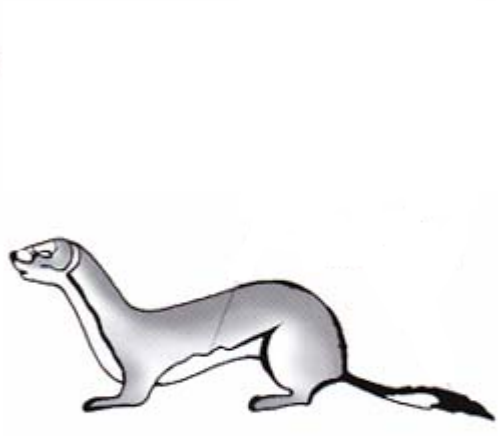
The Mother's Curse

An investigation into the use and efficacy of the Trojan Female Technique as a revolutionary approach to pest control.



Benjamin Atkins

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Chapter 1

Introduction

From the spread of disease to destruction of food crops, pests are considered the cause of countless problems worldwide. Conventional methods attempting to control these abundant and often prolific species use lethal action such as poisons and traps to reduce the population of pests; however these methods are often inefficient, expensive to maintain over long periods, can be damaging to local ecosystems and rarely result in complete eradication [8]. These issues have lead to new approaches to pest control.

A new area of investigation, which is receiving growing support, is the management of populations through control of reproductive output, or 'fertility control' methods [4, 10]. The 'Sterile Male Technique' (SMT) is considered to be one of the most successful fertility control methods to date [7, 8]. It involves flooding the population with sterile males, reducing the number of offspring in the next generation. Although this method is efficient in reducing population numbers over one generation, repeated releases are required, else the population quickly recovers and all benefits are lost. This is an unrealistic and costly approach in the long term, leaving much room for improvement.

In this paper we investigate the use and efficacy of a new fertility control method known as the 'Trojan Female Technique' (TFT), which promises to be a cost effective way of reducing population levels and keeping them down in the long run [8]. This approach utilises naturally occurring mitochondrial (mtDNA) mutations in females that result in male offspring having greatly reduced, even non-existent, fertility, while having negligible effects on female offspring. Females and males with the mutation are coined 'Trojan females' and 'Trojan males' respectively. Since the mutation occurs in the mtDNA, it is passed down maternally. Thus, the offspring of a Trojan Female will also have the muta-

tion, causing them to either be sterile if they are male, or the next generation of Trojan females. It is this self repeating behaviour that promises to make the TFT an effective long term solution for pest control.

In this paper we hope to quantify the effect of the Trojan Female Technique on pest populations and its practicality as a long-term solution.

Chapter 2 introduces the first model taken from [8], explaining how the model was constructed, defining the variables and parameters that will be used throughout this report and giving an example of what the behaviour of the model looks like.

Chapter 3 addresses the problem of including the effect of the juvenile stage in our model [1, 5]. We offer an extension to the model from Chapter 2 which involves a time lag component. We also justify approximating this extended model with the original model for short juvenile stages.

Chapter 4 contains the bulk of our analysis and results. We start by transforming the system of equations from a 4-dimensional system to a 2-dimensional system and then analyse the long term behaviour of this system. In doing so we find that we can split the long term solutions into three groups depending on the size of the initial introduction of Trojan females:

1. If the initial introduction is above a certain level the population will become extinct in the long run. We find an approximate representation of this "extinction boundary".

2. If the initial introduction is below the current size of the population, the population will tend towards an equilibrium that lies on a specific attracting manifold. We define this manifold implicitly but the "lower bound" and "upper bound", between which the equilibrium must lie, are defined explicitly in terms of the parameter values used, with the upper bound corresponding to the equilibrium solution of the population before Trojan females are introduced.

3. If the initial introduction is between the extinction boundary and the current population size we cannot be certain whether the population will become extinct or end at an equilibrium on the attracting manifold.

Lastly in this chapter we explore how the extinction boundary and lower and upper bounds mentioned above change with changes in parameters. We find that the proportion of Trojan females needed to bring the population to extinction falls with increases in the birth rate and rises with increases in the death rate. Increases in the birth also cause a reduction in the distance between the upper and lower bounds, while increases in the death rate increase this distance.

Finally, in Chapter 5 we introduce the use of Wolbachia bacteria [9, 12] and develop an extended model which incorporates the effect of this bacteria. We find that the addition of Wolbachia into our model can aid our goal of pest eradication, but only when Trojan females and Wolbachia infected females, or a combination of males and females, are introduced separately. If introduced together the combination of the two can actually reduce the effects of the TFT and work against our goal.

Chapter 2

Continuous Time Model

In this chapter we formulate a mathematical model used to analyse the behaviour of the Trojan Female Technique. Our starting point is the model introduced in [8], which we now review.

2.1 Parameters

The model is based around the parameters, variables and functions defined in Table 2.1.

Variables		
Notation	Name	Description
N	Population Density	Total number of individuals in the population per 100 ha
M	Density of non-Trojan males	Number of non-Trojan males in the population per 100 ha
F	Density of non-Trojan females	Number of non-Trojan females in the population per 100 ha
M^*	Density of Trojan males	Number of Trojan males in the population per 100 ha
F^*	Density of Trojan females	Number of Trojan females in the population per 100 ha
Parameters		
r	Gender Ratio	Expected proportion of males at birth
l	Litter Size	Number of offspring a female produces monthly
μ	Death rate	Proportion of population that dies each month
k	Mating frequency	Number of males a female will mate with in order to give birth
q	Maturation Rate	Average proportion of mature adults in the population
t	Time	Measure of time in months
Functions		
$b(N)$	Proportion of females breeding	The proportion of females able to breed with finite resources from the environment
$P(M, M^*)$	Female mating rate	Probability that a female will mate with a healthy male

Table 2.1: Description of the parameters used in the models

Of particular interest are the functions used to model the proportion of females breeding, $b(N)$, and the female mating rate, $P(M, M^*)$, which we now discuss.

The female mating rate represents the probability of a female encountering (and breed-

ing with) a healthy, non-Trojan male in a closed population and is calculated by

$$P(M, M^*) = \frac{M}{M + M^* + 1}. \tag{2.1}$$

This is an example of a rectangular hyperbolic fertilization rate, commonly used for its mathematical simplicity, with a weak Allee effect [8]. An Allee effect is a positive relationship between the density and reproductive ability of a population, i.e. at low densities the growth rate of the population is less than at high densities [3]. Notice that P depends almost solely on the relative proportions of non-Trojan and Trojan males in the population, rather than the actual numbers. We are implicitly making the assumption that male individuals are not limited in the number of offspring they are able to produce.

The parameter $b(N)$ introduces density dependence into our models. It is derived from the well-known Beverton-Holt Equation [2]

$$N_{t+1} = \frac{R}{\frac{N_t}{M} + 1} N_t, \tag{2.2}$$

where N_t is the density of the population at time t, R is the proliferation rate of the population and M is the density at which the growth of the population is halved due to limited resources. The Beverton-Holt Equation is used to model the dynamics of a population that displays contest competitive behaviour, where individuals are competing for limited resources rather than sharing resources between themselves. Since pests are often highly abundant and competitive, this is an important parameter of the models to come. In the following models we set the proportion R of females breeding as 0.9 and the density M as 500, from [8], so that

$$b(N) = \frac{0.9}{\frac{N}{500} + 1}. \tag{2.3}$$

Finally, in order to simplify the model equations in the coming chapters, we define the "Overall Birth Rate" as

$$B(N) = lb(N)(1 - (1 - P(M, M^*))^k). \tag{2.4}$$

The term $(1 - (1 - P(M, M^*))^k)$ represents the probability that a female will mate with at least one healthy male, given that they choose k mating partners. If females are monogamous this equals $P(M, M^*)$.

2.2 Model Construction

Here we introduce the continuous time model found in [8]. In this model breeding is assumed to take place continuously throughout the year. The behaviour of this model is determined by the following system of differential equations:

$$\begin{aligned}
\dot{M} &= rqB(N)F - \mu M; \\
\dot{F} &= (1-r)qB(N)F - \mu F; \\
\dot{M^*} &= rqB(N)F^* - \mu M^*; \\
\dot{F^*} &= (1-r)qB(N)F^* - \mu F^*;
\end{aligned}$$

where

$$N = M + F + M^* + F^*.$$

We now review how these equations were constructed. Looking at the first equation we have that in any (small) time interval the number of non-Trojan males that die is approximately μM. The number of non-Trojan males that are born is approximately equal to the number of non-Trojan females (F) multiplied by the proportion of those females that are mature q, the density dependent birth rate $B(N)$ and the probability r that an offspring is male. The other equations are derived in the same way, noting that the probability an offspring is female is $(1-r)$ and that Trojan males and females have Trojan mothers.

This system of four equations appears at first glance to be two separate systems of two equations each. However, the Trojan equations (involving M^* and F^*) are linked to the non-Trojan equations (involving M and F) through the component $B(N)$, which depends on the ratio between M and M^* as discussed earlier. An increase in the number of Trojan males will cause the growth of the population, both non-Trojan and Trojan, to slow down due to the increased probability of a female mating with a sterile male. The overall birth rate $B(N)$ also depends on the total population size, with a larger population resulting in a lower growth rate through the Beverton-Holt component, also mentioned previously. Thus it is the growth rate $B(N)$ that contains most of the information about our model.

2.2.1 Assumptions

In this model the following assumptions have been made:

- Breeding occurs continuously over time.

- Males born with the mtDNA mutation are fully infertile.
- Female reproductive fitness is unaffected by the mutation.
- All individuals have the same mortality rate, i.e. neither age nor the mutation effect the individual's ability to survive.

2.3 Example of Model Behaviour

Simulations of the continuous time model were carried out in MATLAB using ODE45. The code used for simulations throughout this report can be found in Appendix 2.

Figure 2.1 below shows an example of the behaviour of TFT with the above model under a specific set of parameters. The simulation starts with 50 non-Trojan males and females then allows the population to grow for 300 months before introducing a group of adult Trojan females, the size of which is 10% of the current population. The growth of the population after introduction is then simulated for another 300 months (50 years in total). The specific parameter values used were chosen arbitrarily within viable ranges from [8]:

$$l = 8;$$
$$\mu = 0.1;$$
$$r = 0.51;$$
$$k = 1;$$
$$q = 0.5.$$

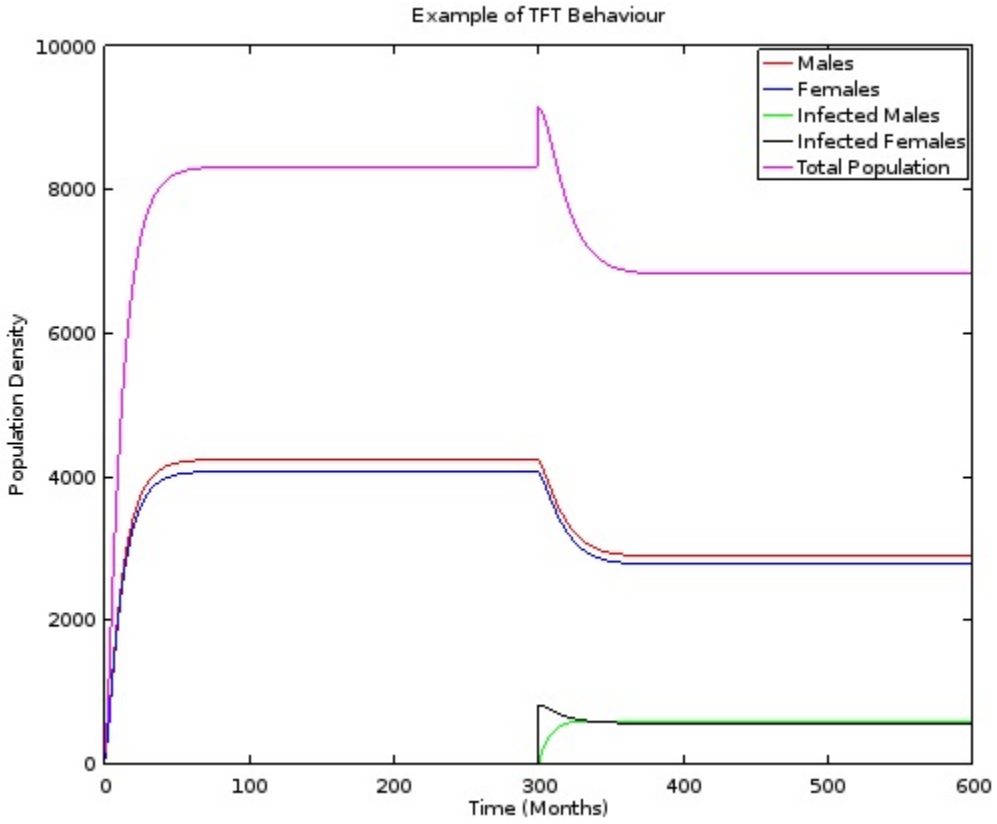

Figure 2.1: Example of TFT behaviour using the continuous time model under specific conditions.

We see that the population, in the absence of Trojan males and females, quickly grows towards a steady equilibrium (we discuss an analytic representation of this equilibrium in Section 2.2). After 300 months there is a spike in the size of the population caused by the 10% introduction of Trojan females. The total size of the population then proceeds to decrease towards and remain steady at a new reduced equilibrium. The size of the new equilibrium after Trojan female introduction is of particular interest and is investigated in detail in Chapter 4.

Chapter 3

The Juvenile Stage

Before carrying out an analysis of the model we wish to address the issue of the time lag caused by the time taken for a juvenile individual to mature into an adult that is able to reproduce [1, 5]. In the model introduced in the previous chapter we approximate this behaviour through the use of the maturation rate q, representing the average proportion of the population that is mature enough to reproduce. The problem with this method is that we are using a fixed value for a proportion that may be changing, especially when we introduce a group of all adult Trojan females. In this chapter we offer an extension to the model that more accurately portrays the effect of this maturation lag. We also show, however, that under certain conditions q can be used as a good approximation.

3.1 Extension

We adapt the continuous time model from the previous chapter, deriving the new system of equations below.

$$\begin{aligned}
\dot{M} &= rB(N)e^{-\mu\tau}F(t-\tau) - \mu M; \\
\dot{F} &= (1-r)B(N)e^{-\mu\tau}F(t-\tau) - \mu F; \\
\dot{M}^* &= rB(N)e^{-\mu\tau}F^*(t-\tau) - \mu M^*; \\
\dot{F}^* &= (1-r)B(N)e^{-\mu\tau}F^*(t-\tau) - \mu F^*;
\end{aligned}$$

where

$$N = M + F + M^* + F^*,$$

as before.

Where before we had the expressions qF and qF^* we now have $e^{-\mu\tau}F(t-\tau)$ and $e^{-\mu\tau}F^*(t-\tau)$. Here the parameter τ has been introduced and represents the time taken for a juvenile to mature into an adult (in months). These equations were derived as follows: in order to calculate the current growth of the population we need to know the number of adult females, which can breed, rather than the total number of females which includes juveniles who cannot add to the population growth. To do this we take the number of adult females from τ months prior, $F(t-\tau)$ (or $F^*(t-\tau)$ for Trojan females) , and multiply this by the probability that an individual survives τ months, $e^{-\mu\tau}$, giving the current number of surviving adults. Any individual born within this time will not be old enough to reproduce and therefore does not add to the growth of the population at the current time.

In the equation above, the variables M, F, M^* and F^* represent the total number of males, females, Trojan males and Trojan females respectively. The juvenile stage could also be accounted for by changing the variables so that they represent only the number of adults. This would take away the need for the $e^{-\mu\tau}F(t-\tau)$ and $e^{-\mu\tau}F^*(t-\tau)$ components, however another lag component would need to be added to the function $B(N)$ so that the increase in the number of adults is defined by the number of juveniles that were born τ months ago. The advantages and disadvantages of such a model will be investigated in future work.

3.1.1 Example of Model Behaviour

The graph below shows an example of the behaviour of the above system, using the parameter values $l = 8$, $\mu = 0.1$, $r = 0.51$, $k = 1$ and $\tau = 2$.

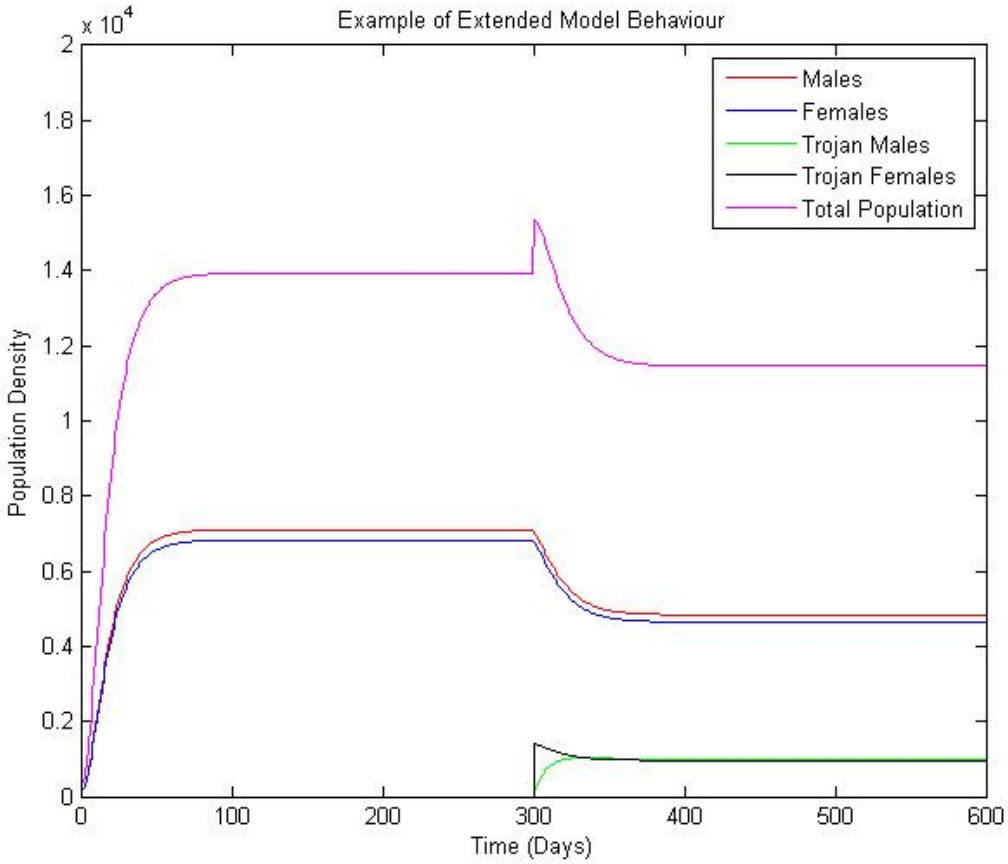

Figure 3.1: Example of TFT behaviour using the extended continuous time model under specific conditions.

This shows very similar to behaviour as the original model.

3.2 Approximation

Although the extended model described above better represents the behaviour of a population, it greatly increases the complexity of the model as it moves us away from the widely studied area of Ordinary Differential Equations into Delay Differential Equations [1]. This will cause the analysis to become very difficult [5]. To avoid this we show that our original model involving q can be used to closely approximate the extended model.

Due to the short length of the juvenile stage, the time lag caused by it has only a small effect on the long term behaviour of the system, which is what we are really interested in. Figure 3.2 below shows that q can be fit to minimise the difference between the two

models. The extended model is simulated with a time lag of 2 months and the original model with $q = 0.815$ (the other parameter values used were $l = 8$, $r = 0.51$, $\mu = 0.1$ and $k = 1$, as above).

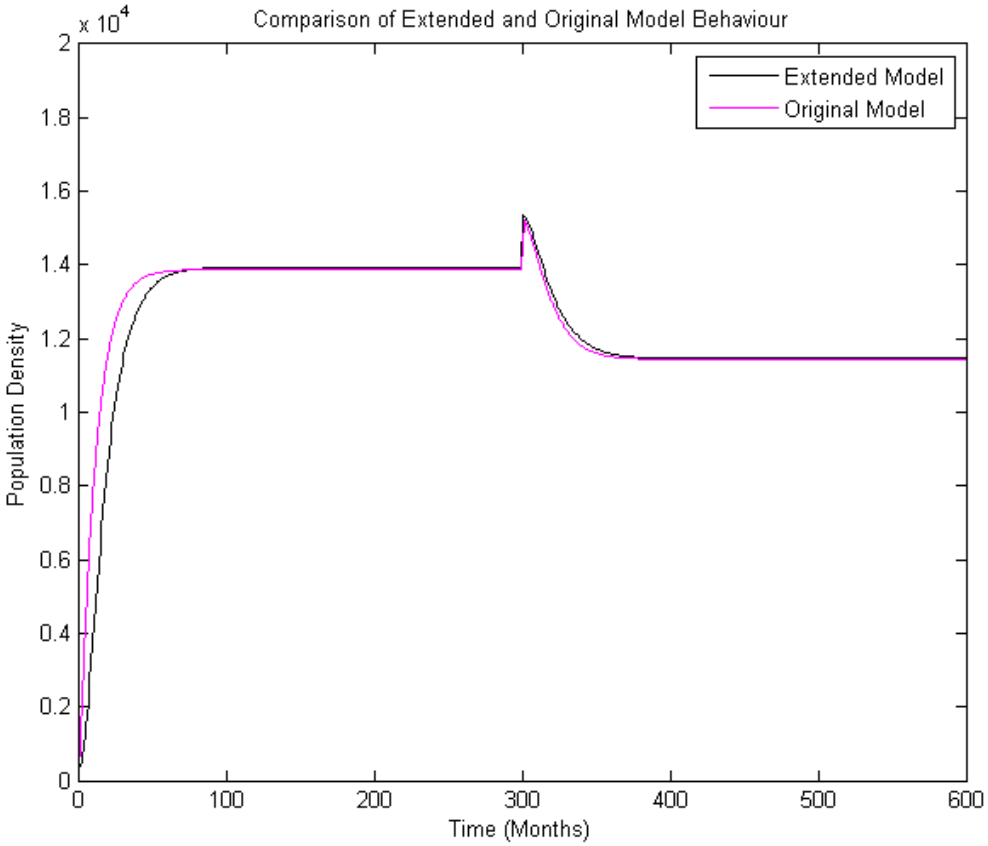

Figure 3.2: Graph displaying the behaviour of our original system with $\tau = 2$ versus the simplified system with $q = 0.815$.

We can see that the greatest point of difference is during the growth of the healthy population before Trojan females are introduced, an aspect of the model behaviour which we are not interested in here. As the juvenile stage gets longer, say 12 months instead of 2, the difference between the two models increases slightly, so care needs to be taken in these cases.

Chapter 4

Analysis

In this section we focus on trying to predict the long term behaviour of the continuous time model given a set of parameter values and initial conditions. The fact that the system is 4-dimensional makes analysis and visualisation difficult. In the following sections we employ a technique to reduce the model to a 2-dimensional system of equations and in turn gain an understanding of the approximate long term behaviour of our model.

4.1 2-Dimensional Reduction

In order to gain a better understanding of our model we wish to reduce it to a 2-dimensional system of ordinary differential equations, which is much simpler to analyse than the current 4-dimensional system. For readability, we assume that $k = 1$ throughout.

To reduce the dimensions of the model we replace the variables M and F with T and S, where T represents the total of the two $(M + F)$ and S corresponds to the extent to which the proportion of males and females differs to the equilibrium proportion r. Similarly M^* and F^* are replaced by T^* and S^*. This transformation allows us to reduce the system to two variables T and T^*, without approximation, revealing much about the structure of the original system of equations. The details of this reduction are shown below.

We make the following transformation

$$\begin{bmatrix} S \\ T \end{bmatrix} = \begin{bmatrix} 1-r & -r \\ 1 & 1 \end{bmatrix} \begin{bmatrix} M \\ F \end{bmatrix},$$

and similarly for S^* and T^*.

This is clearly invertible with

$$\begin{bmatrix} M \\ F \end{bmatrix} = \begin{bmatrix} 1 & r \\ -1 & 1-r \end{bmatrix} \begin{bmatrix} S \\ T \end{bmatrix}.$$

We can now look at the system of equations involving S, T, S^* and T^*. First notice that

$$\begin{aligned} \dot{S} &= (1-r)\dot{M} - r\dot{F}, \\ &= (1-r)(rB(N)qF - \mu M) - r((1-r)B(N)qF - \mu F), \\ &= -(1-r)\mu M + r\mu F, \\ &= -\mu S. \end{aligned}$$

Thus, solving for S, we get

$$S = S_0 e^{-\mu t},$$

where $S_0 = (1-r)M_0 - rF_0$.

Next we have that

$$\begin{aligned} \dot{T} &= \dot{M} + \dot{F}, \\ &= rB(N)qF - \mu M + (1-r)B(N)qF - \mu F, \\ &= B(N)qF - \mu T, \\ &= B(N)q((1-r)T - S) - \mu T, \end{aligned}$$

using the substitution $F = (1-r)T - S$. We then expand $B(N)$ using the substitution $M = rT + S$ to get

$$\dot{T} = \frac{0.9lq(rT+S)((1-r)T - S)}{\left(\frac{T+T^*}{500} + 1\right)(S + S^* + r(T+T^*) + 1)} - \mu T.$$

Similarly for S^* and T^* we have

$$\begin{aligned} S^* &= S_0^* e^{-\mu t}, \quad \text{with } S_0^* = (1-r)M_0^* - rF_0^*, \text{ and} \\ \dot{T^*} &= \frac{0.9lq(rT+S)((1-r)T^* - S^*)}{\left(\frac{T+T^*}{500} + 1\right)(S + S^* + r(T+T^*) + 1)} - \mu T^*. \end{aligned}$$

Thus we have reduced the problem to the following 2-dimensional non-linear system of equations

$$\begin{bmatrix} \dot{T} \\ \dot{T^*} \end{bmatrix} = \begin{bmatrix} \frac{0.9lq(rT+S_0e^{-\mu t})((1-r)T-S_0e^{-\mu t})}{\left(\frac{T+T^*}{500}+1\right)((S_0+S_0^*)e^{-\mu t}+r(T+T^*)+1)} - \mu T \\ \frac{0.9lq(rT+S_0e^{-\mu t})((1-r)T^*-S_0^*e^{-\mu t})}{\left(\frac{T+T^*}{500}+1\right)((S_0+S_0^*)e^{-\mu t}+r(T+T^*)+1)} - \mu T^* \end{bmatrix},$$

with S_0 and S_0^* as defined earlier. This system represents the behaviour of the healthy population T together with the Trojan population T^*.

4.2 Long-Term Behaviour

We can now analyse the behaviour of this 2-dimensional system, which relates directly back to our original model. Given that the system is non-linear, an analytical solution is unlikely. However we can explore the long term behaviour and possible equilibrium solutions of the system. Taking $t \to \infty$, it follows that $e^{-\mu t} \to 0$ and hence, as t gets larger, the system converges to

$$\begin{bmatrix} \dot{T} \\ \dot{T^*} \end{bmatrix} = \begin{bmatrix} \frac{0.9lqr(1-r)T^2}{\left(\frac{T+T^*}{500}+1\right)(r(T+T^*)+1)} - \mu T \\ \frac{0.9lqr(1-r)TT^*}{\left(\frac{T+T^*}{500}+1\right)(r(T+T^*)+1)} - \mu T^* \end{bmatrix}.$$

Using the parameter values $l = 8$, $q = 0.5$, $r = 0.51$ and $\mu = 0.1$ we produce the phase plot shown in Figure 4.1 below (note that these will be the parameter values used throughout the remainder of this chapter).

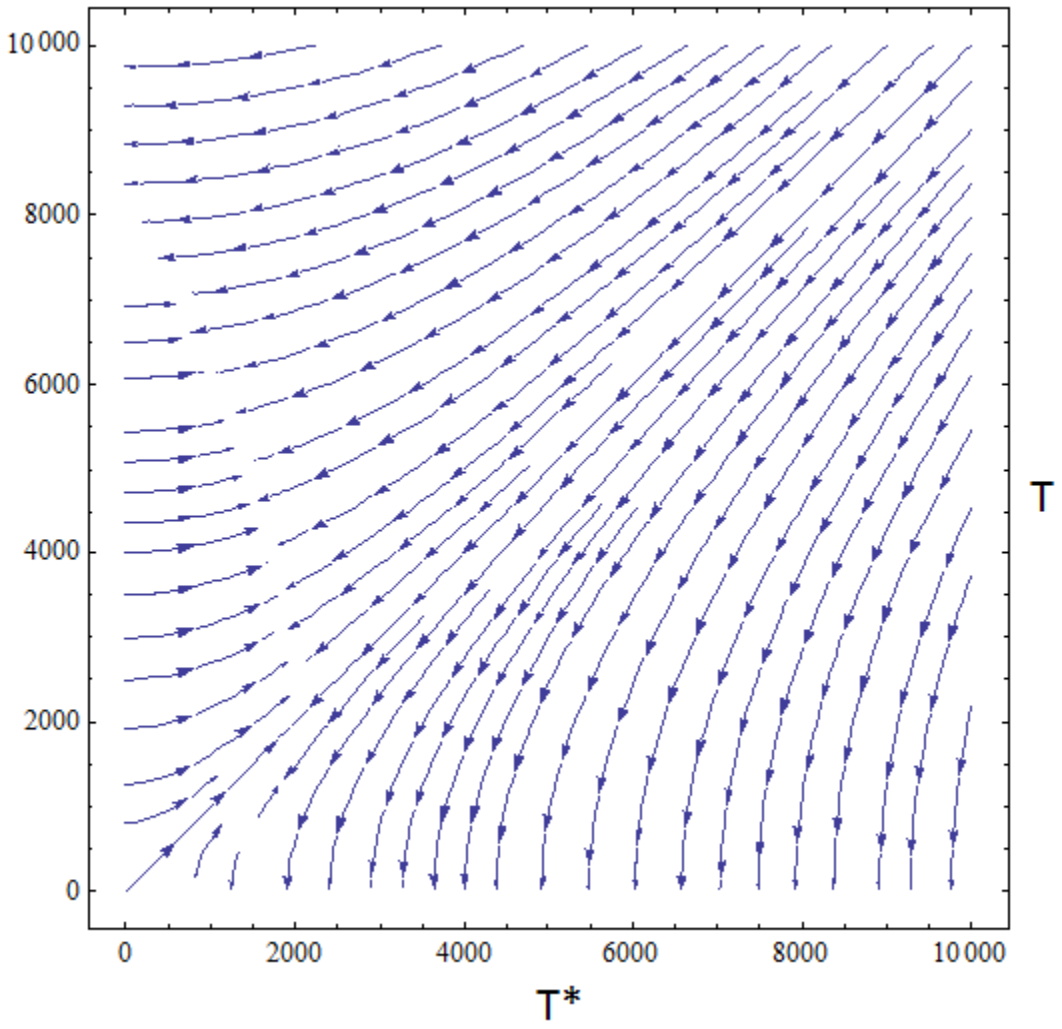

Figure 4.1: Phase plot showing the effect the long term behaviour of the reduced 2D model.

The phase plot shows a clear divide between where the density of the healthy population is increasing and where it is decreasing. Where the two sides meet is likely where the equilibrium solutions occur. To check this we take $\dot{T}, \dot{T^*} = 0$ and $t \to \infty$ as before. We are then left with the equation

$$\begin{bmatrix} 0 \\ 0 \end{bmatrix} = \begin{bmatrix} \frac{0.9lqr(1-r)T^2}{\left(\frac{T+T^*}{500}+1\right)(r(T+T^*)+1)} - \mu T \\ \frac{0.9lqr(1-r)TT^*}{\left(\frac{T+T^*}{500}+1\right)(r(T+T^*)+1)} - \mu T^* \end{bmatrix}.$$

Since the two equations differ only slightly, we make the following substitution:

$$W = \frac{0.9lqr(1-r)T}{\left(\frac{T+T^*}{500}+1\right)(r(T+T^*)+1)}.$$

The we wish to solve the set of simultaneous equations

$$WT = \mu T,$$
$$WT^* = \mu T^*.$$

Clearly $T = T^* = 0$ satisfies the equations, however we are most interested in the circumstances where T and T^* are non-zero. Thus we focus on the solution $W = \mu$. We have

$$W = \mu \Rightarrow \frac{0.9lqr(1-r)T}{\left(\frac{T+T^*}{500}+1\right)\left(r(T+T^*)+1\right)} = \mu, \tag{4.1}$$
$$\Rightarrow \frac{450lqr(1-r)T}{(T+T^*+500)(r(T+T^*)+1)} = \mu, \tag{4.2}$$
$$\Rightarrow \frac{450lqr(1-r)}{\mu}T = (T+T^*+500)(r(T+T^*)+1). \tag{4.3}$$

Plotting this implicitly using the same parameters as above gives the graph shown in Figure 4.2.

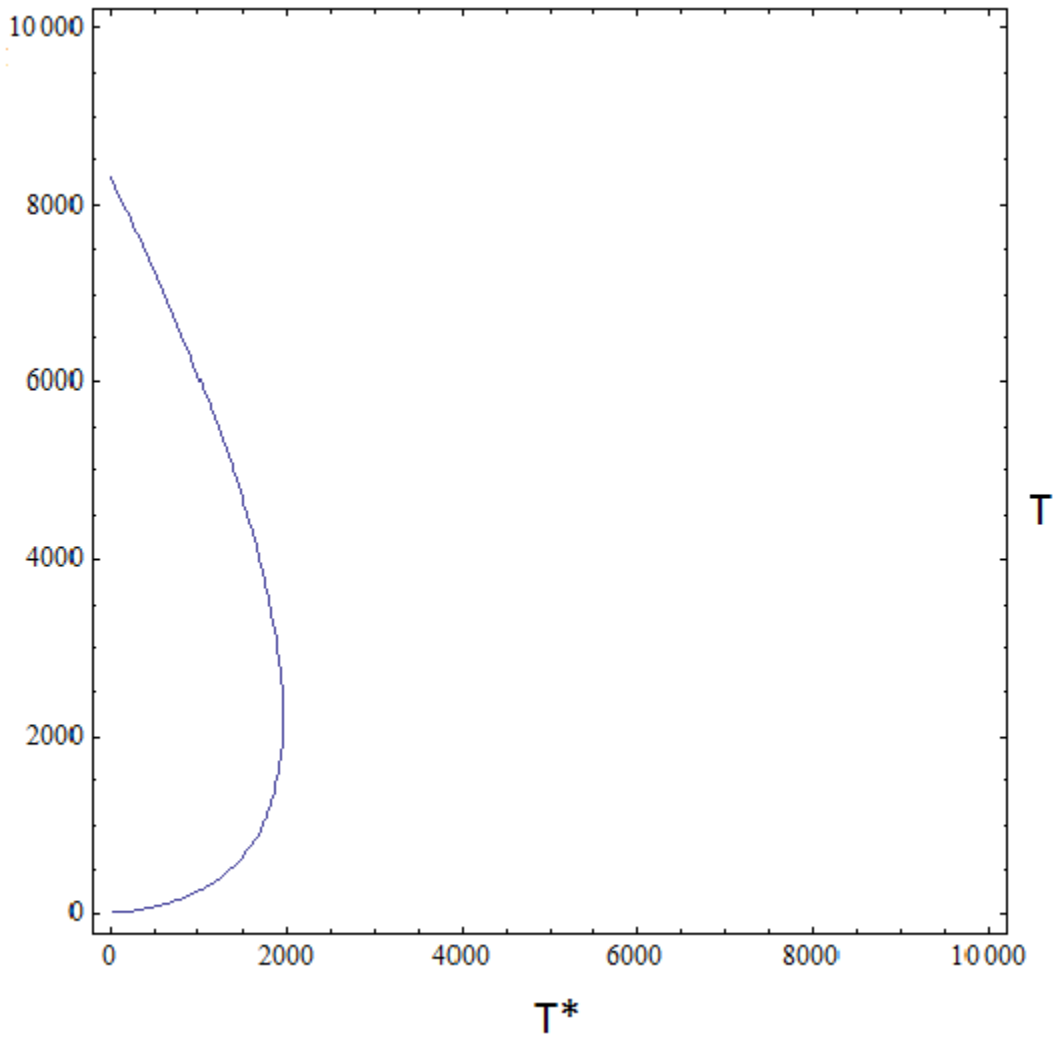

Figure 4.2: Graph showing the long term equilibrium points for the 2D model.

The equilibrium solutions lie along the divide identified in the phase plot from Figure 4.1. As expected, if the initial introduction of Trojan females is large enough (we will define "large enough" later) then the population will become extinct, with the density of the healthy population falling to zero which in turn causes the population to die out. Otherwise, if the size of the introduction is small, the population will approach an equilibrium along the line shown in Figure 4.2. We call this an attracting manifold. The exact equilibrium solution depends on both the size of the introduction of Trojan females and the density of the healthy population at the time of introduction. The greater the introduction size the lower the resultant equilibrium density will be and vice versa.

We wish to learn more about the attracting manifold displayed in Figure 4.2; namely, the point of intersection with the y axis and the size of initial introduction of Trojan females above which extinction is ensured.

To find where the curve crosses the y axis we set $T^* = 0$ in equation (4.3), giving

$$\begin{aligned}\frac{450lqr(1-r)}{\mu}T &= (T+500)(rT+1),\\ &= rT^2 + T(500r+1) + 500.\end{aligned}$$

Hence we wish to solve the quadratic

$$rT^2 + T\left(500r + 1 - \frac{450lqr(1-r)}{\mu}\right) + 500 = 0, \tag{4.4}$$

giving the solutions

$$T = \frac{-(500r + 1 - \frac{450lqr(1-r)}{\mu}) \pm \sqrt{\left(500r + 1 - \frac{450lqr(1-r)}{\mu}\right)^2 - 2000r}}{2r}. \tag{4.5}$$

These two solutions correspond to the equilibrium densities that the population would reach in the absence of the mutation, restricted only by limited resources in the environment (need to show proof of this?). The larger of the two is also an upper bound for the density of the population after Trojan female introduction. The smaller solution will be very close to zero (may not be exactly zero due to the continuous nature of the variables in a discrete context) and represents the obvious equilibrium solution where $T = T^* = 0$.

Another important aspect of the curve in Figure 4.2 is where it crosses the $T = T^*$ line. Since the phase plot is linear along this line, we can use this information to predict the equilibrium that the population will reach if the number of Trojans introduced is equal to the current density of the population. Letting $T = T^*$ in equation (4.3) gives

$$\frac{450lqr(1-r)}{\mu}T = (2T+500)(2rT+1).$$

Thus we can find T by solving the quadratic

$$4rT^2 + \left(2 + 1000r - \frac{450lqr(1-r)}{\mu}\right)T + 500 = 0,$$

which results in

$$T = \frac{-\left(2 + 1000r - \frac{450lqr(1-r)}{\mu}\right) \pm \sqrt{\left(2 + 1000r - \frac{450lqr(1-r)}{\mu}\right)^2 - 2000r}}{8r}. \tag{4.6}$$

Again one of the solutions will be approximately zero and the other corresponds to the equilibrium solution of T given that the number of Trojans introduced is equal to the current density of the population.

Thus we have found that if the number of Trojan females introduced is less than or equal to the current density of the population, the resulting equilibrium will be within the range bounded above by (4.5) and below by two times the value produced in (4.6) (using the non-trivial solutions in each case).

Finally we wish to be able to predict the size of introduction needed to reduce the population to extinction. We can see from the phase plot in Figure 4.1 that the boundary above which this occurs, the "extinction boundary", is close to the $T = T^*$ line, especially for large values of T and T^*. However, for small population sizes this is clearly not the case. The curve that defines this boundary is difficult to find explicitly, however we can approximate it with a straight line that has two properties:

1. the line must have a gradient of 1;

2. the line must touch the curve only once (and therefore must not cross it).

Hence we are looking for a tangent line to the curve with a gradient of 1. To find this we must first compute the implicit derivative of the curve using (4.3):

$$\left(\frac{450lqr(1-r)}{\mu}T\right)' = ((T+T^*+500)(r(T+T^*)+1))'$$
$$\Rightarrow \frac{450lqr(1-r)}{\mu}\frac{dT}{dT^*} = 2rT\frac{dT}{dT^*} + 2rT^*\frac{dT}{dT^*} + 2rT + 2rT^* + (500r+1)\frac{dT}{dT^*} + 500r + 1,$$
$$\Rightarrow \frac{dT}{dT^*}(\frac{450lqr(1-r)}{\mu} - 2r(T+T^*) - 500r - 1) = 2r(T+T^*) + 500r.$$

Thus we have

$$\frac{dT}{dT^*} = \frac{2r(T+T^*)+500r}{\left(\frac{450lqr(1-r)}{\mu} - 2r(T+T^*) - 500r - 1\right)}. \tag{4.7}$$

Solving $\frac{dT}{dT^*} = 1$ gives the point where the tangent to the curve has a gradient of 1:

$$T_0 = \frac{\mu^2(1-500r)^2 - 50625l^2q^2(r-1)^2r^2}{1800lq\mu(r-1)r^2},$$
$$T_0^* = \frac{\mu^2(1-500r)^2 - 151875l^2q^2(r-1)^2r^2 + 900lq\mu(r-1)(1+500r)r}{1800lq\mu(r-1)r^2}.$$

We can now define the extinction boundary as a line with gradient 1, shifted to the right by the difference $T_0^* - T_0$:

$$T = T^* - (T_0^* - T_0). \tag{4.8}$$

Figure 4.3 shows the extinction boundary for our example from before. The red line is the calculated boundary and the $T = T^*$ line is emphasised in blue. If the size of the introduction of Trojan females places the system beyond the red line we can conclude that the population will eventually become extinct. However if it places the system between the two lines we cannot be certain whether or not extinction will occur.

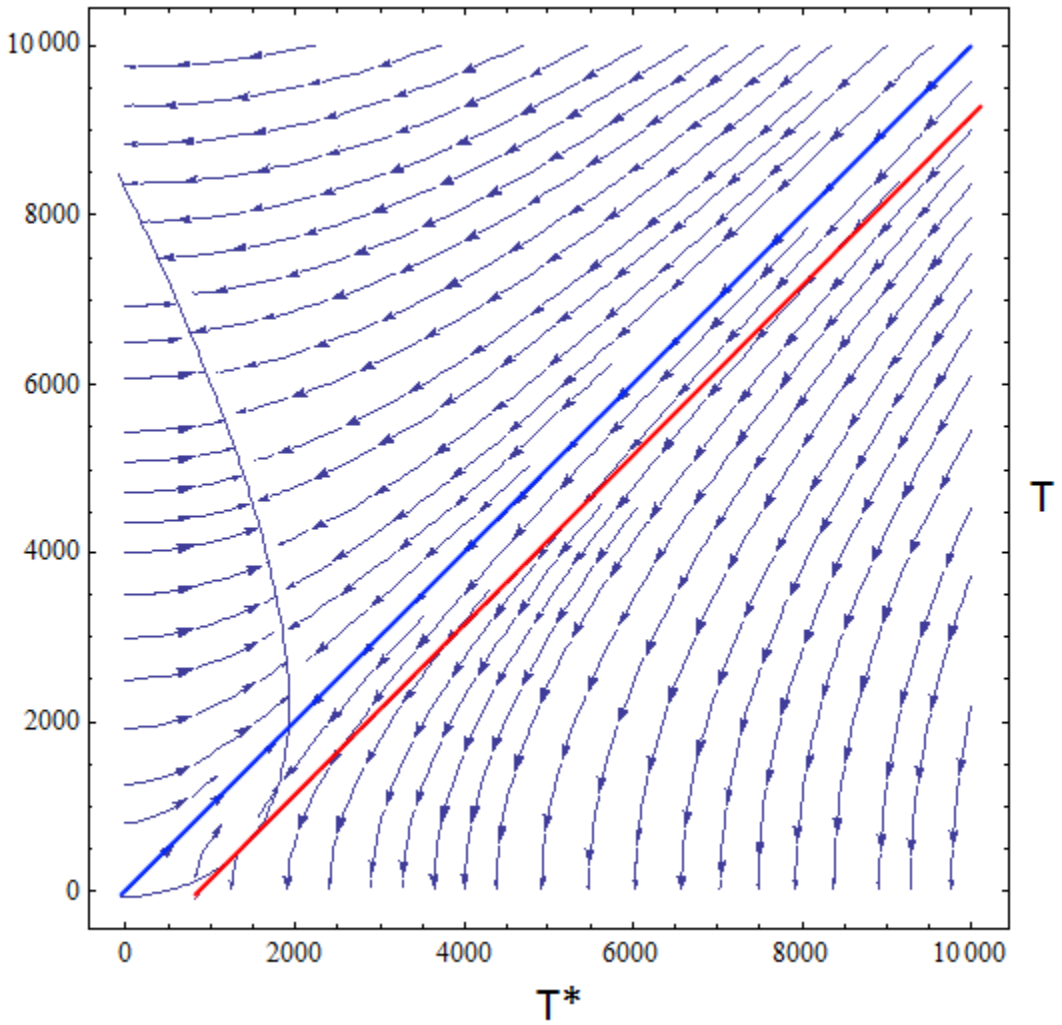

Figure 4.3: Graph showing the boundary above which the population will go extinct.

4.2.1 Effect of Limited Time

In the previous sections we assumed that time was able to tend to infinity, allowing us to observe the long term behaviour of the system. This is equivalent to assuming that $S = 0$ and $S^* = 0$, that is, both the Trojan and non-Trojan populations had equilibrium proportions of males and females. While it may be reasonable to assume that equilibrium holds in the wild population, the strategy for introducing the Trojan mutation involves introducing large numbers of Trojan females, disrupting the gender proportions in the Trojan population. In this section we examine the effect of this temporary gender imbalance on the long term behaviour of the system.

The only places where we encounter t in our system are the terms $S_0 e^{-\mu t}$ and $S_0^* e^{-\mu t}$, where

$$S_0 = (1-r)M_0 - rF_0,$$
$$S_0^* = (1-r)M_0^* - rF_0^*.$$

Since the healthy population is assumed to have been settled in the environment for some time prior to the introduction of Trojan females, it is likely that the proportion of males in the population will have reached its equilibrium proportion r. Thus for S_0 we have

$$S_0 = (1-r)M_0 - rF_0 = (1-r)rT - r(1-r)T = 0.$$

Hence we can deem the effect of $S_0 e^{-\mu t}$ to be negligible.

The same cannot be said for the Trojan equivalent, $S_0^* e^{-\mu t}$. Unlike for the non-Trojan population, the ratio of Trojan males and females will not initially be equal to r, since we only introduce Trojan females into the population. Hence we have

$$S_0^* = (1-r)M_0^* - rF_0^* = -rF_0^*,$$

and therefore

$$-S_0^* e^{-\mu t} = rF_0^* e^{-\mu t} \leq rF_0^*.$$

So what effect does this have on the behaviour of our model? To study this we consider the ratio $\frac{\dot{T}}{\dot{T}^*}$, the rate of change of T with respect to the rate of change of T^*, with the gender imbalance included and compare this to the ratio when the gender imbalance is excluded,

as in the previous section. To simplify calculations we make the following substitutions:

$$W = 0.9lqrT,$$
$$Z = \left(\frac{T+T^*}{500}+1\right)((S_0+S_0^*)e^{-\mu t}+r(T+T^*)+1).$$

We then have

$$\begin{aligned}
\frac{\dot{T}}{\dot{T^*}} &= \frac{\frac{W((1-r)T-S_0e^{-\mu t})}{Z}-\mu T}{\frac{W((1-r)T^*-S_0^*e^{-\mu t})}{Z}-\mu T^*}, \\
&= \frac{W(1-r)T-\mu ZT}{W((1-r)T^*-S_0^*e^{-\mu t})-\mu ZT^*}, \text{ by taking } S_0=0, \\
&= \frac{W(1-r)T-\mu ZT}{W((1-r)T^*+rF_0^*e^{-\mu t})-\mu ZT^*}, \\
&\leq \frac{W(1-r)T-\mu ZT}{W(1-r)T^*-\mu ZT^*}, \\
&= \frac{T}{T^*}.
\end{aligned}$$

Finally, we compare this to the ratio ignoring the gender imbalance:

$$\begin{aligned}
\frac{\dot{T}}{\dot{T^*}} &= \frac{\frac{0.9lqr(1-r)T^2}{\left(\frac{T+T^*}{500}+1\right)(r(T+T^*)+1)}-\mu T}{\frac{0.9lqr(1-r)TT^*}{\left(\frac{T+T^*}{500}+1\right)(r(T+T^*)+1)}-\mu T^*}, \\
&= \frac{T}{T^*}.
\end{aligned}$$

Thus we have shown that the rate of change of T with respect to the rate of change of T^* is less, or more negative, when the effect of gender imbalance within the Trojan population is taken into account. This is a positive sign and suggests our previous predictions were pessimistic, with the healthy population dying out faster, or growing slower, than we predicted.

4.3 Sensitivity to Parameter Changes

In this next section we explore the effect that changing parameters has on our equilibrium solutions. The attracting manifold in (4.3), which defines our equilibrium solutions, depends on the parameters l, q, r and μ, so we will explore the effect that each one has on three things:

1. the upper bound defined in (4.5),

2. the lower bound defined in (4.6), and

3. the horizontal distance between the $T = T^*$ line and the boundary beyond which extinction is ensured, i.e. $T_0^* - T_0$.

In each case the parameter of interest will take on 100 values equally spaced within a suitable range ($(0, 1)$ for r, q and μ, and $(0, 20)$ for l). The solution of interest is then calculated at each value and a line is plotted through the points.

4.3.1 Upper Bound

We are interested in how the "upper bound" of the equilibrium population size changes under different values of l, m, q and r. Recall that this upper bound represents the equilibrium that population tends to in the absence of Trojan females and is the largest possible equilibrium that the population can reach after TF introduction. We defined the upper bound explicitly as

$$UB = \frac{-(500r + 1 - \frac{450lqr(1-r)}{\mu}) + \sqrt{\left(500r + 1 - \frac{450lqr(1-r)}{\mu}\right)^2 - 2000r}}{2r}.$$

Below are four graphs displaying the relationship between the upper bound and each parameter.

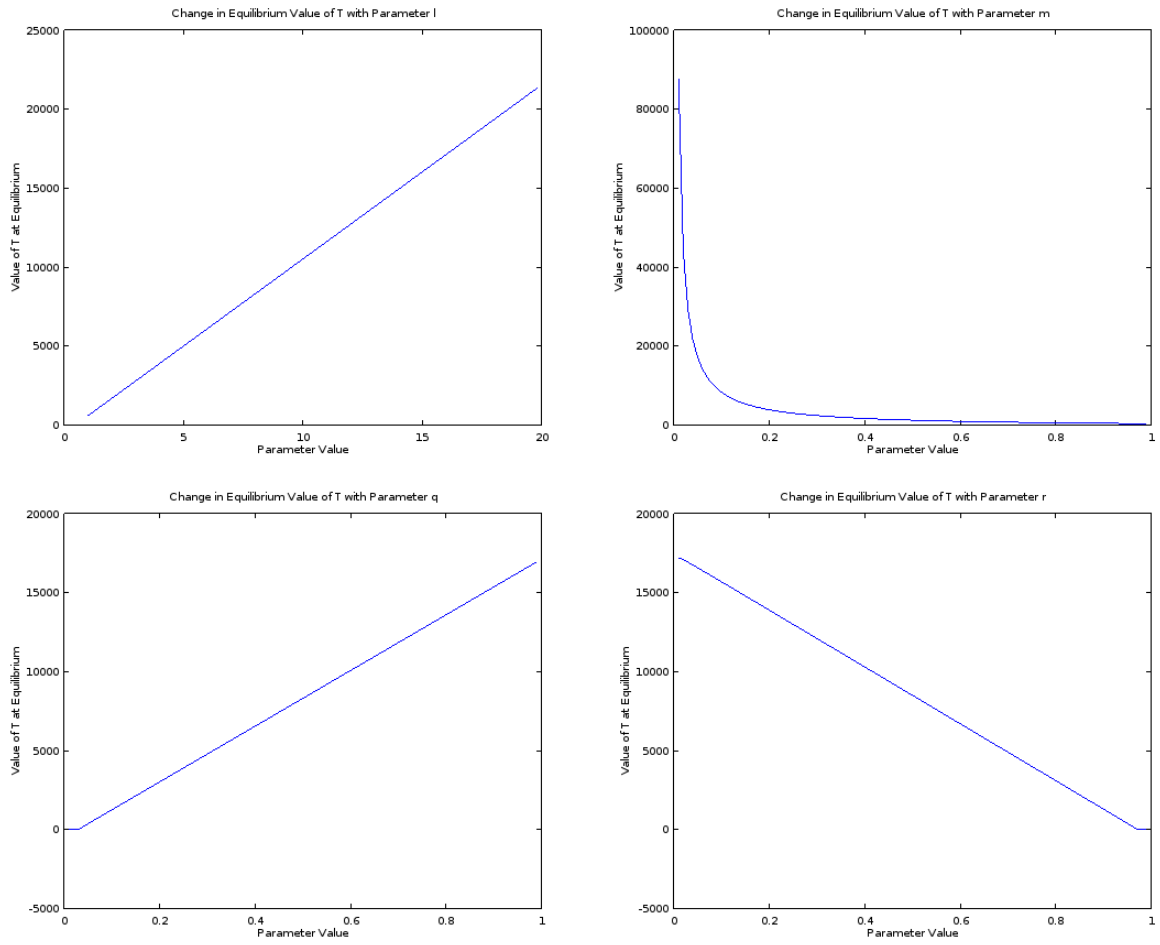

Figure 4.4: Graphs showing how the equilibrium solution in (4.5) changes with respect to each parameter.

We can see that the value of the solution increases linearly with l and q, decreases linearly with r and decreases exponentially with μ.

4.3.2 Lower Bound

The "lower bound" defines the lowest equilibrium value that the population can reach given that the number of Trojan females introduced is less than or equal to the current size of the population. We found that the lower bound was equal to

$$LB = \frac{-\left(2 + 1000r - \frac{450lqr(1-r)}{\mu}\right) + \sqrt{\left(2 + 1000r - \frac{450lqr(1-r)}{\mu}\right)^2 - 2000r}}{8r}.$$

Again we produce four plots displaying the relationship with each parameter.

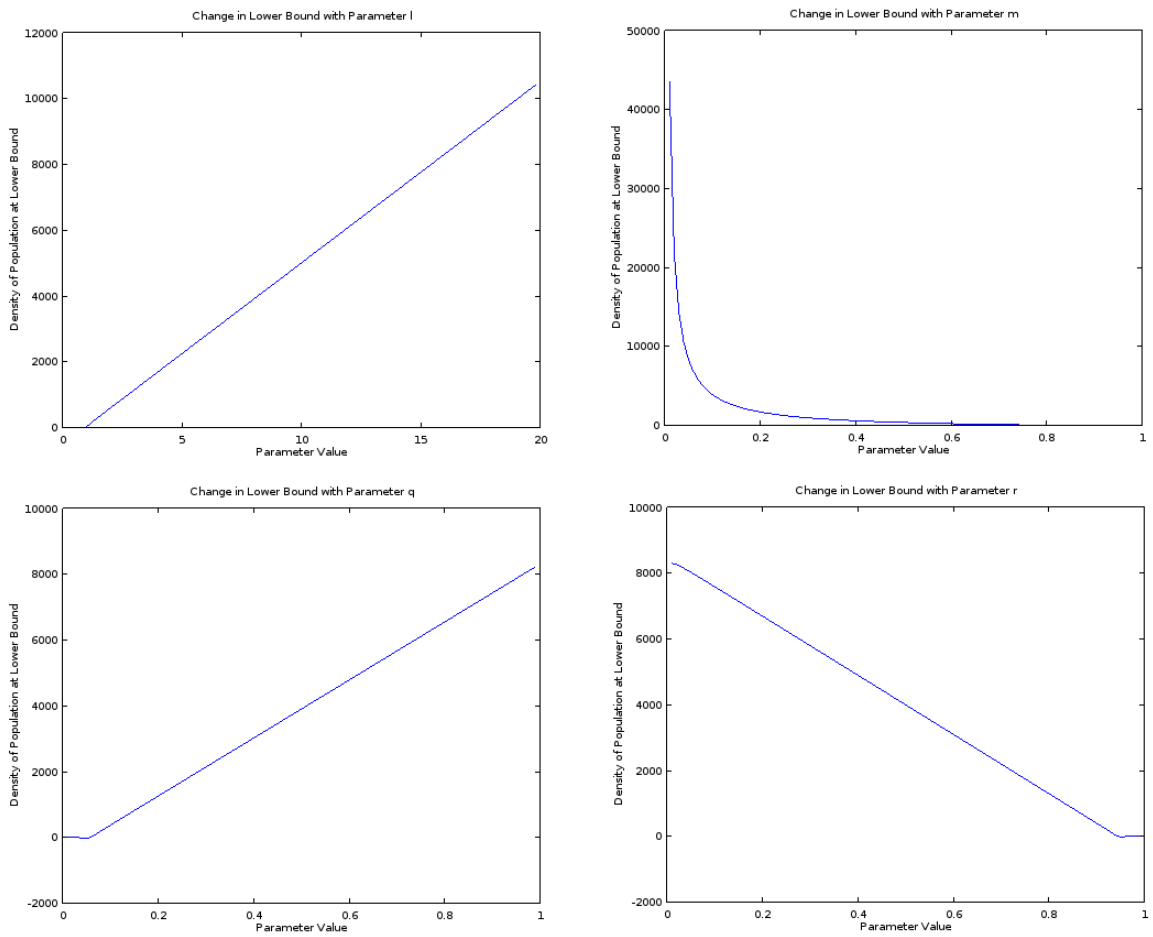

Figure 4.5: Graphs showing how the solution in (4.6) changes with respect to each parameter.

These results are very similar to that of the upper bound, with l and q increasing linearly and r and μ decreasing linearly and exponentially respectively.

4.3.3 Extinction Boundary

The final aspect of the curve we wish to measure with respect to varying parameters is the distance between the $T = T^*$ line and the extinction boundary that defines the number of Trojan females needed to ensure extinction. The results are displayed in Figure 4.6.

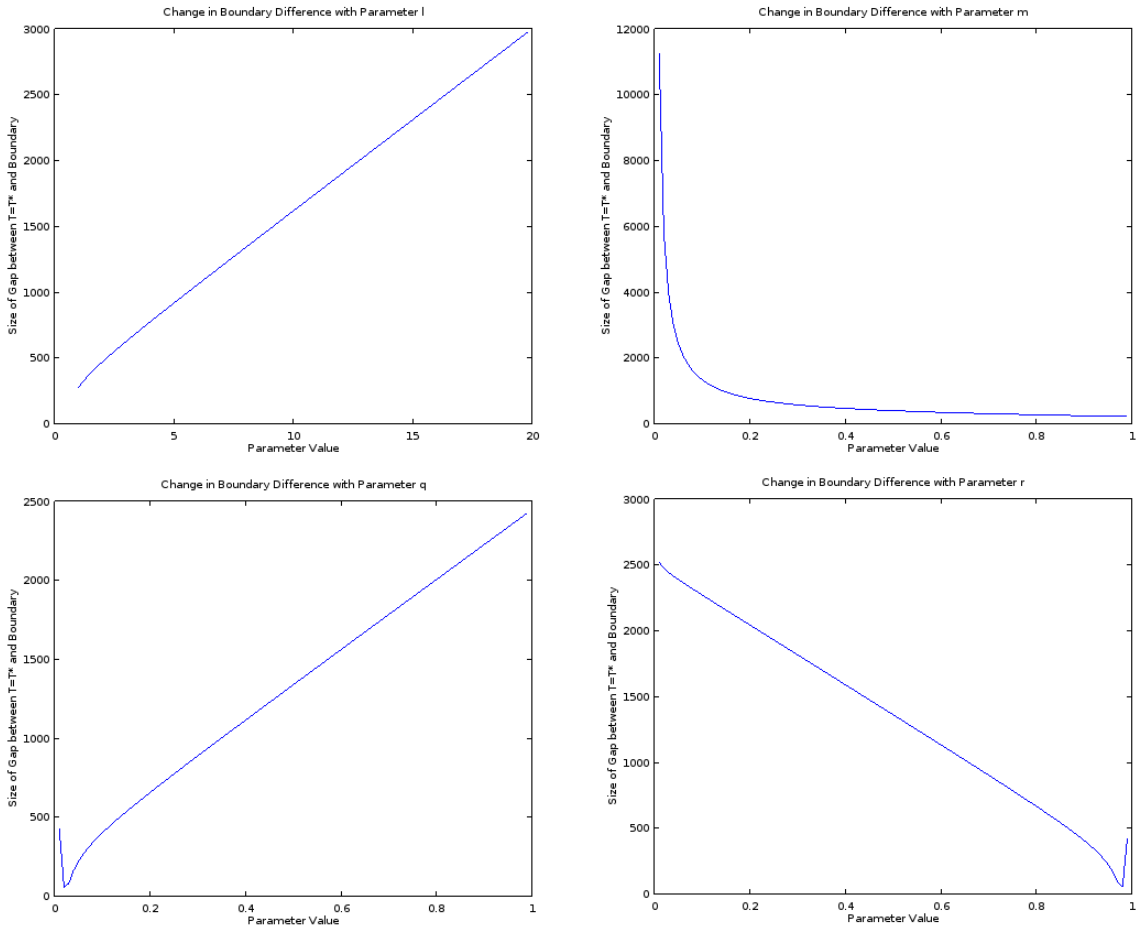

Figure 4.6: Graphs showing how the difference $T_0^* - T_0$ changes with respect to each parameter.

Again we have very similar relationships to the upper and lower bounds, although r and q behave unusually at values close to zero.

4.3.4 Interpretation

We now apply the information from the three sets of graphs above to the behaviour of the system.

Firstly, it is clear that as l and q increase, the extinction boundary is pushed further and further to the right of the $T = T^*$ line. However, when plotted relative to the upper bound, we see that the size of the gap is staying constant relative to the size of the population for changes in q (ignoring values close to zero). For increases in l, the gap is in fact decreasing relative to the size of the population, shown in Figure 4.7. Thus the proportion

of Trojan females needed to bring the population to extinction falls with increased birth rates.

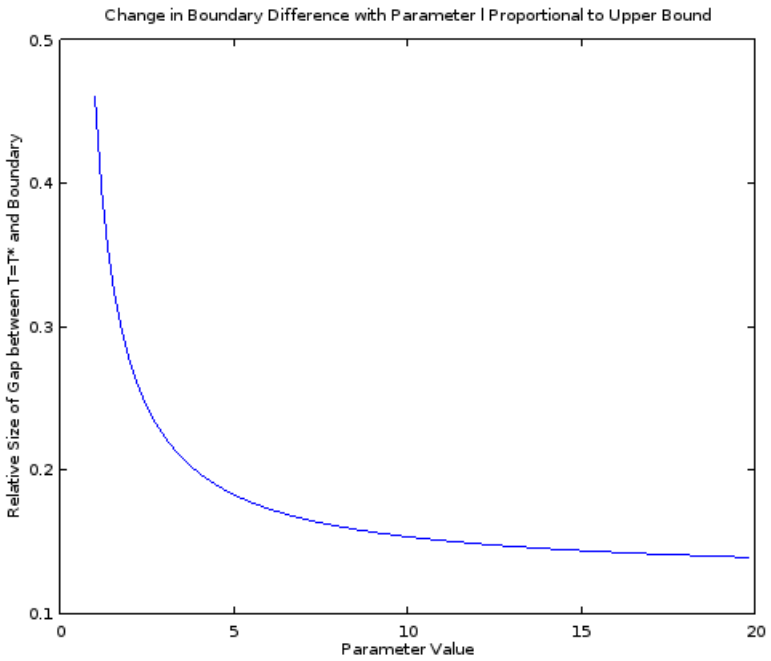

Figure 4.7: Graph showing how the difference $T_0^* - T_0$ changes with l relative to the upper bound.

We find similar results for changes in r and μ. Although the boundary gap appears to decrease with increasing r, it actually remains constant relative to the population size. On the other hand, the death rate μ increases the relative size of the gap, contrary to what the graph in Figure 4.6 suggests.

Thus, the litter size l and death rate μ affect the relative size of the gap in opposing directions, not surprisingly, while the gender ratio r and maturation rate q have little relative effect.

We can do a similar analysis with the upper and lower bounds. The graphs in Figure 4.4 and Figure 4.5 show us that l and q increase both bounds and μ and r decrease them, which is what we would predict. However we obtain more interesting information by looking at the distance between the two bounds, relative to the size of the upper bound. An example of how this value changes with the litter size l is shown below.

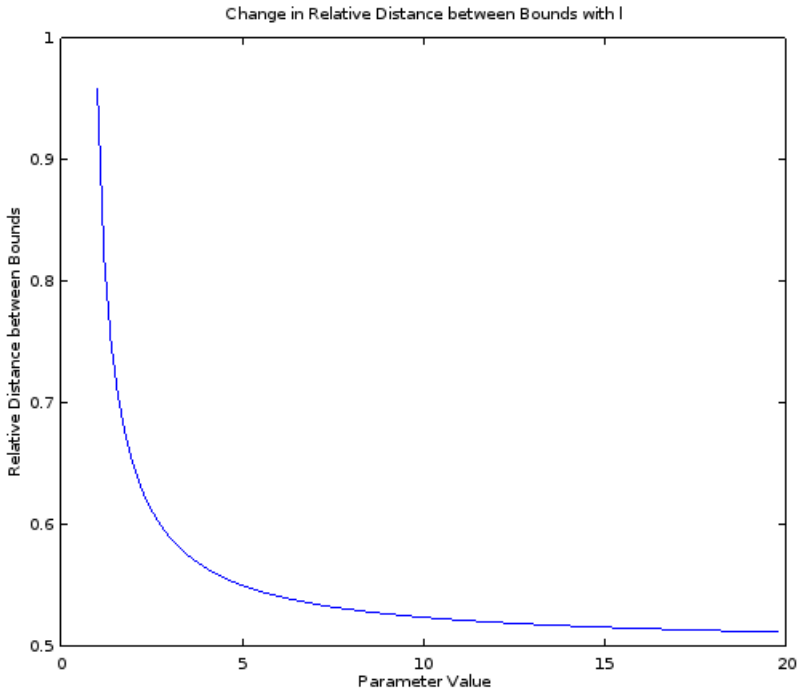

Figure 4.8: Graph showing how the relative distance between bounds changes with l.

We see that as l increases the relative distance between the upper and lower bounds falls. Hence there is a relatively smaller range of possible equilibrium values when the number of Trojan females introduced is less than or equal to the current population size.

Similar simulations for the other parameters show that q also decreases the relative difference while μ and r have the opposite effect.

Chapter 5

Wolbachia

In this chapter we investigate a possible extension to the model in the form of the Wolbachia Bacteria, explained below, a common bacteria found in insects and other arthropods [9, 12]. We extend our model to incorporate the effects of Wolbachia and try to determine whether this inclusion aids, hinders or has no effect on our goal to eradicate pests.

5.1 Background

Wolbachia are endosymbiotic bacteria (bacteria which live within the body or cells of another organism) that are commonly found in insects and other arthropods. They are inherited maternally and can have complex interactions with their host, known to be able to alter reproductive fitness in four ways [12]:

1. Male killing: infected males die during the larval stage.
2. Feminization: infected males develop as females or infertile pseudo-females.
3. Parthenogenesis: reproduction of infected females without males.
4. Cytoplasmic incompatibility (CI): infected males have reduced ability to reproduce with uninfected females, and similarly for infected females mating with uninfected males.

Here we focus on the effect of CI on the behaviour of our model.

5.2 Derivation

5.2.1 Non-Trojan, Non-Wolbachia Model

We use the model from [9] as a basis for our extended model. To justify this, we show below that the dynamic equations defining the basic behaviour of insect growth without Wolbachia is equivalent to our model without Trojans. However we first introduce some new notation, adopted from [9]. Notice that, in the context of insects, the variables and parameters are taken on a daily timescale, rather than the monthly scale we have been using so far. Hence, for the remainder of this chapter, any parameters and models used will adopt this new scale. The model introduced in [9] also takes into account the juvenile stage of insects. Thus we use our model involving the lag term from Chapter 3 throughout this chapter.

Variables	
Notation	Description
$L(t,l)$	Number of larvae that have been in the larval stage for l days
$S(t,a)$	Number of adults that have been in the adult stage for a days
$\tilde{L}(t)$	Total number of larvae of any age
$\tilde{S}(t)$	Total number of adults of any age
Parameters	
λ	Reproductive rate of females
T	Maximum length of larval stage
Functions	
$\theta_L(t,l)$	Probability a larva survives until time l (may be density dependent)
$\theta_S(a)$	Probability an adult survives until time a (depends only on age)
$\mu_L(\tilde{L}(t))$	Density dependent larval mortality rate
$\mu_S(a)$	Age dependent adult mortality rate

Table 5.1: Description of the parameters used in the model from [9]

Given these parameters, and assuming the sex ratio is equality, the dynamics of this model are determined by the following

$$L(t,l) = \frac{\lambda}{2}\tilde{S}(t-l)\theta_L(t,l), \quad l \leq T, \tag{5.1}$$

$$S(t,a) = L(t-a,T)\theta_S(a), \tag{5.2}$$

with

$$\theta_L(t,l) = exp(-\int_{t-l}^{t} \mu_L(\tilde{L}(\tau))d\tau),$$
$$\mu_L(\tilde{L}(t)) = \mu + \alpha(\tilde{L}(t))^{\beta}, \quad \mu, \alpha \text{ and } \beta \text{ constants},$$
$$\theta_S(a) = exp(-\int_{0}^{a} \mu_S(\tau)d\tau),$$
$$\mu_S(a) = c + \gamma r(ra)^{\gamma-1}, \quad c \text{ constant, } \gamma \text{ and } r \text{ Weibull shape and rate parameters.}$$

To convert this to our own model we take $\mu_L(\tilde{L}(t))$ and $\mu_S(a)$ to be density and age independent by letting $\alpha = \gamma = r = 0$ and $c = \mu$. Then $\mu_L(\tilde{L}(t)) = \mu_S(a) = \mu$ and hence

$$\theta_L(t,l) = exp(-\int_{t-l}^{t} \mu d\tau) = e^{-\mu l},$$
$$\theta_S(a) = exp(-\int_{0}^{a} \mu d\tau) = e^{-\mu a}.$$

Thus equations (5.1) and (5.2) become

$$L(t,l) = \frac{\lambda}{2}\tilde{S}(t-l)e^{-\mu l}, \quad l \leq T,$$
$$S(t,a) = L(t-a,T)e^{-\mu a}.$$

We characterise this behaviour with the following system of differential equations in terms of $\dot{\tilde{L}}(t)$ and $\dot{\tilde{S}}(t)$

$$\dot{\tilde{L}}(t) = \frac{\lambda}{2}\tilde{S}(t) - \mu\tilde{L}(t) - L(t,T),$$
$$\dot{\tilde{S}}(t) = L(t,T) - \mu\tilde{S}(t).$$

We derived these equations using that:

- The increase in the total number of larvae of any age is the birth rate λ multiplied by the number of adult females, which is half the total number of adults.
- The decrease in the total number of larvae is a combination of the number of larvae that die ($\mu\tilde{L}(t)$) and the number of larvae that mature into adults within the next time step. The latter is equal to the number of larvae that have been larvae for T days, $L(t,T)$, since these larvae will become adults given any small increase in t.
- The increase in the total number of adults is the number of larvae that become adults $L(t,T)$.

- The decrease in the total number of adults is the number of adults that die $\mu\tilde{S}(t)$.

Define $N(t) = \tilde{L}(t) + \tilde{S}(t)$. Then

$$\begin{aligned}\dot{N}(t) &= \frac{\lambda}{2}\tilde{S}(t) - \mu\tilde{L}(t) - L(t,T) + L(t,T) - \mu\tilde{S}(t),\\ &= \frac{\lambda}{2}\tilde{S}(t) - \mu N(t),\\ &= \frac{\lambda}{2}N(t-T)e^{-\mu T} - \mu N(t),\end{aligned}$$

using the fact that $\tilde{S}(t) = \tilde{S}(t-T)e^{-\mu T} + \tilde{L}(t-T)e^{-\mu T}$.

Finally we split this equation into males M and females F:

$$\dot{M}(t) = \frac{1}{2}\lambda F(t-T)e^{-\mu T} - \mu M(t), \tag{5.3}$$

$$\dot{F}(t) = \frac{1}{2}\lambda F(t-T)e^{-\mu T} - \mu F(t). \tag{5.4}$$

This clearly corresponds to our continuous time model from Chapter 2, excluding Trojans, with $r = \frac{1}{2}$, $B(N) = \lambda$, $\mu = \mu$ and $\tau = T$. Thus we have shown that our non-Trojan model is in fact an example of the type of model introduced in [9], thus we are justified in using a similar extension to model the effect of Wolbachia.

5.2.2 Wolbachia Model without Trojans

To introduce Wolbachia into the equations we make use of the following new parameters [9]:

Parameters	
Notation	Description
$p(t)$	Proportion of adults infected by Wolbachia
S_h	Fraction of offspring that fail to develop when an infected male mates with an uninfected female or vice versa
ω	Fraction of offspring from infected female that do not inherit the infection

Table 5.2: Description of the new parameters used to describe Wolbachia behaviour

We also carry through the same notation from before, using the subscripts U and W to signify uninfected and infected respectively.

There are four possible outcomes when two adults mate depending on which are healthy and which are infected. These four options are outlined in the table below

Parents	Healthy Proportion	Infected Proportion	Proportion of Healthy that Develop	Proportion of Infected that Develop
$F_U \times M_U$	1	0	1	NA
$F_U \times M_W$	1	0	$1 - S_h$	NA
$F_W \times M_U$	ω	$1 - \omega$	$1 - S_h$	1
$F_W \times M_W$	ω	$1 - \omega$	1	1

Table 5.3: Possible outcomes depending on type of parents

From this we derive equations (7) in [9]

$$L_W(t,l) = \frac{\lambda_W}{2}(1-\omega)\tilde{S_W}(t-l)\theta_{L,W}(t,l), \quad l \leq T_W,$$
$$L_U(t,l) = [(1 - S_h p(t-l))\frac{\lambda_U}{2}\tilde{S_U}(t-l) + (1 - S_h(1-p(t-l))\omega\frac{\lambda_W}{2}\tilde{S_W}(t-l)]\theta_{L,U}(t,l), \quad l \leq T_U,$$
$$S_W(t,a) = L_W(t-a, T_W)\theta_{S,W}(a),$$
$$S_U(t,a) = L_U(t-a, T_U)\theta_{S,U}(a).$$

(Notice that the second equation differs slightly to that found in [9], however we are confident that this is a minor error on their behalf and hence we continue our analysis with our version of these equations.)

Again we rewrite these as a system of differential equations involving $\dot{\tilde{L_W}}(t)$, $\dot{\tilde{L_U}}(t)$, $\dot{\tilde{S_W}}(t)$ and $\dot{\tilde{S_U}}(t)$, making the assumptions that the mortality rate for all individuals, juveniles, adults, healthy and infected, is a constant μ and the maturation time is not affected by the Wolbachia, i.e. $T_W = T_U = T$, for some constant T. We have

$$\dot{\tilde{L_W}}(t) = \frac{\lambda_W}{2}(1-\omega)\tilde{S_W}(t) - \mu\tilde{L_W}(t) - L_W(t,T),$$
$$\dot{\tilde{L_U}}(t) = (1 - S_h p(t))\frac{\lambda_U}{2}\tilde{S_U}(t) + (1 - S_h(1-p(t))\omega\frac{\lambda_W}{2}\tilde{S_W}(t) - \mu\tilde{L_U}(t) - L_U(t,T),$$
$$\dot{\tilde{S_W}}(t) = L_W(t,T) - \mu\tilde{S_W}(t),$$
$$\dot{\tilde{S_U}}(t) = L_U(t,T) - \mu\tilde{S_U}(t).$$

Letting $N_U = \tilde{L}_U + \tilde{S}_U$ and $N_W = \tilde{L}_W + \tilde{S}_W$ gives

$$\dot{N}_W(t) = \frac{\lambda_W}{2}(1-\omega)N_W(t-T)e^{-\mu T} - \mu N_W(t),$$
$$\dot{N}_U(t) = [(1-S_h p(t))\frac{\lambda_U}{2}N_U(t-T) + (1-S_h(1-p(t))\omega\frac{\lambda_W}{2}N_W(t-T)]e^{-\mu T} - \mu N_U(t).$$

Finally, we split N_U and N_W into M_U, F_U, M_W and F_W using the gender ratio $r = 0.5$, giving

$$\dot{M}_W(t) = \frac{\lambda_W}{2}(1-\omega)F_W(t-T)e^{-\mu T} - \mu M_W(t), \tag{5.5}$$
$$\dot{F}_W(t) = \frac{\lambda_W}{2}(1-\omega)F_W(t-T)e^{-\mu T} - \mu F_W(t), \tag{5.6}$$
$$\dot{M}_U(t) = [(1-S_h p(t))\frac{\lambda_U}{2}F_U(t-T) + (1-S_h(1-p(t))\omega\frac{\lambda_W}{2}F_W(t-T)]e^{-\mu T} - \mu M_U(t), \tag{5.7}$$
$$\dot{F}_U(t) = [(1-S_h p(t))\frac{\lambda_U}{2}F_U(t-T) + (1-S_h(1-p(t))\omega\frac{\lambda_W}{2}F_W(t-T)]e^{-\mu T} - \mu F_U(t), \tag{5.8}$$

where

- $\lambda_U = B(N)$ in the absence of Trojans,
- $\lambda_W = (1-S_f)\lambda_U$, with S_f representing the proportional reduction of female reproduction due to the Wolbachia [9],
- $p(t) = \frac{M_W+F_W}{M_W+F_W+M_U+F_U}$.

5.2.3 Wolbachia Model with Trojans

The final step in the derivation of our extended Wolbachia model is to incorporate the addition of Trojan females and sterile males into equations (5.5) - (5.8). In a similar manner to before, we list all the possible outcomes of reproduction given the category that the parents fall into. We bring in the usual $*$ notation to represent Trojan females or sterile males.

Parents	Healthy Trojan	Infected Trojan	Healthy non-Trojan	Infected non-Trojan
$F_U \times M_U$	0	0	1	0
$F_U \times M_W$	0	0	$1 - S_h$	0
$F_U \times M_U^*$	0	0	0	0
$F_U \times M_W^*$	0	0	0	0
$F_W \times M_U$	0	0	$\omega(1 - S_h)$	$1 - \omega$
$F_W \times M_W$	0	0	ω	$1 - \omega$
$F_W \times M_U^*$	0	0	0	0
$F_W \times M_W^*$	0	0	0	0
$F_U^* \times M_U$	1	0	0	0
$F_U^* \times M_W$	$1 - S_h$	0	0	0
$F_U^* \times M_U^*$	0	0	0	0
$F_U^* \times M_W^*$	0	0	0	0
$F_W^* \times M_U$	$\omega(1 - S_h)$	$1 - \omega$	0	0
$F_W^* \times M_W$	ω	$1 - \omega$	0	0
$F_W^* \times M_U^*$	0	0	0	0
$F_W^* \times M_W^*$	0	0	0	0

Table 5.4: Possible outcomes depending on type of parents

We use this information in the same way as in the previous section to obtain the system of equations (5.9) - (5.16) which describe the behaviour of the population with both Wolbachia and Trojans included:

$$\dot{M}_W(t) = \frac{\lambda_W}{2}(1-\omega)F_W(t-T)e^{-\mu T} - \mu M_W(t), \tag{5.9}$$

$$\dot{F}_W(t) = \frac{\lambda_W}{2}(1-\omega)F_W(t-T)e^{-\mu T} - \mu F_W(t), \tag{5.10}$$

$$\dot{M}_U(t) = [(1-S_h p(t))\frac{\lambda_U}{2}F_U(t-T) + (1-S_h(1-p(t))\omega\frac{\lambda_W}{2}F_W(t-T)]e^{-\mu T} - \mu M_U(t), \tag{5.11}$$

$$\dot{F}_U(t) = [(1-S_h p(t))\frac{\lambda_U}{2}F_U(t-T) + (1-S_h(1-p(t))\omega\frac{\lambda_W}{2}F_W(t-T)]e^{-\mu T} - \mu F_U(t), \tag{5.12}$$

$$\dot{M}^*_W(t) = \frac{\lambda_W}{2}(1-\omega)F^*_W(t-T)e^{-\mu T} - \mu M^*_W(t), \tag{5.13}$$

$$\dot{F}^*_W(t) = \frac{\lambda_W}{2}(1-\omega)F^*_W(t-T)e^{-\mu T} - \mu F^*_W(t), \tag{5.14}$$

$$\dot{M}^*_U(t) = [(1-S_h p^*(t))\frac{\lambda_U}{2}F^*_U(t-T) + (1-S_h(1-p^*(t))\omega\frac{\lambda_W}{2}F^*_W(t-T)]e^{-\mu T} - \mu M^*_U(t), \tag{5.15}$$

$$\dot{F}^*_U(t) = [(1-S_h p^*(t))\frac{\lambda_U}{2}F^*_U(t-T) + (1-S_h(1-p^*(t))\omega\frac{\lambda_W}{2}F^*_W(t-T)]e^{-\mu T} - \mu F^*_U(t), \tag{5.16}$$

where

- $\lambda_U = B(N)$,
- $\lambda_W = (1-S_f)\lambda_U$, with S_f as before,
- $p(t) = \frac{M_W+F_W}{M_W+F_W+M_U+F_U}$ and $p^*(t) = \frac{M^*_W+F^*_W}{M^*_W+F^*_W+M^*_U+F^*_U}$,
- we assume that the Wolbachia parameters ω and S_h are the same for Trojans and non-Trojans.

5.3 Effect of Wolbachia

Now that we have models characterising the behaviour of Wolbachia in our population, both with and without Trojans, we wish to investigate the affect this has on the long term behaviour of the population size. Given the high dimensions and complexity of the models involving Wolbachia, analytic solutions will be hard to come by. However, we can run numerical simulations of the Wolbachia models and compare them to our original continuous time model in order to gain a better understanding of the effect that Wolbachia has

and whether we could use it to increase the efficacy of the TFT as a pest control method.

We first run the model under a specific set of parameters to observe how the different populations react to each other. We use the parameter values from Hancock et al (2011), $r = 0.5$, $l = 15$, $\mu = 0.1$, $k = 1$, $S_f = 0.05$, $S_h = 0.99$, $\omega = 0.01$ and $T = 10$. In this case we allow the population to grow freely to its equilibrium before introducing a group of Wolbachia infected Trojan females, whose size is equivalent to 20% of the total population size at the time of introduction. The graph below shows the behaviour of each of the populations over a 2000 day period.

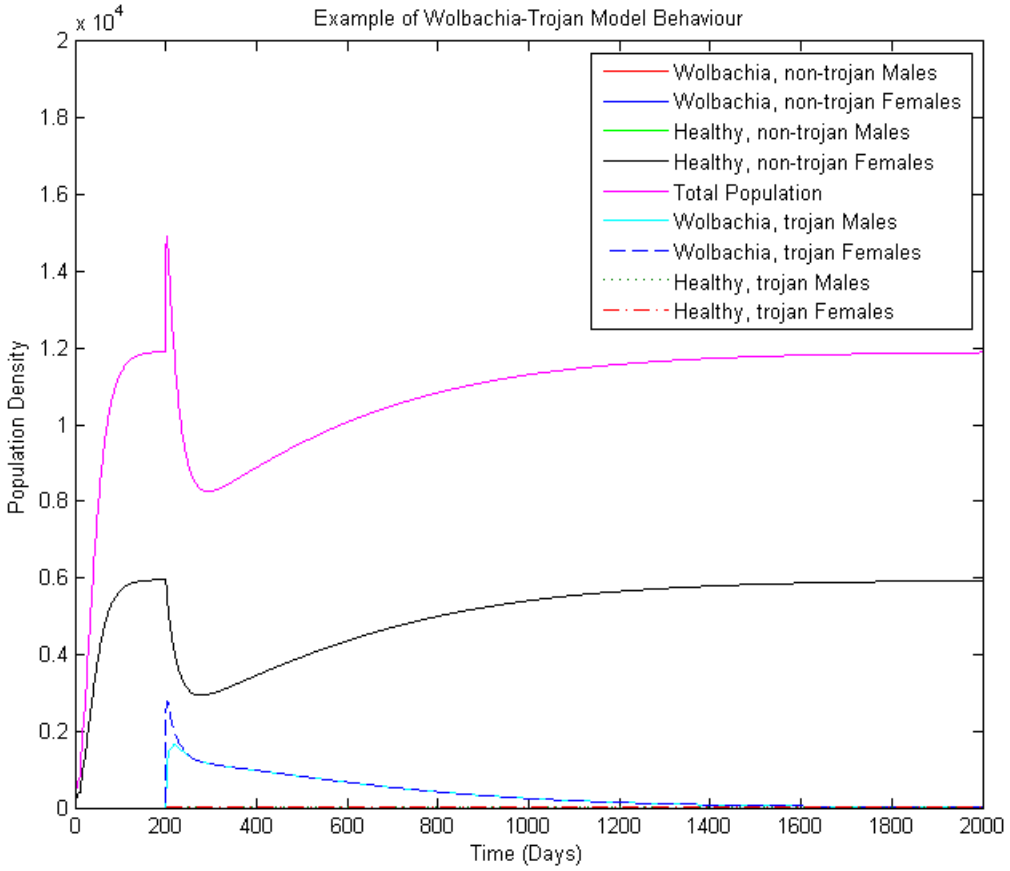

Figure 5.1: Graph showing the behaviour of the different populations under specific conditions.

This initial test does not give a positive outlook for the effect of Wolbachia on our pest control technique. When the Wolbachia Trojan females are first introduced we see an instantaneous rise in the population size due to the 20% introduction, followed by a

short decrease. The number of healthy, non-Trojan males and females also follows this pattern. However, the population of Wolbachia Trojan females consistently decreases after the initial introduction. Since Wolbachia and the Trojan mutation are both inherited maternally, this decline in the number of Wolbachia Trojan females causes the healthy, non-Trojan population to recover after a short amount of time. In the end the population returns to its original equilibrium.

We also wish to investigate how changing the method of release of Trojan females and Wolbachia affects the behaviour of the model. To do this we run the model multiple times, changing the number of Trojan females and Wolbachia that are introduced, whilst using the parameter values from above. In each case the population is allowed to grow freely to its equilibrium before a certain proportion of Trojan females and Wolbachia infected individuals (male or female) are introduced to the population. The total number of individuals introduced is constant at 20% of the total population size. The total population size over 2000 days for each case is shown below.

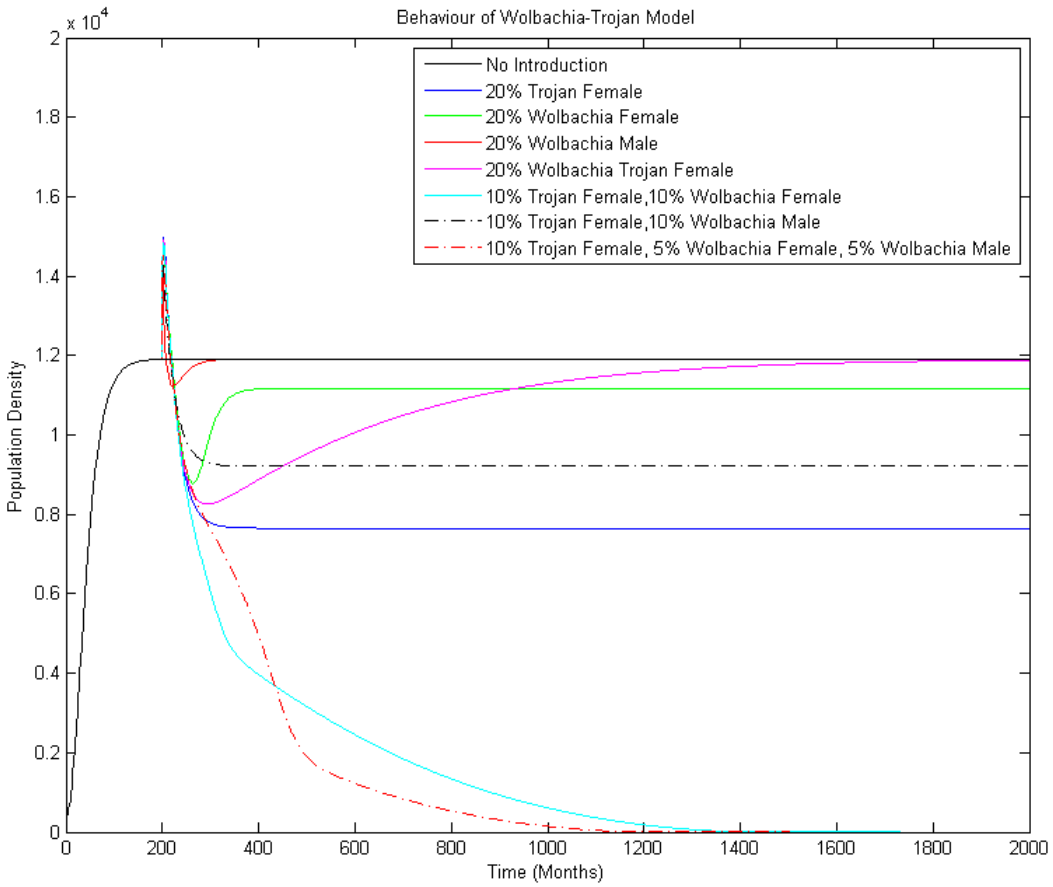

Figure 5.2: Graph showing the behaviour of the joint Trojan, Wolbachia model under different initial introduction proportions

It is clear from this graph that the resulting equilibrium of our system is very sensitive to how we introduce the Wolbachia along with the Trojan females. Firstly, we can see that introducing the Wolbachia through females or a combination of males and females is far more effective than introducing it through males alone. The best results, leading to a rapid drop to extinction, come through introducing a combination of Trojan females without Wolbachia and healthy females with Wolbachia or both healthy males and females with Wolbachia. It is vital, however, that the Trojan mutation and Wolbachia bacteria are not combined within the individuals, as an introduction of only Trojan females with Wolbachia leads to a full recovery of the population.

Chapter 6

Summary

In conclusion, the Trojan Female Technique appears to be an efficient method to reduce the size of a pest population, possibly to extinction, and keep it down. Through the analysis of the continuous time model we have found that we can split the long term solutions into three groups depending on the size of the initial introduction of Trojan females:

- If the initial introduction is above the extinction boundary the population will become extinct in the long run. We have found an approximate representation of this extinction boundary, defined by a straight line parallel to the $T = T^*$ line, shifted to the right by the amount $T_0^* - T_0$. Through simulation we also found that, as the birth rate l increases the size of $T_0^* - T_0$ decreases relative to the population size. This suggests that proportionally fewer Trojan females are needed to bring the population to extinction. The death rate parameter μ has the opposite effect.

- If the initial introduction is below the $T^* = T$ line, the population tends towards an equilibrium that lies on an attracting manifold which we define implicitly by

$$\frac{450lqr(1-r)}{\mu}T = (T + T^* + 500)(r(T + T^*) + 1).$$

The "lower bound" and "upper bound", between which the equilibrium must lie, are defined explicitly in terms of the parameter values used by

$$UB = \frac{-(500r + 1 - \frac{450lqr(1-r)}{\mu}) + \sqrt{\left(500r + 1 - \frac{450lqr(1-r)}{\mu}\right)^2 - 2000r}}{2r},$$

$$LB = \frac{-\left(2 + 1000r - \frac{450lqr(1-r)}{\mu}\right) + \sqrt{\left(2 + 1000r - \frac{450lqr(1-r)}{\mu}\right)^2 - 2000r}}{8r}.$$

The upper bound corresponds to the equilibrium solution of the population before Trojan females are introduced and the lower bound is the point where the $T^* = T$ line crosses the attracting manifold. These equations were derived assuming that the gender proportions in the population were at equilibrium. We found that this has little effect on the long term solutions and any effect it does have will actually act in favour of extinction.

Again through simulation we found that increases in the parameters l and q cause a decrease in the distance between the two bounds relative to the population size, allowing for relatively fewer possible equilibrium points. The parameters r and μ had an opposite effect.

- If the initial introduction is between the $T^* = T$ line and the extinction boundary, we cannot be certain whether the population will go extinct or end up at an equilibrium on the attracting manifold.

We also explored the use of the Wolbachia bacteria in conjunction with the Trojan Female Technique. We found that this can aid our goal of extinction, but only if Trojan females and Wolbachia infected females, or a combination of males and females, are introduced separately. When introduced together (i.e. Trojan-Wolbachia females) the combination actually has a negative effect on the efficacy of the TFT.

In the ongoing research on the Trojan Female Technique we wish to explore further the following areas:

- The effect of including the juvenile stage, introduced in Chapter 3, in our model. This will include looking into a different representation of the population behaviour, using only the density of adults rather than the total density.

- Analysis of the discrete and stochastic models that are attached in Appendix 1. We derived these models from the continuous time model, however have yet to carry out an in depth analysis. The effect of stochasticity on the long term solutions will be of particular interest in future work.

- Investigation into the other effects of Wolbachia and how this could be combined with our current model. So far we have only looked into the effect of cytoplasmic incompatibility (CI), however there are three other ways in which Wolbachia are

known to affect the reproductive fitness of individuals and we wish to explore the application of these to the TFT.

- A spatial extension to our model. Currently the dynamics of the population only depend on time, under the assumption that we have a closed population. We wish to extend this to incorporate a spatial component to study how the migratory behaviour of pests affects the efficacy of the TFT.

Appendices

Appendix 1: Other Models

Before carrying out an extensive analysis of the continuous time model we also spent some time developing a discrete time model and a stochastic model. We consider the stochastic model to be an important area for future investigation, thus we include its derivation and some preliminary results here. Note that the models here include the time lag component from Chapter 3 to better model the juvenile stage.

A1.1: Discrete Time Model

The second model we derived is an adaption of the continuous time model in a discrete time context. Discrete time models are based on the idea that breeding occurs at specific points in time separated by a constant time interval, though they can also be viewed as convenient approximations of continuous time models. Our discrete time model is governed by the system of equations

$$\begin{aligned}
M_{t+1} &= M_t + rB(N_t)(1-\mu)^\tau F_{t-\tau} - \mu M_t; \\
F_{t+1} &= F_t + (1-r)B(N_t)(1-\mu)^\tau F_{t-\tau} - \mu F_t; \\
M^*_{t+1} &= M^*_t + rB(N_t)(1-\mu)^\tau F^*_{t-\tau} - \mu M^*_t; \\
F^*_{t+1} &= F^*_t + (1-r)B(N_t)(1-\mu)^\tau F^*_{t-\tau} - \mu F^*_t,
\end{aligned}$$

with

$$N_t = M_t + F_t + M^*_t + F^*_t.$$

The components of this model are very similar to that of the continuous time model, with the major difference appearing between $(1-\mu)^\tau$ and $e^{-\mu\tau}$. Both these terms represent the probability that an adult individual survives τ months, however in the discrete time context the formulation of this changes slightly to accommodate the discrete time intervals.

Assumptions

In this model we have made the following assumptions:

- Breeding occurs monthly.
- Males born with the mtDNA mutation are fully infertile.
- Female reproductive fitness is unaffected by the mutation.
- All individuals have the same mortality rate, i.e. neither age nor the mutation effect the individual's ability to survive.

Example of Model Behaviour

Figure 6.1 below shows an example of the behaviour of TFT with the Discrete Time Model under the same set of parameters as in Figure 3.1.

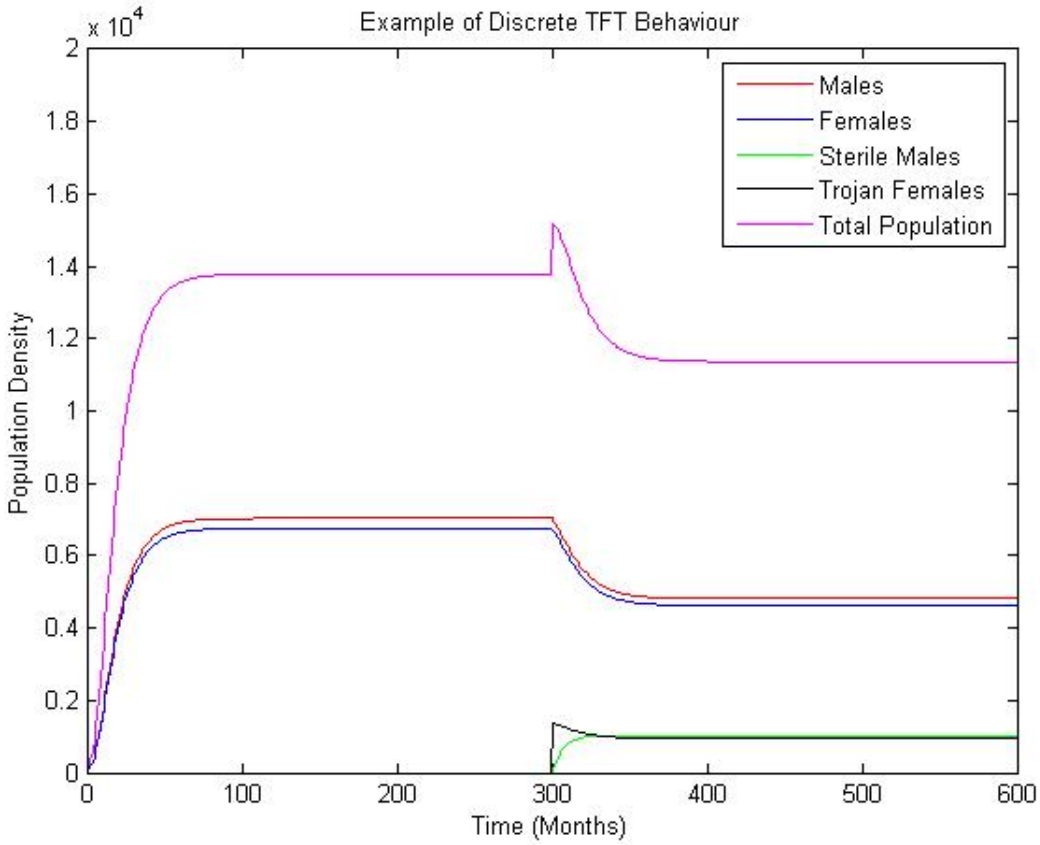

Figure 6.1: Example of TFT behaviour using the Discrete Time Model under specific conditions.

We see that with discrete time intervals of only one month the discrete model is an excellent approximation of the continuous time model. As we shall see, the discrete time model also provides us with a convenient basis for a stochastic model.

A1.2: Stochastic Model

The continuous time and discrete time models are deterministic in nature, that is, given a set of parameters, we can determine the exact density of the population after a certain amount of time. This assumes that there is no inherent stochasticity in the growth of a population, which is often not the case. Our next model, the 'Stochastic Model', addresses this problem through the addition of a probabilistic component.

The Moran Model

The Moran Model is a stochastic, finite population model first proposed by Patrick Moran in 1958 [11]. It describes the probabilistic process of competition between two alleles A and B in a finite population of size N and can be used to model the effects of genetic drift, natural selection and mutation within populations.
A process is considered to follow the Moran Model if the following conditions are met:

- The population has constant size N.
- Generations are allowed to overlap.
- At discrete time intervals, two individuals are chosen at random; one reproduces and the other dies (they can be the same individual).

Extension and Application of the Moran Model

We wish to use the Moran Model to describe the behaviour of this mtDNA mutation in a finite population, hence we can think of the mutation as the allele A and the absence of the mutation as the allele B. Clearly the Moran Model as described above does not fit our problem; for one, we are mainly interested in the change in population density which is assumed fixed under the Moran Model. Thus, in order to apply it to our situation, we extend it to fit certain conditions.

The first adjustment we make is to allow the population size N to change. To do this we set up the following recursion [6]:

1. At discrete time intervals, Δt, two individuals a and b are chosen at random from the population (again they can be the same individual).

2. Individual a dies.

3. Individual b gives birth to U offspring of the same type, where $U \sim Pois(\lambda)$ with expected value λ.

Thus, at each interval, we have $N_{t+\Delta t} = N_t + U - 1$. To further relate this to our problem we wish to group the recursion into monthly time intervals, as with the previous discrete time model. We define $\alpha = \frac{1}{\Delta t}$. Then, using the properties of Poisson random variables, we have that

$$\begin{aligned} N_{t+1} &= N_t + \sum_{i=1}^{\alpha}(U_i - 1), \quad \text{where } U_i \sim Pois(\lambda) \text{ for each } i = 1, ..., \alpha, \\ &= N_t + \sum_{i=1}^{\alpha} U_i - \alpha, \\ &= N_t + U - \alpha, \quad \text{where } U \sim Pois(\alpha\lambda). \end{aligned}$$

The growth of the population can therefore be controlled by α and λ. We can estimate the values of these parameters by comparing the equation above to the discrete time model from before:

$$N_{t+1} = N_t + U - \alpha, \quad \text{and} \quad M_{t+1} = M_t + B(N_t)(1-d)^{\tau}F_{t-\tau} - dM_t, \tag{6.1}$$

giving the approximations

$$\begin{aligned} \alpha &= dM_t, \\ \lambda &= \frac{B(N_t)(1-d)^{\tau}F_{t-\tau}}{dM_t}. \end{aligned}$$

We get similar approximations for the expectation of F, F^* and M^*.

The resulting model is outlined in the section below.

Proposed Model

Using the extensions of the Moran Model explained above we obtain the following system of equations that guide the behaviour of this model:

$$\begin{aligned} M_{t+1} &= M_t + U_1 - dM_t, \\ F_{t+1} &= F_t + U_2 - dF_t, \\ M^*_{t+1} &= M^*_t + U_3 - dM^*_t, \\ F^*_{t+1} &= F^*_t + U_4 - dF^*_t, \end{aligned}$$

where

$$\begin{aligned} U_1 &\sim Pois(rB(N_t)(1-d)^\tau F_{t-\tau}), \\ U_2 &\sim Pois((1-r)B(N_t)(1-d)^\tau F_{t-\tau}), \\ U_3 &\sim Pois(rB(N_t)(1-d)^\tau F^*_{t-\tau}) \; and \\ U_4 &\sim Pois((1-r)B(N_t)(1-d)^\tau F^*_{t-\tau}). \end{aligned}$$

This clearly resembles the discrete time model, except the monthly growth of the population now has a stochastic component and is not solely determined by the density of the population.

Example of Model Behaviour

Figure 6.2 below shows an example of the behaviour of TFT with the Stochastic Model under the same set of parameters as in the discrete and continuous model examples.

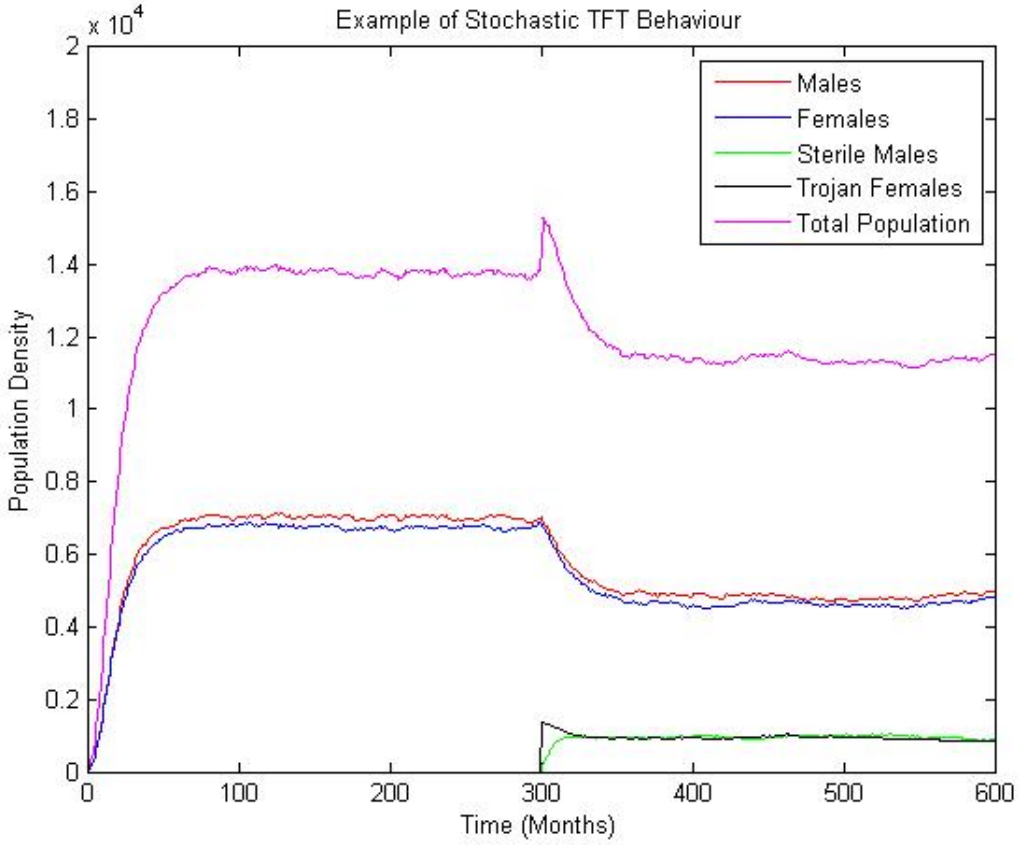

Figure 6.2: Example of TFT behaviour using the Stochastic Model under specific conditions.

As expected, the Stochastic Model displays far more variation than the two deterministic models. The level of this variation and how it effects the model (e.g. probability of extinction) will be of particular interest in future analysis of this model.

A1.3: Preliminary Results

Finally, we provide a few preliminary results for the stochastic model.

Variability

We can gauge a visual representation of the variation within the stochastic model by simulating the model a number of times under the same conditions. The graph below shows the paths of ten identical simulations of the model (with the same paramters as above) over 600 months, where Trojan female introduction occurs in the 300th month.

There is some variation in the size of the population after 600 months, however all trials show an overall decrease in the population size after Trojan female introduction.

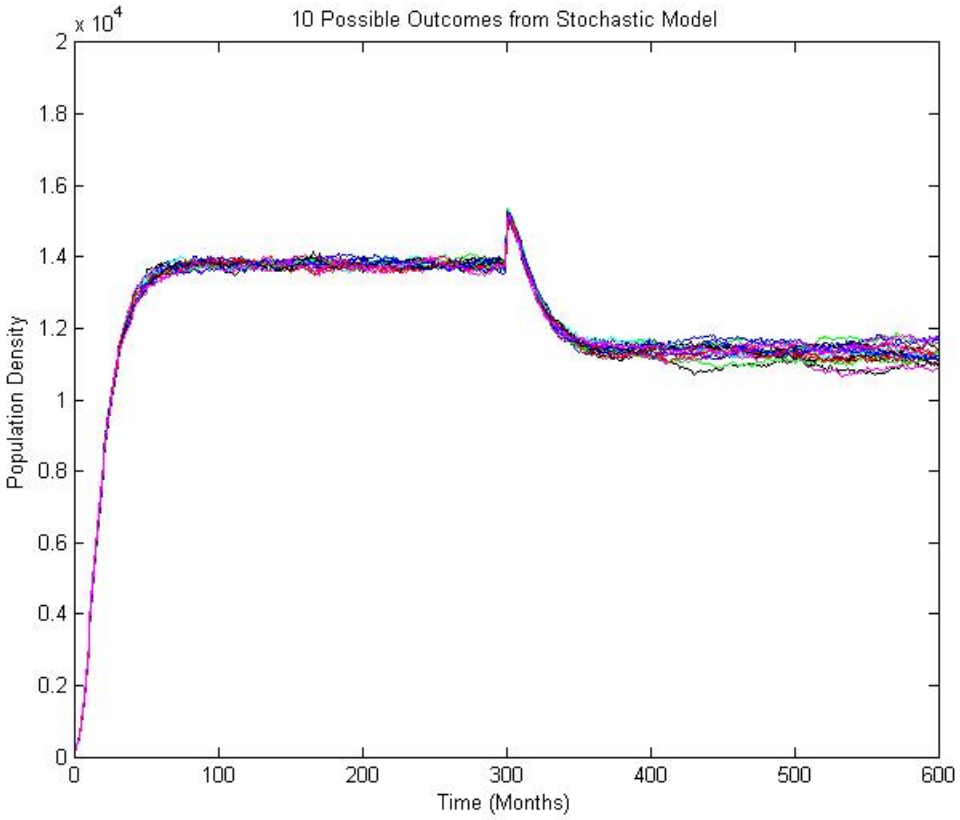

Figure 6.3: An example of the variation found within the Stochastic Model when using a single 10% release. The model is run 10 times with the same parameters and each outcome plotted.

Average Behaviour

As expected, the stochastic model behaves differently to the discrete time model due to the added stochastic component. However we wish to see whether the average of many stochastic trials produces similar behaviour to the discrete model. We do this by running the model 1000 times and plotting the average of the trials. The graph below displays the results.

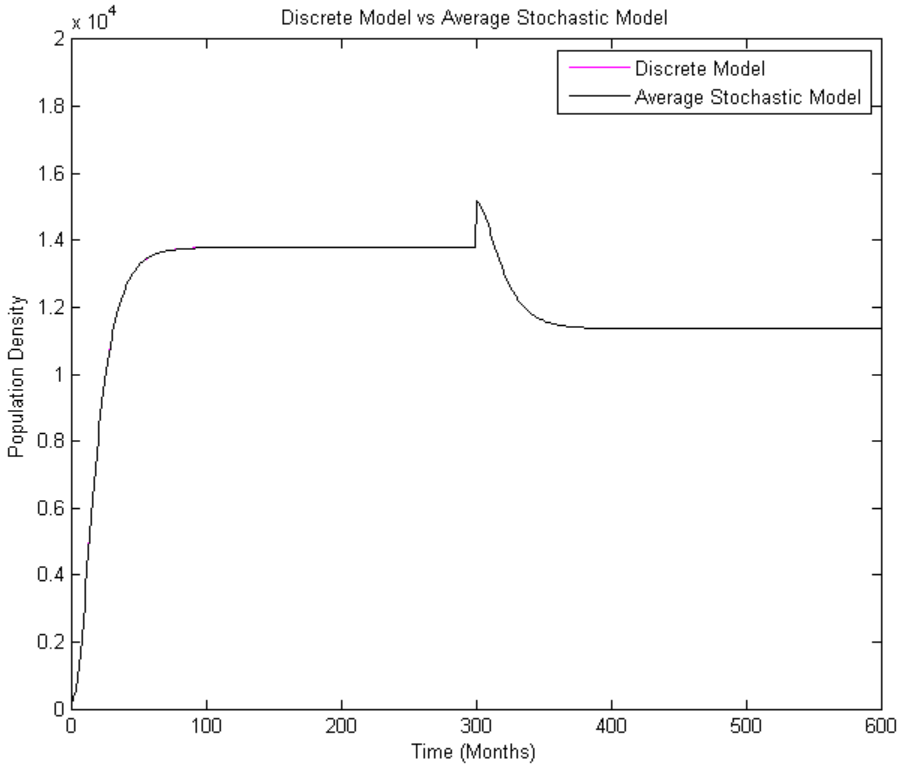

Figure 6.4: Average of 1000 stochastic trials vs discrete model.

We can see that the average of 1000 runs of the stochastic model is almost indistinguishable from the discrete time model. This is to be expected as the discrete time model was used as the basis for the stochastic model.

Appendix 2: MATLAB Code

Continuous Time Model

Model Function

```
function [dy] = cModel (t, y)
dy = zeros(4,1);

N=sum(y);  %total population size
P=y(1)/(y(1)+y(3)+1);  %probability of female fertilization
r=0.51;  %gender ratio
l=8;  %monthly litter size
q=0.5;  %maturation rate
k=1;  %number of male partners
b=0.9/((N/500)+1);  %proportion of females breeding
```

```
B=b*(1-(1-P)^k);  %probability of successful conception
D=0.1;  %monthly death rate
l*B*q;


dy(1) = r*l*q*B*y(2)-D*y(1);  %males
dy(2) = (1-r)*l*q*B*y(2)-D*y(2);  %females
dy(3) = r*l*q*B*y(4)-D*y(3);  %trojan males
dy(4) = (1-r)*l*q*B*y(4)-D*y(4);  %trojan females

end
```

Run Model Script

```
introMonth = 300;  %month that trojan females are introduced
runtime = 300;  %number of months the model runs after introduction
initF = 50;  %initial number of females
initM = 50;  %initial number of males
introProp = 0.1;  %number of trojan females introduced as a proportion of the total population

options=odeset('RelTol',1e-4,'AbsTol',[1 1 1 1],'InitialStep',1,'MaxStep',1);
[T,Y]=ode45(@cModel,[0,(introMonth-1)],[initM,initF,0,0],options);  %run until TF introduction
[S,Z]=ode45(@cModel,[introMonth,(introMonth + runtime)],[Y(introMonth,1),Y(introMonth,2),0,
(introProp*(Y(introMonth,1)+Y(introMonth,2)))],options);
%run after TF introduction

Y=[Y' Z']';
T=[T' S']';
popTotal = sum(Y,2);

plot(T,Y(:,1),'r',T,Y(:,2),'b',T,Y(:,3),'g',T,Y(:,4),'k',T,popTotal,'m')
title('Example of TFT Behaviour');
legend({'Males','Females','Infected Males','Infected Females','Total Population'},'Location','NorthEast');
```

Extended Continuous Time Model (Lag)

Model Function

```
function dy = cTimeDelayModel(t,y,yd)

dy = zeros(4,1);

N=sum(y);  %total population size
P=y(1)/(y(1)+y(3)+1);  %probability of female fertilization
r=0.51;  %gender ratio
l=8;  %monthly litter size
k=1;  %number of male partners
b=0.9/((N/500)+1);  %proportion of females breeding
B=b*(1-(1-P)^k);  %probability of successful conception
D=0.1;  %monthly death rate

lag = 2;  %time lag (months)
```

```
R = l*B*exp(-D*lag);

dy(1) = r*R*yd(2,1)-D*y(1);  %males
dy(2) = (1-r)*R*yd(2,1)-D*y(2);  %females
dy(3) = r*R*yd(4,1)-D*y(3);  %infected males
dy(4) = (1-r)*R*yd(4,1)-D*y(4);  %infected females

end
```

Run Model Script

```
lag = [2];

introMonth = 300;  %month that trojan females are introduced
runtime = 300;  %number of months the model runs after introduction
initM = 50;  %initial number of males
initF = 50;  %initial number of females
introProp = 0.1;  %number of trojan females introduced as a proportion of the total population
D = 0.1;  %death rate

options=ddeset('RelTol',1e-4,'AbsTol',[1 1 1 1],'InitialStep',1,'MaxStep',1);

Y = dde23(@cTimeDelayModel, lag,[initM;initF;0;0],[0,introMonth],options);
%history for t<0 does not effect long term dynamics

Z = dde23(@cTimeDelayModel,lag,@cLagHist,[introMonth,(introMonth + runtime)],options);
% assumes we are at a stable level when introduction occurs

T=[Y.x Z.x]';
Y=[Y.y Z.y]';
popTotal = sum(Y,2);

plot(T,Y(:,1),'r',T,Y(:,2),'b',T,Y(:,3),'g',T,Y(:,4),'k',T,popTotal,'m')
xlabel('Time (Months)');
ylabel('Population Density');
title('Example of Extended Model Behaviour');
legend({'Males','Females','Infected Males','Infected Females','Total Population'},'Location','NorthEast');

function s = cLagHist(t)
D = 0.1;
introMonth=300;
introProp=0.1;
%equilibrium prior to TF introduction with lag = 2
M =  7.1096e+03;
F =  6.8308e+03;
%equilibrium prior to TF introduction with lag = 10
%M = 5.9528e+03;
%F = 5.9528e+03;

s = [M;F;0;introProp*(M+F)*exp(-D*(t-introMonth))];
end
```

Trojan-Wolbachia Model

Model Function

```
function dy = cWolbachiaModel(t,y,yd)

dy = zeros(8,1);

N=sum(y);  %total population size
P=(y(1)+y(3))/(y(1)+y(3)+y(5)+y(7)+1);  %probability of female fertilization
r=0.5;  %gender ratio
l=15;  %daily litter size
k=1;  %number of male partners
b=0.9/((N/500)+1);  %proportion of females breeding
B=b*(1-(1-P)^k);  %probability of successful conception
D=0.1;  %daily death rate

ph=(y(1)+y(2))/(y(3)+y(4)+y(1)+y(2));  %proportion of non-trojans with Wolbachia
pt=(y(5)+y(6))/(y(5)+y(6)+y(7)+y(8)+0.0001);  %proportion of trojans with Wolbachia


Sf=0.05;  %proportional reduction in female reproductivity due to wolbachia
Sh=0.99;  %proportion of offspring that fail to develop through incompatible mating
w=0.01;  %proportion of offspring from infected female that are not infected

lag = 10;  %time lag (days)
R = l*B*exp(-D*lag);

dy(1) = r*(1-Sf)*R*(1-w)*yd(2,1)-D*y(1);  %Wolbachia, non-trojan males
dy(2) = (1-r)*(1-Sf)*R*(1-w)*yd(2,1)-D*y(2);  %Wolbachia, non-trojan females
dy(3) = r*((1-Sh*ph)*R*yd(4,1)+(1-Sh*(1-ph))*w*(1-Sf)*R*yd(2,1)) - D*y(3); %healthy, non-trojan males
dy(4) = (1-r)*((1-Sh*ph)*R*yd(4,1)+(1-Sh*(1-ph))*w*(1-Sf)*R*yd(2,1)) - D*y(4); %healthy, non-trojan females
dy(5) = r*(1-Sf)*R*(1-w)*yd(6,1)-D*y(5);  %Wolbachia, trojan males
dy(6) = (1-r)*(1-Sf)*R*(1-w)*yd(6,1)-D*y(6);  %Wolbachia, trojan females
dy(7) = r*((1-Sh*pt)*R*yd(8,1)+(1-Sh*(1-pt))*w*(1-Sf)*R*yd(6,1)) - D*y(7); %healthy, trojan males
dy(8) = (1-r)*((1-Sh*pt)*R*yd(8,1)+(1-Sh*(1-pt))*w*(1-Sf)*R*yd(6,1)) - D*y(8); %healthy, trojan females

end
```

Run Model Script

```
lag = [10];

introMonth = 200;  %month that trojan females/Wolbachia are introduced
runtime = 1800;  %number of days the model runs after introduction
initM = 50;   %initial number of males
initF = 50;   %initial number of females
introProp = 0.2;  %number of trojan females introduced as a proportion of the total population
D = 0.1;  %death rate

options=ddeset('RelTol',1e-4,'AbsTol',[1 1 1 1 1 1 1 1],'InitialStep',1,'MaxStep',1);

Y = dde23(@cWolbachiaModel, lag,[0;0;initM;initF;0;0;0;0],[0,introMonth],options);
% history for t<0 does not effect long term dynamics
```

```
Z = dde23(@cWolbachiaModel,lag,@cWolHist,[introMonth,(introMonth + runtime)],options);
% assumes we are at a stable level when introduction occurs

T=[Y.x Z.x]';
Y=[Y.y Z.y]';
popTotal = sum(Y,2);

plot(T,Y(:,1),'r',T,Y(:,2),'b',T,Y(:,3),'g',T,Y(:,4),'k',T,popTotal,'m',T,Y(:,5),'c',T,Y(:,6),'--',
T,Y(:,7),':',T,Y(:,8),'-.')
title('Example of Wolbachia-Trojan Model Behaviour')
xlabel('Time (Days)');
ylabel('Population Density');
ylim([0,20000]);
legend({'Wolbachia, non-trojan Males','Wolbachia, non-trojan Females','Healthy, non-trojan Males',
'Healthy, non-trojan Females','Total Population','Wolbachia, trojan Males','Wolbachia, trojan Females',
'Healthy, trojan Males','Healthy, trojan Females'},'Location','NorthEast');

function s = cWolHist(t)
D = 0.1;
introMonth=200;
introProp=0.2;
%equilibrium prior to TF introduction with lag = 10
M = 5.9528e+03;
F = 5.9528e+03;

s = [(introProp*(M+F)*exp(-D*(t-introMonth)))/4;(introProp*(M+F)*exp(-D*(t-introMonth)))/4;M;F;0;0;0;
(introProp*(M+F)*exp(-D*(t-introMonth)))/2];
end
```

Discrete Time Model

```
lag = 2; %time to maturation (months)

r = 0.51; %gender ratio
b = 8;  %litter size per month
d = 0.1; %death rate per month
L = 500;  %BH parameter

runtime = 602;  %number of months to run simulation for
introMonth = 300;  %month in which trojan females are introduced
introProp = 0.1;  %number of trojan females introduced as a proportion of the total population

M=zeros(runtime,1);
F=zeros(runtime,1);
Mstar=zeros(runtime,1);
Fstar=zeros(runtime,1);
N=zeros(runtime,1);
P=zeros(runtime,1);
B=zeros(runtime,1);
T=1:runtime;

M(1)=50;
```

```
F(1)=50;
Mstar(1)=0;
Fstar(1)=0;

for n = 1:(runtime-1)
    N(n) = M(n)+F(n)+Mstar(n)+Fstar(n);
    P(n) = M(n)/(M(n)+Mstar(n)+1);
    B(n) = b*P(n)*(0.9/(N(n)/L+1));
    if (n==(introMonth-1)) %introduce trojan females
        M(n+1) = M(n) + r*B(n)*F(n-lag)*(1-d)^lag - d*M(n);
        F(n+1) = F(n) + (1-r)*B(n)*F(n-lag)*(1-d)^lag - d*F(n);
        Mstar(n+1) = 0;
        Fstar(n+1) = introProp*N(n);
    else if (n<=lag)  %special case for 1st generation
            M(n+1) = M(n) + r*B(n)*F(1)*(1-d)^lag - d*M(n);
            F(n+1) = F(n) + (1-r)*B(n)*F(1)*(1-d)^lag - d*F(n);
            Mstar(n+1) = Mstar(n) + r*B(n)*Fstar(1)*(1-d)^lag - d*Mstar(n);
            Fstar(n+1) = Fstar(n) + (1-r)*B(n)*Fstar(1)*(1-d)^lag - d*Fstar(n);
        else if (n<=introMonth+lag && n>=introMonth)  %special case for first generation of trojan females
                M(n+1) = M(n) + r*B(n)*F(n-lag)*(1-d)^lag - d*M(n);
                F(n+1) = F(n) + (1-r)*B(n)*F(n-lag)*(1-d)^lag - d*F(n);
                Mstar(n+1) = Mstar(n) + r*B(n)*Fstar(introMonth)*(1-d)^lag - d*Mstar(n);
                Fstar(n+1) = Fstar(n) + (1-r)*B(n)*Fstar(introMonth)*(1-d)^lag- d*Fstar(n);
            else  %normal behaviour everywhere else
                M(n+1) = M(n) + r*B(n)*F(n-lag)*(1-d)^lag - d*M(n);
                F(n+1) = F(n) + (1-r)*B(n)*F(n-lag)*(1-d)^lag - d*F(n);
                Mstar(n+1) = Mstar(n) + r*B(n)*Fstar(n-lag)*(1-d)^lag - d*Mstar(n);
                Fstar(n+1) = Fstar(n) + (1-r)*B(n)*Fstar(n-lag)*(1-d)^lag - d*Fstar(n);
            end
        end
    end
end

popTotal = M+F+Mstar+Fstar;

plot(T,M,'r',T,F,'b',T,Mstar,'g',T,Fstar,'k',T,popTotal,'m')
xlabel('Time (Months)');
ylabel('Population Density');
title('Example of Discrete TFT Behaviour');
legend({'Males','Females','Sterile Males','Trojan Females','Total Population'},'Location','NorthEast');
```

Stochastic Model

```
lag = 2; %time to maturation (months)

r = 0.51; %gender ratio
b = 8;  %births per litter per female
d = 0.1; %death rate per time step
L = 500;  %BH parameter

runtime = 602;  %number of months to run simulation for
introMonth = 300;  %month in which trojan females are introduced
introProp = 0.1;  %number of trojan females introduced as a proportion of the total population
```

```
M=zeros(runtime,1);
F=zeros(runtime,1);
Mstar=zeros(runtime,1);
Fstar=zeros(runtime,1);
N=zeros(runtime,1);
P=zeros(runtime,1);
B=zeros(runtime,1);
T=1:runtime;

M(1)=50;
F(1)=50;
Mstar(1)=0;
Fstar(1)=0;

for n = 1:(runtime-1)
    N(n) = M(n)+F(n)+Mstar(n)+Fstar(n);
    P(n) = M(n)/(M(n)+Mstar(n)+1);
    B(n) = b*P(n)*(0.9/(N(n)/L+1));
    if (n==(introMonth-1)) %introduce trojan females
        M(n+1) = (1-d)*M(n) + poissrnd((r*B(n)*F(n-lag)*(1-d)^lag));
        F(n+1) = (1-d)*F(n) + poissrnd(((1-r)*B(n)*F(n-lag)*(1-d)^lag));
        Mstar(n+1) = 0;
        Fstar(n+1) = introProp*N(n);
    else if (n<=lag)  %special case for 1st generation
            M(n+1) = (1-d)*M(n) + poissrnd((r*B(n)*F(1)*(1-d)^lag));
            F(n+1) = (1-d)*F(n) + poissrnd(((1-r)*B(n)*F(1)*(1-d)^lag));
            Mstar(n+1) = (1-d)*Mstar(n) + poissrnd((r*B(n)*Fstar(1)*(1-d)^lag));
            Fstar(n+1) = (1-d)*Fstar(n) + poissrnd(((1-r)*B(n)*Fstar(1)*(1-d)^lag));
        else if (n<=introMonth+lag && n>=introMonth)  %special case for first generation of trojan females
                M(n+1) = (1-d)*M(n) + poissrnd((r*B(n)*F(n-lag)*(1-d)^lag));
                F(n+1) = (1-d)*F(n) + poissrnd(((1-r)*B(n)*F(n-lag)*(1-d)^lag));
                Mstar(n+1) = (1-d)*Mstar(n) + poissrnd(r*B(n)*Fstar(introMonth)*(1-d)^lag);
                Fstar(n+1) = (1-d)*Fstar(n) + poissrnd((1-r)*B(n)*Fstar(introMonth)*(1-d)^lag);
            else  %normal behaviour everywhere else
                M(n+1) = (1-d)*M(n) + poissrnd((r*B(n)*F(n-lag)*(1-d)^lag));
                F(n+1) = (1-d)*F(n) + poissrnd(((1-r)*B(n)*F(n-lag)*(1-d)^lag));
                Mstar(n+1) = (1-d)*Mstar(n) + poissrnd((r*B(n)*Fstar(n-lag)*(1-d)^lag));
                Fstar(n+1) = (1-d)*Fstar(n) + poissrnd(((1-r)*B(n)*Fstar(n-lag)*(1-d)^lag));
            end
        end
    end
end
plot(T,M,'r',T,F,'b',T,Mstar,'g',T,Fstar,'k',T,N,'m')
title('Example of Stochastic TFT Behaviour')
xlabel('Time (Months)');
ylabel('Population Density');
legend({'Males','Females','Sterile Males','Trojan Females','Total Population'},'Location','NorthEast');
```

Bibliography

[1] Julien Arino, Lin Wang, and Gail SK Wolkowicz. An alternative formulation for a delayed logistic equation. *Journal of theoretical biology*, 241(1):109–119, 2006.

[2] Åke Brännström and David JT Sumpter. The role of competition and clustering in population dynamics. *Proceedings of the Royal Society B: Biological Sciences*, 272(1576):2065–2072, 2005.

[3] Franck Courchamp, Ludek Berec, and Joanna Gascoigne. Allee effects in ecology and conservation. *Environ. Conserv*, 36:80–85, 2008.

[4] PHIL Cowan, ROGER Pech, and PAUL Curtis. Field applications of fertility control for wildlife management. *CONSERVATION BIOLOGY SERIES-CAMBRIDGE-*, pages 305–318, 2003.

[5] W Jack Cunningham. A nonlinear differential-difference equation of growth. *Proceedings of the National Academy of Sciences of the United States of America*, 40(8):708, 1954.

[6] Peter Donnelly. A genealogical approach to variable-population-size models in population genetics. *Journal of applied probability*, pages 283–296, 1986.

[7] V Arnold Dyck, Jorge Hendrichs, and Alan S Robinson. *Sterile insect technique*. Springer, 2005.

[8] Neil J Gemmell, Aidin Jalilzadeh, Raphael K Didham, Tanya Soboleva, and Daniel M Tompkins. The trojan female technique: a novel, effective and humane approach for pest population control. 2013.

[9] Penelope A Hancock, Steven P Sinkins, and H Charles J Godfray. Population dynamic models of the spread of wolbachia. *The American Naturalist*, 177(3):323–333, 2011.

[10] SR McLeod, G Saunders, LE Twigg, Anthony D Arthur, D Ramsey, and LA Hinds. Prospects for the future: is there a role for virally vectored immunocontraception in vertebrate pest management? *Wildlife Research*, 34(7):555–566, 2008.

[11] Patrick Alfred Pierce Moran. Random processes in genetics. In *Mathematical Proceedings of the Cambridge Philosophical Society*, volume 54, pages 60–71. Cambridge Univ Press, 1958.

[12] John H Werren. Biology of wolbachia. *Annual review of entomology*, 42(1):587–609, 1997.