}{\partial x} + p_2 (\gamma_{23} - \gamma_{33}) + p_2^2 (\gamma_{22} - 3 \gamma_{23} + 2 \gamma_{33}) + p_2^3 (-\gamma_{22} + 2 \gamma_{23} - \gamma_{33})\]

\[+ p_1 p_2 (\gamma_{12} - 2 \gamma_{13} - \gamma_{23} + 2 \gamma_{33}) + p_1 p_2^2 (-2 \gamma_{12} + 2 \gamma_{13} + 2 \gamma_{23} - 2 \gamma_{33})\]

\[+ p_1^2 p_2^2 (-\gamma_{11} + 2 \gamma_{13} - \gamma_{33}) ,\]

equation (4.3) \(_2\).
Appendix D

Calculations for the stability of the constant solutions for the system of equations (4.4)

In this appendix, we find the seven constant solutions to the system of equations (4.4), and examine the stability of five of them. The system of equations (4.4) can be written as

\[ p_t = p_{xx} + F(p) \]

where

\[ F(p) = (\Phi(p_1, p_2), \Psi(p_1, p_2)) \quad \text{and} \quad p = (p_1, p_2). \]
Appendix D

The system of equations (4.4) has constant solutions when

\[ \Phi(p_1, p_2) = \Psi(p_1, p_2) = 0. \]

This occurs for seven values of \( p_1 \) and \( p_2 \):

\[
\begin{align*}
(p_1, p_2) &= (0, 0), & (p_1, p_2) &= (0, 1), & (p_1, p_2) &= (1, 0), \\
(p_1, p_2) &= (0, \alpha), & \alpha &= \frac{\gamma_{23} - \gamma_{33}}{-\gamma_{22} + 2\gamma_{23} - \gamma_{33}}, \\
(p_1, p_2) &= (\beta, 0), & \beta &= \frac{\gamma_{13} - \gamma_{33}}{-\gamma_{11} + 2\gamma_{13} - \gamma_{33}}, \\
(p_1, p_2) &= \left( \frac{\gamma_{12} - \gamma_{22}}{-\gamma_{11} + 2\gamma_{12} - \gamma_{22}}, \frac{\gamma_{11} - \gamma_{12}}{\gamma_{11} - 2\gamma_{12} + \gamma_{22}} \right), \\
(p_1, p_2) &= \begin{bmatrix} \gamma_{12}^2 + \gamma_{13}^2 + \gamma_{23}^2 - 2\gamma_{12}\gamma_{13} - 2\gamma_{12}\gamma_{23} - \gamma_{11}\gamma_{33} + 2\gamma_{12}\gamma_{33} \\
-\gamma_{11}\gamma_{22} - 2\gamma_{13}\gamma_{23} - \gamma_{22}\gamma_{33} + 2\gamma_{13}\gamma_{22} + 2\gamma_{11}\gamma_{23} \\
-\gamma_{13}\gamma_{23} + \gamma_{13}\gamma_{22} - \gamma_{12}\gamma_{23} & -\gamma_{12}\gamma_{13} + \gamma_{12}\gamma_{33} - \gamma_{13}\gamma_{23} \\
+\gamma_{12}\gamma_{33} - \gamma_{22}\gamma_{33} + \gamma_{23}^2 & -\gamma_{11}\gamma_{33} + \gamma_{11}\gamma_{23} + \gamma_{13}^2 \end{bmatrix}^{-1} \times \\
&= \begin{bmatrix} \gamma_{12}^2 + \gamma_{13}^2 + \gamma_{23}^2 - 2\gamma_{12}\gamma_{13} - 2\gamma_{12}\gamma_{23} - \gamma_{11}\gamma_{33} + 2\gamma_{12}\gamma_{33} \\
-\gamma_{11}\gamma_{22} - 2\gamma_{13}\gamma_{23} - \gamma_{22}\gamma_{33} + 2\gamma_{13}\gamma_{22} + 2\gamma_{11}\gamma_{23} \\
-\gamma_{13}\gamma_{23} + \gamma_{13}\gamma_{22} - \gamma_{12}\gamma_{23} & -\gamma_{12}\gamma_{13} + \gamma_{12}\gamma_{33} - \gamma_{13}\gamma_{23} \\
+\gamma_{12}\gamma_{33} - \gamma_{22}\gamma_{33} + \gamma_{23}^2 & -\gamma_{11}\gamma_{33} + \gamma_{11}\gamma_{23} + \gamma_{13}^2 \end{bmatrix}.
\end{align*}
\]

To investigate the stability of the constant solutions, we must consider the eigen-value equation

\[ F'(p^*)q = \lambda q \]

where

\[ F'(p) = \begin{bmatrix} \frac{\partial \Phi}{\partial p_1} & \frac{\partial \Phi}{\partial p_2} \\
\frac{\partial \Psi}{\partial p_1} & \frac{\partial \Psi}{\partial p_2} \end{bmatrix} \]

and \( p^* \) is a solution of \( \Phi(p_1, p_2) = \Psi(p_1, p_2) = 0. \)
For this analysis, we assume the case of allele $A_1$ having an advantage so that

$$
\gamma_{11} > \gamma_{12}, \gamma_{13} > \gamma_{22}, \gamma_{23}, \gamma_{33} . \quad (D.1)
$$

We now look for the eigenvalues for the first five constant solutions.

(i) $(p_1, p_2) = (0, 0)$

For this constant solution, we solve

$$
|\mathbf{F'}(\mathbf{p}) - \lambda I| = \begin{vmatrix}
\gamma_{13} - \gamma_{33} - \lambda & 0 \\
0 & \gamma_{23} - \gamma_{33} - \lambda
\end{vmatrix} = 0
$$

to find

$$
\lambda = \gamma_{13} - \gamma_{33} > 0, \quad \gamma_{23} - \gamma_{33},
$$

so that this constant solution is unstable.

(ii) $(p_1, p_2) = (0, 1)$

For this constant solution, we solve

$$
|\mathbf{F'}(\mathbf{p}) - \lambda I| = \begin{vmatrix}
\gamma_{12} - \gamma_{22} - \lambda & -\gamma_{12} + \gamma_{23} \\
0 & -\gamma_{22} + \gamma_{23} - \lambda
\end{vmatrix} = 0
$$

to find

$$
\lambda = \gamma_{12} - \gamma_{22} > 0, \quad -\gamma_{22} + \gamma_{23},
$$

so that this constant solution is unstable.
Appendix D

(iii) \((p_1, p_2) = (1,0)\)

For this constant solution, we solve

\[
|F'(p) - \lambda I| = \begin{vmatrix} -\gamma_{11} + \gamma_{13} - \lambda & 0 \\ -\gamma_{12} + \gamma_{13} & -\gamma_{11} + \gamma_{12} - \lambda \end{vmatrix} = 0
\]

to find

\[
\lambda = -\gamma_{11} - \gamma_{13} < 0, \quad -\gamma_{11} + \gamma_{12} < 0.
\]

Since both of these eigenvalues are negative for the chosen restrictions on the \(\gamma_{ij}\) (D.1), this constant solution is stable.

(iv) \((p_1, p_2) = (0, \alpha)\)

For this constant solution, we solve

\[
|F'(p) - \lambda I| = \begin{vmatrix} \gamma_{13} - \gamma_{33} & \alpha(\gamma_{12} - 2\gamma_{13} - \gamma_{23} + 2\gamma_{33}) \\ +\alpha(\gamma_{12} - \gamma_{13} - \gamma_{23} + \gamma_{33}) - \lambda & +2\alpha^2(-\gamma_{12} + \gamma_{13} + \gamma_{23} - \gamma_{33}) \end{vmatrix} = 0
\]

to find

\[
\lambda = \gamma_{13} - \gamma_{33} + \alpha(\gamma_{12} - \gamma_{13} - \gamma_{23} + \gamma_{33}),
\]

\[
\gamma_{23} - \gamma_{33} + \alpha(2\gamma_{22} - 3\gamma_{23} + \gamma_{33}).
\]
In general, we cannot comment on whether these values for \( \lambda \) are positive or negative, so we are unable to determine the stability of this constant solution.

\[(v) \quad (p_1, p_2) = (\beta, 0)\]

For this constant solution, we solve

\[
|F'(p) - \lambda I| = \begin{vmatrix}
\gamma_{13} - \gamma_{33} & 0 \\
+\beta(2\gamma_{11} - 3\gamma_{13} + \gamma_{33}) - \lambda & \\
\beta(\gamma_{12} - \gamma_{13} - 2\gamma_{23} + 2\gamma_{33}) & \gamma_{23} - \gamma_{33} \\
+2\beta^2(-\gamma_{12} + \gamma_{13} + \gamma_{23} - \gamma_{33}) + \beta(\gamma_{12} - \gamma_{13} - \gamma_{23} + \gamma_{33}) - \lambda
\end{vmatrix} = 0
\]

to find

\[
\lambda = \gamma_{13} - \gamma_{33} + \beta(2\gamma_{11} - 3\gamma_{13} + \gamma_{33}),
\]

\[
\gamma_{23} - \gamma_{33} + \beta(\gamma_{12} - \gamma_{13} - \gamma_{23} + \gamma_{33}).
\]

In general, we cannot comment on whether these values for \( \lambda \) are positive or negative, so we are unable to determine the stability of this constant solution.
Appendix E

A second travelling wave solution to the system of equations

In Chapter 4, we find a travelling wave solution to equations (4.4) using the boundary conditions \((p_1, p_2)(-\infty) = (1, 0), (p_1, p_2)(\infty) = (0, \alpha)\). Using the same method, we can find a travelling wave solution using the boundary conditions

\[
(p_1, p_2)(-\infty) = (0, 1) \\
(p_1, p_2)(\infty) = (\beta, 0),
\]

where

\[
\beta = \frac{\gamma_{13} - \gamma_{33}}{-\gamma_{11} + 2\gamma_{13} - \gamma_{33}} \quad , \quad 0 \leq \beta \leq 1.
\]

We first rewrite the equations in terms of the travelling wave coordinate, \(z = x - ct\) to obtain equations (4.5). Choosing \(p_2\) as the new independent variable we
look for solutions that satisfy

\[ \frac{dp_2}{dz} = F(p_2), \quad p_1 = G(p_2), \quad (E.2) \]

where \( F \) and \( G \) are polynomials in \( p_2 \). Applying this transformation gives

\[ F^2 \frac{d^2G}{dp_2^2} + F \frac{dF}{dp_2} \frac{dG}{dp_2} + cF \frac{dG}{dp_2} + \Phi(G, p_2) = 0 \]
\[ F \frac{dF}{dp_2} + cF + \Psi(G, p_2) = 0. \quad (E.3) \]

Following the same procedure as used in Chapter 4, we assume that \( F(p_2) \) and \( G(p_2) \) are polynomials in \( p_2 \), i.e. let

\[ F(p_2) = \sum_{n=0}^{\nu} a_n p_2^n, \quad G(p_2) = \sum_{n=0}^{\sigma} b_n p_2^n \]

where \( \nu, \sigma, a_n \) and \( b_n \) are constants to be determined. Substituting this into equations (E.3) gives

\[ \left( \sum_{n=0}^{\nu} a_n p_2^n \right)^2 \left( \sum_{n=2}^{\sigma} nb_n p_2^{n-2} \right) + \left( \sum_{n=0}^{\nu} a_n p_2^n \right) \left( \sum_{n=1}^{\nu} na_n p_2^{n-1} \right) \left( \sum_{n=1}^{\sigma} nb_n p_2^{n-1} \right) \]
\[ + c \left( \sum_{n=0}^{\nu} a_n p_2^n \right) \left( \sum_{n=1}^{\sigma} nb_n p_2^{n-1} \right) + \Phi(G, p_2) = 0 \]
\[ \left( \sum_{n=0}^{\nu} a_n p_2^n \right) \left( \sum_{n=1}^{\nu} na_n p_2^{n-1} \right) + c \left( \sum_{n=0}^{\nu} a_n p_2^n \right) + \Psi(G, p_2) = 0 \]

By balancing the exponents of the highest order derivative terms with the exponents of the highest order non-linear terms, we find that a solution may be found if

\[ \nu = 2, \quad \sigma = 1. \]

We can now write \( F(p_2) \) and \( G(p_2) \) as

\[ F(p_2) = a_0 + a_1 p_2 + a_2 p_2^2 \]
\[ G(p_2) = b_0 + b_1 p_2. \]
From the boundary conditions, we deduce that

\[ a_0 = 0, \quad b_0 = \beta, \]
\[ -a_1 = a_2 = a, \quad b_1 = -\beta, \]

so that

\[ F(p_2) = ap_2^2 - ap_2 \]
\[ G(p_2) = \beta - \beta p_2. \]

Substituting this into equations (E.3) and equating coefficients of powers of \( p_2 \) to zero, we obtain seven equations for \( a \) and \( c \) which can be reduced to three independent equations:

\[
\begin{align*}
    a^2 - ca - (\gamma_{12} - 2\gamma_{13} - 2\gamma_{23} + 3\gamma_{33}) - \beta(-2\gamma_{11} - 2\gamma_{12} + 5\gamma_{13} + 2\gamma_{23} - 3\gamma_{33}) &= 0 \\
    a^2 - ca + (\gamma_{23} - \gamma_{33}) + \beta(\gamma_{12} - \gamma_{13} - \gamma_{23} + \gamma_{33}) &= 0 \\
    2a^2 + (-\gamma_{22} + 2\gamma_{23} - \gamma_{33}) + \beta(2\gamma_{12} - \gamma_{13} - 2\gamma_{23} + \gamma_{33}) &= 0
\end{align*}
\]

Solving these equations, we can obtain expressions for the constant \( a \) and the wave speed \( c \) providing that \( \beta = 1 \) or \( \gamma_{12} = \gamma_{23} \). Once again, the most interesting case is when \( \beta \neq 1 \). We therefore set

\[ \gamma_{12} = \gamma_{23} \]

and \( a \) and \( c \) can be written as

\[ a = \frac{1}{\sqrt{2}} \sqrt{(\gamma_{22} - 2\gamma_{23} + \gamma_{33}) + \beta(\gamma_{13} - \gamma_{33})}, \]
\[ c = \frac{1}{2a} \left[ (4\gamma_{13} + \gamma_{22} - 5\gamma_{33}) + \beta(4\gamma_{11} - 9\gamma_{13} + 5\gamma_{33}) \right]. \]
Using (E.4), we integrate the first equation in (E.2) and substitute the result into the second to obtain

\[ p_1(z) = \frac{-A \beta \exp az}{1 - A \exp az} \]
\[ p_2(z) = \frac{1}{1 - A \exp az} \]

where \( A \) is a constant. We can choose \( p_2(0) = 1/2 \) (i.e. we can centre the coordinate system where \( p_2 = 1/2 \)), so that a solution to the system of equations (4.5) with boundary conditions (E.1) and \( \gamma_{12} = \gamma_{23} \) is

\[ p_1(z) = \frac{\beta \exp az}{1 + A \exp az} \]
\[ p_2(z) = \frac{1}{1 + A \exp az} \]  \hspace{1cm} (E.5)

The solution curves are shown in Figure E.1. The birth rates have been chosen as \( \gamma_{11} = 0.6, \gamma_{12} = \gamma_{23} = 0.3, \gamma_{13} = 0.4, \gamma_{22} = 0.2, \gamma_{33} = 0.5 \) so that \( \beta = 1/3, a \approx 0.183 \) and \( c \approx -0.730 \).
Figure E.1: Travelling wave solution (E.5) for the system of equations (4.5) with boundary conditions (E.1). The waves are moving to the left.
Appendix F

Using Dimsym and Maple to find classical and nonclassical symmetries

F.1 Dimsym

The following is the output generated by Dimsym when we analyse equation (5.2). It shows that Dimsym has assumed a number of expressions are linearly independent, from which we obtain the ODE (5.14) for $g(x)$.

load sym;
\%x(1)=t, x(2)=x, U(1)=u
freeunknown(g);
depend g,x(2);
Appendix F

loaddeq( u(1,2,2) = u(1,1) - g*u(1)^2*(1 - u(1)) );

%ie look for point symmetries;

mkdets(point);
showdets();
solvedets(std);
mk gens();

showdets();
end;

load sym;

Dimsym 2.2, 1-Jan-99

Symmetry determination and linear D.E. package

(c) 1992, 1993 James Sherring; 1999 James Sherring and Geoff Prince

Any publication resulting from these calculations must reference this program.

Users are free to modify this program but it is not to be redistributed in modified form.

%x(1)=t, x(2)=x, U(1)=u

freeunknown(g);

depend g,x(2);

loaddeq( u(1,2,2) = u(1,1) - g*u(1)^2*(1 - u(1)) );

1

%ie look for point symmetries;
There are 1 determining equations remaining, which are...

\[
deteqn(1) = \phi(1,2,2) - \phi(1,1) - 3*\phi(1)*u(1) + 2*\phi(1)*u(1)*g - 2^3 - \xi(2)*df(g,x(2))*u(1) + \xi(2)*df(g,x(2))*u(1)
\]

The remaining dependencies are ...

\[
(\phi 1) \text{ depends on } ((u 1) (x 2) (x 1))
\]

\[
(xi 2) \text{ depends on } ((u 1) (x 2) (x 1))
\]

\[
(xi 1) \text{ depends on } ((u 1) (x 2) (x 1))
\]

The dunkns in the remaining equations are: 

\[
((xi 2) (phi 1) (phi 1 1) (phi 1 2 2))
\]

The leading derivatives are: 

\[
((phi 1 2 2))
\]

The parametric derviatives in the remaining equations are: 

\[
((xi 2) (phi 1) (phi 1 1))
\]

solvedets(std);

Solving equations using std algorithm.

*** free or special functions found when dividing by 

g

Must have all of 

\[
df(g,x(2))*x(2)
\]

\[
df(g,x(2))
\]

\[
2
\]

\[
x(2) * g
\]
Appendix F

There are 0 equations remaining.

mkgens();

There are 1 symmetries found.

The generators of the finite algebra are:

Gen(1) = @
    x(1)

showdets();

There are no determining equations remaining.

The remaining dependencies are ...
end;

F.2 Maple

The following is the Maple program used to look for forms of \( g(x) \) that enable equation (5.2) to admit additional symmetries.

\[
\text{Nonclassical symmetry analysis for equation (5.2).} \\
> \text{restart;}
> \text{de1 := pt-pxx-G(x)*p^2*(1-p);} \\
> \text{dx := proc(f)} \\
> \text{diff(f,x) + diff(f,p)*px + diff(f,px)*pxx + diff(f,pt)*pxt} \\
> \text{+ diff(f,pxx)*pxxx;} \\
> \text{end;
}
> dt := proc(f)
> diff(f, t) + diff(f, p)*pt + diff(f, px)*pxt + diff(f, pt)*ptt;
> end;
> pr2 := proc(f)
> diff(f, x)*cx(x, t, p) + diff(f, t)*ct(x, t, p) + diff(f, p)*cp(x, t, p)
> + diff(f, px)*cpx + diff(f, pt)*cpt + diff(f, pxx)*cpxx
> + diff(f, pxt)*cpxt + diff(f, ptt)*cptt;
> end;
> cpx := dx(cp(x, t, p)) - dx(cx(x, t, p))*px - dx(ct(x, t, p))*pt;
> cpt := dt(cp(x, t, p)) - dt(cx(x, t, p))*px - dt(ct(x, t, p))*pt;
> cpxx := dx(cpx) - dx(cx(x, t, p))*px x - dx(ct(x, t, p))*pxt;
> cpxt := dt(cpx) - dt(cx(x, t, p))*px - dt(ct(x, t, p))*pxt;
> cptt := dt(cpt) - dt(cx(x, t, p))*pxt - dt(ct(x, t, p))*ptt;
> eqn1 := pr2(de1);
> pxt := dx(cp(x, t, p)) - cx(x, t, p)*px;
> pt := cp(x, t, p) - cx(x, t, p)*px;
> pxx := pt - G(x)*p^2*(1-p);
> ct(x, t, p) := 1;
> 2
de1 := pt - pxx - G(x)*p*(1 - p)

dx := proc(f)
    diff(f, x) + diff(f, p)*px + diff(f, px)*pxx
    + diff(f, pt)*pxt + diff(f, pxx)*pxxx
end

dt := proc(f)
    diff(f, t) + diff(f, p)*pt + diff(f, px)*pxt
    + diff(f, pt)*ptt
end

pr2 := proc(f)
    diff(f, x)*cx(x, t, p) + diff(f, t)*ct(x, t, p)
    + diff(f, p)*cp(x, t, p) + diff(f, px)*cpx
    + diff(f, pt)*cpt + diff(f, pxx)*cpxx
    + diff(f, pxt)*cpxt + diff(f, ptt)*cptt
end

p_\text{xt} := \frac{\partial \text{cp}(x, t, p)}{\partial x} - \frac{\partial \text{cx}(x, t, p)}{\partial x} \frac{\partial x}{\partial x}
\[ \begin{align*} 
\pm \left( \frac{\partial}{\partial t} \right) &= \frac{1}{2} \left( \frac{\partial}{\partial x} \right)^2 \left( -\frac{\partial}{\partial p} \right) \left( \frac{\partial}{\partial x} \right)^2 \\
&- \frac{1}{2} \left( \frac{\partial}{\partial x} \right)^2 \left( -\frac{\partial}{\partial p} \right) \left( \frac{\partial}{\partial x} \right)^2 \\
&+ \frac{1}{2} \left( \frac{\partial}{\partial x} \right)^2 \left( \frac{\partial}{\partial p} \right) \left( \frac{\partial}{\partial x} \right)^2 \\
&- \frac{1}{2} \left( \frac{\partial}{\partial x} \right)^2 \left( \frac{\partial}{\partial p} \right) \left( \frac{\partial}{\partial x} \right)^2 \\
&+ \frac{1}{2} \left( \frac{\partial}{\partial x} \right)^2 \left( \frac{\partial}{\partial p} \right) \left( \frac{\partial}{\partial x} \right)^2 
\end{align*} \]

\[ pt := \frac{1}{2} \left( \frac{\partial}{\partial x} \right)^2 \left( -\frac{\partial}{\partial p} \right) \left( \frac{\partial}{\partial x} \right)^2 \\
ct(x, t, p) := 1 \]

\[ > \text{eqn1} := \text{numer(eqn1)}; \]

\[ \begin{align*} 
\text{eqn1} &:= \frac{1}{2} \left( \frac{\partial}{\partial x} \right)^2 \left( -\frac{\partial}{\partial p} \right) \left( \frac{\partial}{\partial x} \right)^2 \\
&+ \frac{1}{2} \left( \frac{\partial}{\partial x} \right)^2 \left( -\frac{\partial}{\partial p} \right) \left( \frac{\partial}{\partial x} \right)^2 \\
&- \frac{1}{2} \left( \frac{\partial}{\partial x} \right)^2 \left( -\frac{\partial}{\partial p} \right) \left( \frac{\partial}{\partial x} \right)^2 \\
&+ \frac{1}{2} \left( \frac{\partial}{\partial x} \right)^2 \left( -\frac{\partial}{\partial p} \right) \left( \frac{\partial}{\partial x} \right)^2 \\
&+ \frac{1}{2} \left( \frac{\partial}{\partial x} \right)^2 \left( -\frac{\partial}{\partial p} \right) \left( \frac{\partial}{\partial x} \right)^2 
\end{align*} \]
\[ \begin{align*} 
+ 3 \frac{\partial}{\partial p} G(x) p - 2 \frac{\partial}{\partial x} c(x, t, p) c(x, t, p) p x \\
+ 2 p x \frac{\partial}{\partial p} c(x, t, p) c(x, t, p) p x \\
\frac{\partial}{\partial p} c(x, t, p) c(x, t, p) p x \\
\frac{\partial}{\partial x} \frac{\partial}{\partial p} c(x, t, p) c(x, t, p) p x \\
- 2 \frac{\partial}{\partial x} \frac{\partial}{\partial p} c(x, t, p) c(x, t, p) p x \\
\frac{\partial}{\partial x} \frac{\partial}{\partial dt} c(x, t, p) c(x, t, p) p x \\
\frac{\partial}{\partial x} \frac{\partial}{\partial dt} c(x, t, p) c(x, t, p) p x \\
\frac{\partial}{\partial p} \frac{\partial}{\partial dt} c(x, t, p) c(x, t, p) p x \\
+ 3 \frac{\partial}{\partial p} G(x) p + 3 \frac{\partial}{\partial p} c(x, t, p) c(x, t, p) p x \\
\frac{\partial}{\partial p} c(x, t, p) c(x, t, p) p x \\
\end{align*} \]

> d0 := coeff(eqn1,px,0): d1 := coeff(eqn1,px,1): d2 := coeff(eqn1,px,2):
> d3 := coeff(eqn1,px,3);

\[ d3 := \frac{2}{2} \frac{\partial}{\partial p} c(x, t, p) \]

From d3 we know:

\[ c(x, t, p) := f1(x, t) p + f2(x, t); \]

\[ c(x, t, p) := f1(x, t) p + f2(x, t) \]
We can solve $d_2$:

\[
\frac{\partial}{\partial x} \left( -\frac{1}{2} f_1(x, t) p + \frac{1}{3} f_1(x, t) p^2 - f_1(x, t) f_2(x, t) p + f_3(x, t) p + f_4(x, t) \right)
\]
Try $f_1(x,t) = 0, \pm 3\sqrt{G/2}$

```maple
> f1(x,t) := 0;
f1(x, t) := 0
> eval(d1): eval(d0): eval(e00): eval(e01): eval(e02): eval(e03):
> eval(e04); 0
> eval(e10):
> eval(e11); 0
> eval(e12); 0
> eval(e13); 0
> simplify(e03+e02);

\[ f_3(x, t) G(x) + 3 f_4(x, t) G(x) \]

\[ f_3(x, t) := -3 f_4(x, t); \]

\[ f_3(x, t) := -3 f_4(x, t) \]

> eval(e00): eval(e01):
> eval(e02);

\[
\frac{d}{dx} \left( 6 f_4(x, t) G(x) - 2 \frac{d}{dx} f_2(x, t) G(x) - \frac{d}{dx} G(x) f_2(x, t) \right)
\]

\[ \text{temp4} := \text{solve(e02,f4(x,t))}; \]

\[
\frac{d}{dx} \left( 2 \frac{d}{dx} f_2(x, t) G(x) + \frac{d}{dx} G(x) f_2(x, t) \right)
\]

\[ \text{temp4} := 1/6 \frac{1}{G(x)} \]

> e00 := simplify(subs(f4(x,t)=temp4,e00)):
> e01 := simplify(subs(f4(x,t)=temp4,e01));
Appendix F

> e02 := simplify(subs(f4(x,t)=temp4,e02));

\[ e02 := 0 \]

> e03 := simplify(subs(f4(x,t)=temp4,e03));

\[ e03 := 0 \]

> e04 := simplify(subs(f4(x,t)=temp4,e04));

\[ e04 := 0 \]

> e10 := simplify(subs(f4(x,t)=temp4,e10));
> e11 := simplify(subs(f4(x,t)=temp4,e11));

\[ e11 := 0 \]

> e12 := simplify(subs(f4(x,t)=temp4,e12));

\[ e12 := 0 \]

> e13 := simplify(subs(f4(x,t)=temp4,e13));

\[ e13 := 0 \]

ie, 3 equations for \( f_2(x,t) \) and \( G(x) \).
> simplify(3*e00+e01);

\[
- \frac{2}{3} \frac{\partial}{\partial x} f_2(x,t) G(x) - \frac{1}{3} \frac{\partial}{\partial x} G(x) f_2(x,t)
\]

> dsolve(%,f2(x,t));

\[
_f1(t) \frac{\partial}{\partial t} f_2(x,t) = \frac{\partial}{\partial x} f_2(x,t) G(x) - \frac{\partial}{\partial x} G(x) f_2(x,t)
\]

\[ f_2(x,t) = \frac{f_5(t)}{\sqrt{G(x)}} \]

> f2(x,t) := f5(t)/(sqrt(G(x)));
> f4(x,t):= temp4;
f4(x, t) := 0

> simplify(e00);
0

> simplify(e01);
0

> e10 := simplify(e10);

\[
\begin{array}{c}
\frac{1}{4} \frac{d}{dx} \left( -3 f5(t) G(x) \right) + 2 f5(t) G(x) \frac{d}{dx} G(x) \\
- 4 f5(t) \sqrt{G(x)} + 4 f5(t) G(x) \\
(5/2) G(x)
\end{array}
\]

> simplify(eqn1);

\[
\begin{array}{c}
\frac{1}{4} \frac{d}{dx} \left( -3 f5(t) G(x) \right) + 2 f5(t) G(x) \frac{d}{dx} G(x) \\
+ 4 \frac{d}{dx} G(x) - 4 f5(t) \frac{d}{dx} G(x) \\
(9/2) G(x)
\end{array}
\]
Bibliography


[8] Bateman Manuscript Project, Higher Transcendental functions (Based, in part, on notes left by Harry Bateman, and compiled by the staff of the Bateman Manuscript Project), McGraw-Hill, New York, 1953.


Bibliography


Publications associated with this thesis


(2) B.H. Bradshaw-Hajek, P. Broadbridge, G. Williams and M. Rodrigo, Advance of a new gene over two pre-existing alternatives, submitted.

