

# Branching processes, extinction probabilities with application to pest eradication

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# Abstract

This project introduces branching processes as a stochastic tool for estimating the number of the population of individuals at any generation  $n$ . This estimation was done by finding the mean, variance, probability, and the time to extinction of the individual's population. An application is presented, modelling the life history of tsetse flies. Some of the known control measures of tsetse flies such as sterile insemination technique (SIT) and mortality reduction (bait technology) are also included in the model and subsequently analysed.

# Contents

<b>Abstract</b>	<b>i</b>
<b>1 Introduction</b>	<b>1</b>
1.1 The life cycle of a tsetse fly . . . . .	1
<b>2 Theoretical review of branching processes</b>	<b>2</b>
2.1 Fundamental branching process equation . . . . .	2
2.2 Examples of branching processes . . . . .	2
2.3 The mean and variance of a branching process . . . . .	3
2.4 Generating functions of a branching process . . . . .	6
2.5 Extinction probabilities . . . . .	7
2.6 Time to extinction . . . . .	9
2.6.1 Extinction by time $n$ . . . . .	9
<b>3 Application of branching processes, extinction probabilities to tsetse flies</b>	<b>11</b>
3.1 Theoretical development . . . . .	11
3.2 Mean and variance of the female tsetse population at generation $n$ . . . . .	17
3.3 Time for the population of the female tsetse flies to become extinct . . . . .	19
3.4 Results and analysis . . . . .	20
3.4.1 The relationship between extinction probabilities and adult female daily mortality . . . . .	20
3.4.2 The relationship between extinction probabilities and the probability of insemination . . . . .	20
3.4.3 The mean and variance of the population growth . . . . .	22
3.4.4 Expected number of generations to extinction . . . . .	24
<b>4 Conclusion and future work</b>	<b>27</b>
<b>Bibliography</b>	<b>29</b>

# List of Figures

2.1	A graphical representation of a branching process. A dot indicates the birth of an individual. $X_0 = 1$ implies that there is one individual in the initial generation which produces 3 individuals in the next generation. This continues either indefinitely or until extinction. . . . .	2
2.2	Graphs showing extinction probabilities for the three possible cases; supercritical, subcritical and critical. . . . .	9
3.1	Upper graph: A graph of extinction probability against adult mortality for different values of pupal mortality. Lower graph: A graph of extinction probability against adult mortality for different values of initial population at constant pupal mortality ( $\chi = 0.5\%$ ). . . . .	21
3.2	Upper graph: A graph of extinction probability against the probability of insemination for different values of adult mortality at constant pupal mortality ( $\chi = 0.5\%$ ). Lower graph: A graph of extinction probability against the probability of insemination for different values of initial female population; $\psi = \chi = 0.5\%$ . . . . .	22
3.3	Upper graph: A graph of mean (standard deviation) against the number of generations; $\psi = 3\%$ , $\chi = 0.5\%$ . Lower graph: A graph of mean (standard deviation) against the number of generations; $\psi = 4\%$ , $\chi = 0.5\%$ . . . . .	23
3.4	Upper graph: A graph of expected number of generations to extinction against pupal mortality in percentage; $\psi = 7\%$ , $\epsilon = 1$ . Lower graph: A graph of expected number of generations to extinction against the probability of insemination; $\chi = 0.5\%$ , $\psi = 8\%$ . . . . .	25
3.5	Upper graph: A graph of expected number of generations to extinction against adult female daily mortality; $\epsilon = 0.1$ , $\chi = 0.5\%$ . Lower graph: Same graph as the upper graph but this case $\epsilon = 0.5$ . . . . .	26

# 1. Introduction

In modelling animal populations or diseases we most often consider situations where the population size is large enough to be treated as a continuous variable. When the population size is small, however, this may not be appropriate since we cannot then talk about having half a tsetse fly or quarter an HIV virus, and we need different mathematical techniques. The present project will involve understanding the mathematical basis of branching processes and their application in particular areas of biology and medicine.

A branching process is one where an initial random number of particles create more particles of the same or of a different type, and these particles then create other particles, with the system developing in accordance with some probability law [Lan03]. In a branching process, time is measured discretely, particles are considered to behave independently and there exists a certain probability of producing new particles [Lan03, TK84].

The theory of branching processes is of much importance to mathematicians, biologists and statisticians because it enables the estimation of the number of particles at each generation. It also allows us to find the probability of ultimate extinction, and the time to extinction with error bands of these quantities. This theory has so far been applied to diverse areas of biology such as molecular biology, cell biology, evolution and medicine [Lan03, KA02].

In this essay we are looking at the application of branching processes in the particular case of the population dynamics of tsetse flies [*Glossina spp*]. First we give an overview of the life cycle of a tsetse fly, and show how it can be viewed as a branching process. We present a theoretical review of branching processes. We finally use the theory of branching processes to describe the generations of tsetse flies, and find the probability of extinction and the time to extinction.

## 1.1 The life cycle of a tsetse fly

A tsetse fly has a mean life-span of perhaps 30-40 days, but can live in the wild for up to 100 days and gives birth after an interval of 9-10 days to a full-grown larva. This means that a tsetse fly could give birth to about 9-10 offspring in her life. Female tsetse flies mate once and keep the sperm which fertilises the rest of the eggs. This means that if they are mated by sterile males, then they can not produce any offspring [Har05, mus].

The tsetse life cycle is composed of four stages: egg, larva, pupa and adult. The egg and larva stages take place within the female. The female then lays the larva on the ground in a region such as a rain forest. The larva burrows into the soil after being laid and its skin immediately hardens, turning it into a puparium. The pupa develops into an adult after 20 days (at 30°C) - 47 days (at 20°C). The entire life cycle from egg to adult takes about 30 days.

We shall assume that there is one female tsetse fly in the initial generation. This tsetse fly can produce a random number of female tsetse flies in the next generation, which in their turn produce random numbers of females in subsequent generations. The offspring resulting from the first tsetse fly can be regarded as a branching process.

# 2. Theoretical review of branching processes

## 2.1 Fundamental branching process equation

Let us assume that an individual (which can be an atomic particle, or a tsetse fly or a mosquito) produces a random number  $\xi$  of offspring, and let

$$P(\xi = k) = p_k, k = 0, 1, 2, 3, \dots \tag{2.1}$$

be the probability mass function for the number of offspring generated by each individual. Individuals give rise to offspring independently so  $\xi$  is identically, independently distributed for each individual within a generation time  $n$ . Since the individuals behave independently, then the size of each generation  $\{X_n, n \geq 0\}$  follows a discrete-time branching process.

In the  $n$ th generation, the  $X_n$  individuals independently produce other individuals  $\xi_1^{(n)}, \xi_2^{(n)}, \dots, \xi_{X_n}^{(n)}$  and thus the total number of individuals produced in the  $(n + 1)$ th generation is

$$X_{n+1} = \xi_1^{(n)} + \xi_2^{(n)} + \dots + \xi_{X_n}^{(n)}. \tag{2.2}$$

This is the fundamental branching processes equation. Figure (2.1) gives a picture of a branching process.

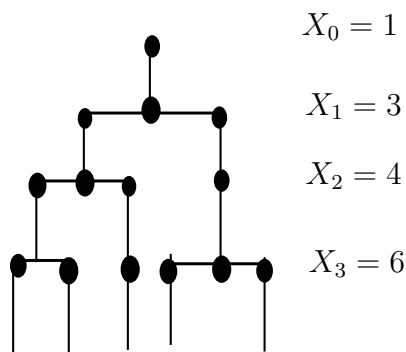


Figure 2.1: A graphical representation of a branching process. A dot indicates the birth of an individual.  $X_0 = 1$  implies that there is one individual in the initial generation which produces 3 individuals in the next generation. This continues either indefinitely or until extinction.

## 2.2 Examples of branching processes

- **Survival of family names.**

The family name is inherited by sons only. A man produces a random number of male offspring during his life time. These male offspring also produce another random number

of male offspring in the subsequent generations. These descendants make up what is called a branching process.

- **Neutron chain reaction.**

An initial number of neutrons hit a nuclei, which then splits and emits a random number of neutrons. These emitted neutrons may hit some other nuclei, producing more neutrons in turn. The process continues and thus constitutes a branching process.

- **Growth of tsetse fly population.**

Suppose there is one female tsetse fly in the initial generation. This female tsetse fly can give birth to a random number of tsetse flies, which can in turn produce other random numbers of tsetse flies in the subsequent generations. The offspring resulting from the first female tsetse fly constitutes a branching process.

- **Cell division**

Biologically, it is believed that a cell either dies or divides. Thus, if cells are assumed to reproduce synchronically at discrete time in generations, starting from a certain number of original cells, then the number of cells in the subsequent generations constitute a branching process.

## 2.3 The mean and variance of a branching process

Let  $\mu = E(\xi)$  and  $\sigma^2 = \text{var}(\xi)$  respectively be the mean and variance of the offspring distribution in (2.1). Let  $M(n) = E(X_n)$  and  $V(n) = \text{Var}(X_n)$  be the respective mean and variance of  $X_n$  under the initial condition  $X_0 = 1$ . Then

$$M(n+1) = \mu M(n) \quad \text{and} \quad (2.3)$$

$$V(n+1) = \sigma^2 M(n) + \mu^2 V(n). \quad (2.4)$$

### Proof

$$\begin{aligned} M(n+1) &= E(X_{n+1}) = E[E(X_{n+1}/X_n = n)] \\ &= E[E(\xi_1^{(n)} + \xi_2^{(n)} + \cdots + \xi_{X_n}^{(n)}/X_n = n)] \\ &= E[E(\xi_1^{(n)} + \xi_2^{(n)} + \cdots + \xi_n^{(n)}/X_n = n)] \\ &= \sum_{n=1}^{\infty} E(\xi_1^{(n)} + \xi_2^{(n)} + \cdots + \xi_n^{(n)}/X_n = n)P(X_n = n) \\ &= \sum_{n=1}^{\infty} nE(\xi)P(X_n = n) \\ &= E(\xi) \sum_{n=1}^{\infty} nP(X_n = n) \\ &= E(\xi)E(X_n), \end{aligned}$$

since  $\xi$  and  $X_n$  are independent random variables. Thus

$$M(n+1) = \mu M(n).$$

Also,

$$\begin{aligned} V(n+1) &= \text{Var}(X_{n+1}) = E[(X_{n+1} - E(X_{n+1}))^2] = E[(X_{n+1} - \mu M(n))^2] \\ &= E[(X_{n+1} - \mu X_n + \mu X_n - \mu M(n))^2], \\ &= E[(X_{n+1} - \mu X_n)^2] + E[(\mu X_n - \mu M(n))^2] + 2E[(X_{n+1} - \mu X_n)(\mu X_n - \mu M(n))]. \end{aligned}$$

Simplifying each term independently, we obtain

(i).

$$\begin{aligned} E[(X_{n+1} - \mu X_n)^2] &= E(E[(\xi_1^{(n)} + \xi_2^{(n)} + \cdots + \xi_{X_n}^{(n)} - \mu X_n)^2 / X_n = n]) \\ &= E(E[(\xi_1^{(n)} + \xi_2^{(n)} + \cdots + \xi_n^{(n)} - \mu n)^2 / X_n = n]) \\ &= \sum_{n=1}^{\infty} E[(\xi_1^{(n)} + \xi_2^{(n)} + \cdots + \xi_n^{(n)} - \mu n)^2 / X_n = n] P(X_n = n) \\ &= \sum_{n=1}^{\infty} n \text{Var}(\xi) P(X_n = n) \\ &= \text{Var}(\xi) \sum_{n=1}^{\infty} n P(X_n = n) \\ &= \text{Var}(\xi) E(X_n) \\ &= \sigma^2 M(n). \end{aligned}$$

(ii).

$$\begin{aligned} E[(\mu X_n - \mu M(n))^2] &= \mu^2 E[(X_n - M(n))^2] \\ &= \mu^2 E[(X_n - E(X_n))^2] \\ &= \mu^2 V(n). \end{aligned}$$

(iii).

$$\begin{aligned} E[(X_{n+1} - \mu X_n)(\mu X_n - \mu M(n))] &= E[(X_{n+1} - \mu X_n)] E[(\mu X_n - \mu M(n))] \\ &= 0, \end{aligned}$$

since

$$\begin{aligned} E[(X_{n+1} - \mu X_n)] &= E(E[(\xi_1^{(n)} + \xi_2^{(n)} + \cdots + \xi_{X_n}^{(n)} - \mu n) / X_n = n]) \\ &= \sum_{n=1}^{\infty} E[(\xi_1^{(n)} + \xi_2^{(n)} + \cdots + \xi_n^{(n)} - \mu n) / X_n = n] P(X_n = n) \\ &= \sum_{n=1}^{\infty} (\mu n - \mu n) P(X_n = n) \\ &= 0. \end{aligned}$$



Putting these results together, we have

$$V(n+1) = \sigma^2 M(n) + \mu^2 V(n).$$

It is also true that the recursions of (2.3) and (2.4) give

$$M(n) = \mu^n \tag{2.5}$$

and

$$V(n) = \begin{cases} n\sigma^2, & \mu = 1 \\ \frac{(1-\mu^n)\sigma^2\mu^{n-1}}{1-\mu}, & \mu \neq 1. \end{cases} \tag{2.6}$$

Equations (2.5) and (2.6) can be proved by induction.

### Proof for Equation (2.5)

When  $n = 0$ , then  $M(0) = \mu^0 = 1$ . Since  $X_0 = 1$ , by assumption, this is true. If we assume that it is true for  $n$ , then we can show that it true for  $(n+1)$ , as shown below

$$\begin{aligned} M(n+1) &= \mu M(n) \\ &= \mu \mu^n \\ &= \mu^{n+1}. \end{aligned}$$

### Proof for equation (2.6)

When  $n = 0$ , then  $V(0) = 0$ . Since  $X_0 = 1$ , this will in fact be the case. If we assume that the equation is true for  $n$ , then we can prove that it is true for  $(n+1)$ . Let us start with the case when  $\mu = 1$

$$\begin{aligned} V(n+1) &= \sigma^2 M(n) + \mu^2 V(n) \\ &= \sigma^2 \mu^n + \mu^2 n\sigma^2 \\ &= \sigma^2 + n\sigma^2 \\ &= \sigma^2(1+n). \end{aligned}$$

Also when  $\mu \neq 1$ , we obtain

$$\begin{aligned} V(n+1) &= \sigma^2 M(n) + \mu^2 V(n) \\ &= \sigma^2 \mu^n + \left( \frac{(1-\mu^n)\sigma^2\mu^{n+1}}{1-\mu} \right) \\ &= \sigma^2 \mu^n \left( 1 + \frac{(1-\mu^n)\mu}{1-\mu} \right) \\ &= \sigma^2 \mu^n \left( \frac{1-\mu + \mu - \mu^{n+1}}{1-\mu} \right) \\ &= \sigma^2 \mu^n \left( \frac{1-\mu^{n+1}}{1-\mu} \right). \end{aligned}$$

Thus,

$$V(n+1) = \begin{cases} \sigma^2(n+1), & \mu = 1 \\ \frac{(1-\mu^{n+1})\sigma^2\mu^n}{1-\mu}, & \mu \neq 1 \end{cases}$$

and so is true for  $(n + 1)$ .

From equations (2.5) and (2.6), it can be seen that if  $\mu = 1$ , then the mean size of the individuals remains constant, but the variance increases linearly. If  $\mu > 1$ , then the mean size and variance grow geometrically. And, if  $\mu < 1$ , the mean size and variance decrease geometrically.

## 2.4 Generating functions of a branching process

A generating function is a power series representation of the probability mass function of a non-negative discrete random variable as a continuous function on the domain  $[0,1]$ . Consider the discrete non-negative random variable given in equation (2.1). This distribution can be represented by a generating function  $\phi(s)$  with  $0 \leq s \leq 1$ , given by;

$$\phi(s) = E(s^{\xi}) = \sum_{k=0}^{\infty} p_k s^k. \quad (2.7)$$

Three major results can be obtained from equation (2.7). These results are:

1. It is clear that the relationship between the probability mass function (2.1) and the generating function (2.7) is one-to-one. This is because for each value of  $p_k$ , there exists one and only one value of  $\phi(s)$ . The question we can ask ourselves is, how can we express  $p_k$  in terms of  $\phi$ ? First, we can notice that

$$\phi(s) = p_0 + p_1 s + p_2 s^2 + \dots \quad (2.8)$$

Substituting  $s=0$ , in this equation gives  $\phi(0) = p_0$

Finding the first derivative of (2.8), and substituting  $s=0$ , also gives

$$\phi'(0) = p_1.$$

Similarly, finding the second derivative of (2.8), and substituting  $s=0$ , gives

$$\frac{\phi''(0)}{2} = p_2.$$

Thus, in general

$$p_k = \frac{1}{k!} \frac{d^k}{ds^k} [\phi(0)]. \quad (2.9)$$

We can conclude that the successive derivatives of the generating function  $\phi(s)$ , evaluated at  $s=0$ , produce the probability mass function  $p_k$ .

2. Let  $\xi_1, \xi_2, \dots, \xi_n$  be independent random variables with generating functions  $\phi_1(s), \phi_2(s), \dots, \phi_n(s)$ . Let  $X = \xi_1 + \xi_2 + \dots + \xi_n$  be the sum of the independent random variables.

The generating function of  $X$  is given by the product of the generating functions of the variables  $\xi$ , that is

$$\phi_X(s) = \phi_1(s)\phi_2(s) \cdots \phi_n(s) \quad (2.10)$$

The result in (2.10) can be used when working with sums of non-identically distributed random variables, and can hence be applied in the analysis of branching processes.

3. It can be seen that differentiating (2.8) leads us to the moments of the random variable  $\xi$ . For example, the first derivative will be

$$\phi'(s) = p_1 + 2p_2s + 3p_3s + \cdots, \quad (2.11)$$

from where

$$\phi'(1) = p_1 + 2p_2 + 3p_3 + \cdots = \sum_{k=1}^{\infty} kp_k = E[\xi]. \quad (2.12)$$

Similarly, from the second derivative, we obtain

$$\phi''(1) = 2p_2 + 6p_3 + 12p_4 + \cdots = \sum_{k=2}^{\infty} k(k-1)p_k = E[\xi(\xi-1)] = E[\xi^2] - E[\xi]. \quad (2.13)$$

Thus from  $\text{Var}(\xi) = E[\xi^2] - E[\xi]^2$ , we have

$$\text{Var}(\xi) = \phi''(1) + \phi'(1) - (\phi'(1))^2. \quad (2.14)$$

We can conclude that the successive derivatives of the generating function  $\phi(s)$ , evaluated at  $s = 1$ , produce the successive moments of the random variable  $\xi$ .

## 2.5 Extinction probabilities

In this section, we are interested in finding the probability that the population dies out after some finite number of generations  $n$ . We try to answer some important questions. What is the probability that an infectious disease dies out before an epidemic is initiated? What is the probability that a family line becomes extinct? What is the probability that a tsetse population will become extinct at generation  $n$ ? Starting with  $X_0 = 1$ , we shall assume that the number of progeny  $X_1 = k$  is produced by  $X_0$ . Let  $T$  be the random time of extinction, that is

$$T = \min_{n \geq 0} \{X_n = 0\},$$

and let

$$\theta_n = P(T \leq n / X_0 = 1) = P(X_n = 0 / X_0 = 1) \quad (2.15)$$

be the probability of extinction at or before the  $n$ th generation. Of course, it is clear that when  $X_n = 0$ , then  $X_{n+i} = 0$  for  $i \geq 0$  since individuals can only be generated if the preceding generation is non-zero.

Since we have assumed that  $X_1 = k$ , we will expect each of the  $k$  offspring to produce a certain random number of descendants. In this case we will obtain  $k$  subpopulations which are independent. The probability that any of these subpopulations will be extinct by generation  $(n-1)$  is  $\theta_{n-1}$ , by definition. The probability that all the  $k$  independent subpopulations will be extinct in generation  $(n-1)$  is  $(\theta_{n-1})^k$ . Thus, using the law of total probability, we obtain the probability of extinction at generation  $n$  as

$$\theta_n = \sum_{k=0}^{\infty} p_k (\theta_{n-1})^k, n = 1, 2, 3, \dots \quad (2.16)$$

Comparing equation (2.16) with equation (2.7), we can re-write equation (2.16) in terms of a moment generating function as

$$\phi(\theta_{n-1}) = \sum_{k=0}^{\infty} p_k (\theta_{n-1})^k = \theta_n. \quad (2.17)$$

Thus, from the above equation one can calculate the extinction probabilities, starting with  $\theta_0 = 0$ ,  $\theta_1 = \phi(\theta_0)$ ,  $\theta_2 = \phi(\theta_1)$ , and continuing iteratively through the generations.

From equation (2.17), we can notice the following:

- The extinction probability  $\theta_n = \phi(\theta_{n-1})$  implies that  $\theta_{n+1} = \phi(\theta_n)$ .
- If we let  $\theta = P(X_m = 0 \text{ for some } m > 0) = \lim_{n \rightarrow \infty} \theta_n$ , and using the fact that  $\phi$  is continuous, we can write that  $\theta = \phi(\theta)$ .
- The function  $\phi(\theta)$  is an analytic function.
- The function  $\phi(1) = E(1^k) = \sum_{k=0}^{\infty} p_k 1^k = 1$ . So  $\theta = 1$  is always a solution.
- The function  $\phi(\theta) = \sum_{k=0}^{\infty} p_k \theta^k > 0$  and  $\phi'(\theta) = \sum_{k=0}^{\infty} k p_k \theta^{k-1} > 0$ . Thus  $\phi(\theta)$  and  $\phi'(\theta)$  are strictly increasing functions for  $0 \leq \theta \leq 1$ .
- The second derivative  $\phi''(\theta) = \sum_{k=0}^{\infty} k(k-1) p_k \theta^{k-2} > 0$  for  $0 \leq \theta \leq 1$ . Thus, the function  $\phi(\theta)$  is a convex function on the given interval of  $\theta$ .
- The first derivative  $\phi'(1) = E(\xi) = \mu$ .

**Theorem 2.5.1.** *If  $E(\xi) > 1$ , then the extinction probability  $\theta$  is the unique root of the equation  $\theta = \phi(\theta)$  which lies strictly between 0 and 1. If  $E(\xi) \leq 1$ , then  $\theta = 1$ .*

### Proof

The proof of this theorem is done graphically. Since we know that  $\phi(0) > 0$ , then the curve of  $\phi(\theta)$  has its vertical intercept above the origin.

When  $\mu > 1$ , then the curve  $\phi(\theta)$  starts by moving in a direction below the line  $t=\theta$  at  $\theta=1$ . This curve has to cross the line  $t=\theta$  in order for it to meet the  $t$ -axis at  $\phi(0)$ , as shown in figure 2.2 (a). Thus, there exists a solution to the equation  $\theta = \phi(\theta)$  between 0 and 1. This solution will be called the extinction probability, since this quantity is always the smallest non-negative solution. Here extinction is not certain since  $E(X_n)$  tends to infinity as  $n$  goes to infinity; this process is then termed supercritical.

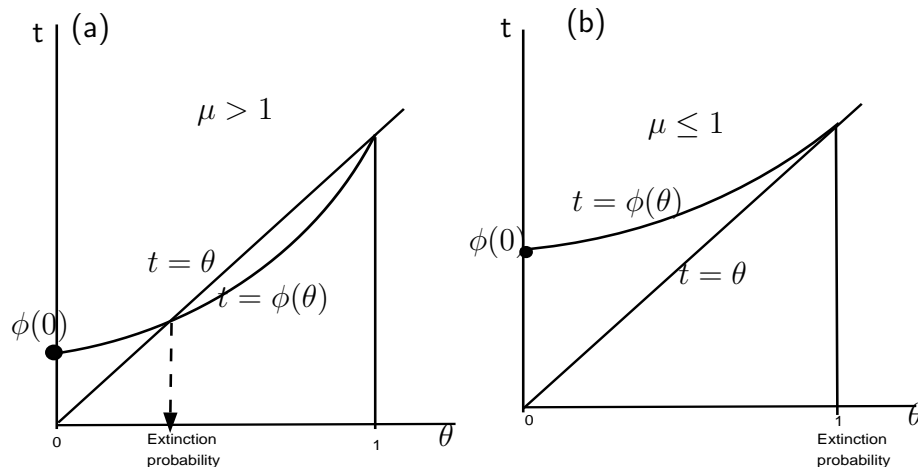


Figure 2.2: Graphs showing extinction probabilities for the three possible cases; supercritical, subcritical and critical.

When  $\mu < 1$ , the curve  $\phi(\theta)$  starts by moving in a direction above the line  $t=\theta$  at  $\theta = 1$ . There is no possibility for this curve to cross the line  $t=\theta$  again before meeting the vertical axis. There is no other solution to the equation  $\theta = \phi(\theta)$  except  $\theta = 1$ . Thus the extinction probability is 1. Here extinction is certain since  $E(X_n)$  tends to zero as  $n$  goes to infinity. This process is termed subcritical. This result is shown in figure 2.2 (b).

The same situation occurs when  $\mu = 1$ , unless  $k=1$ . Here extinction is also certain since  $E(X_n) = \mu^n = 1$  for all  $n$ . This process is termed critical.

## 2.6 Time to extinction

After knowing the probability of extinction, it is useful to know how long it will take for the population to become extinct, the number of generations before extinction. For example, how long do we expect a disease epidemic like AIDS to continue?

### 2.6.1 Extinction by time $n$

We already know that a branching process is extinct by time  $n$  if  $X_n = 0$ . Taking  $\theta_n$  to be the probability of extinction at or before the  $n$ th generation, and  $T$  to be the extinction time

as defined in equation (2.15), then the  $j$ -th moment of  $T$  can be computed from the general formula [Fel71]

$$E(T^j) = \sum_{n=0}^{\infty} [(n+1)^j - n^j](1 - \theta_n), \quad (2.18)$$

where  $(1 - \theta_n) = P(T > n)$ .

To prove equation (2.18), let

$$(1 - \theta_n) = P(T > n) = \sum_{m=n+1}^{\infty} P(T = m),$$

for some  $m$ , then

$$\sum_{n=0}^{\infty} [(n+1)^j - n^j](1 - \theta_n) = \sum_{n=0}^{\infty} [(n+1)^j - n^j] \sum_{m=n+1}^{\infty} P(T = m).$$

If we let  $x_n = (n+1)^j - n^j$ , then we can see that

$$\begin{aligned} \sum_{n=0}^{\infty} x_n \sum_{m=n+1}^{\infty} P(T = m) &= x_0 \sum_{m=1}^{\infty} P(T = m) + x_1 \sum_{m=2}^{\infty} P(T = m) + x_2 \sum_{m=3}^{\infty} P(T = m) + \dots \\ &= \sum_{m=1}^{\infty} P(T = m) \sum_{n=0}^{m-1} x_n. \end{aligned}$$

Thus

$$\begin{aligned} \sum_{n=0}^{\infty} [(n+1)^j - n^j](1 - \theta_n) &= \sum_{m=1}^{\infty} P(T = m) \sum_{n=0}^{m-1} [(n+1)^j - n^j] \\ &= \sum_{m=1}^{\infty} P(T = m) [(1^j - 0) + (2^j - 1^j) + \dots + (m^j - (m-1)^j)] \\ &= \sum_{m=1}^{\infty} P(T = m) m^j \\ &= E(T^j). \end{aligned}$$

From equation (2.18), we can obtain the first two moments of  $T$  as

$$E(T) = \sum_{n=0}^{\infty} (1 - \theta_n) \quad \text{and} \quad (2.19)$$

$$E(T^2) = \sum_{n=0}^{\infty} (2n+1)(1 - \theta_n), \quad (2.20)$$

from which we can approximate the mean  $E(T)$  and variance  $\text{Var}(T) = E(T^2) - [E(T)]^2$ .

### 3. Application of branching processes, extinction probabilities to tsetse flies

This application is based on John Hagrove's article which was published in 2005 [Har05]. In this essay, we give in full detail the derivation of the formulas used.

#### 3.1 Theoretical development

In section (1.1) we looked at the life cycle of a tsetse fly. We realised that a female tsetse fly mates only once, and for this matter it is crucial to include in our model the probability that a female tsetse fly is inseminated by a fertile male. We will also assume that the probability that a deposited pupa is male or female will be the same, that is equal to 0.5. In other words, males and females have equal chances of being produced.

First, we define our parameters as follows;

- $\lambda$  the probability that an adult female tsetse fly survives daily.
- $\varphi$  the probability that an immature female pupa survives daily.
- $\nu$  the number of days a female takes to have its first ovulation.
- $\epsilon$  the probability that a female is inseminated by a fertile male.
- $\tau$  the inter-larval period in days.
- $T$  pupal duration.
- $p_{n,k}$  the probability that a female tsetse fly dies between pregnancy  $n$  and  $(n + 1)$  and produces  $k$  surviving female offspring.
- $\beta$  the probability that a female pupa is deposited. This is assumed to be 0.5.
- $\psi$  the daily mortality rate for adult females =  $-\ln(\lambda)$ .
- $\chi$  the mortality rate for female pupae =  $-\ln(\varphi)$ .

Considering a female that survives one pregnancy and produces one surviving female offspring, we can deduce the probability  $p_{1,1}$  for this case as follows. First, we know that a female tsetse fly is inseminated by a fertile male with a probability  $\epsilon$ , then survives with probability  $\lambda^{(\nu+\tau)}$  up to the time she produces her first pupa, which itself has a probability  $\beta$  of being female. This pupa survives with a probability  $\varphi^T$  and the mother finally dies with a probability  $(1 - \lambda^\tau)$  during the next pregnancy. Thus, combining all these factors, we obtain the probability that a female tsetse fly produces one surviving daughter after surviving one pregnancy as

$$p_{1,1} = \epsilon \lambda^{(\nu+\tau)} \beta \varphi^T (1 - \lambda^\tau). \quad (3.1)$$

In general the probability that a female tsetse fly produces  $k$  surviving daughters after surviving  $n$  pregnancies is given by

$$p_{n,k} = \epsilon \lambda^{(\nu+n\tau)} (1 - \lambda^\tau) \binom{n}{k} \beta^n \varphi^{kT} (1 + (1 - \varphi^T))^{n-k} \quad (3.2)$$

for  $n > 0; 1 \leq k \leq n$ , and where  $\binom{n}{k}$  are the binomial coefficients.

Equation (3.2) can be proved by induction as follows.

Let  $A_n$  be the event "a mother deposits exactly  $n$  pupae", and  $B_{n,k}$  be the event " $n$  pupae produces exactly  $k$  female adults". We can then define

$$\begin{aligned} M_n &= P(A_n) = \epsilon \lambda^{\nu+n\tau} (1 - \lambda^\tau). \\ q_{n,k} &= P(B_{n,k}/A_n). \end{aligned}$$

It is clear that

$$p_{n,k} = P(A_n \cap B_{n,k}) = P(A_n) \cdot P(B_{n,k}/A_n) = M_n \cdot q_{n,k}. \quad (3.3)$$

We notice that  $M_n$  refers to the mother's survival and  $q_{n,k}$  refers to the pupae survival. So we can base our proof by concentrating on the pupal survival since the product of the two gives the result we are interested in, which results from independence.

**Claim:**

$$q_{n,k} = \binom{n}{k} \beta^n \rho^k \gamma^{n-k}, \quad (3.4)$$

where  $\rho = \varphi^T$  and  $\gamma = (\frac{1}{\beta} - \rho)$ , of course with  $\beta=0.5$ .

**Proof:** The proof of the claim is as follows;

$$\begin{aligned} q_{(1,0)} &= P(1 \text{ pupa, no female adults}) \\ &= P(1 \text{ female pupa, 1 female pupa dies}) + P(1 \text{ male pupa}) \\ &= \binom{1}{0} \beta (1 - \rho) + \binom{1}{0} (1 - \beta) \\ &= 1 - \beta \rho = \beta \left( \frac{1}{\beta} - \rho \right) \\ &= \beta \gamma. \end{aligned}$$

By independence  $q_{n,0} = (q_{1,0})^n = (\beta \gamma)^n$ .

$$\begin{aligned} q_{(1,1)} &= P(1 \text{ pupa, 1 female adult}) \\ &= \beta \rho \\ &= \binom{1}{1} \beta \rho \gamma^{1-1}. \end{aligned}$$

$$\begin{aligned} q_{(2,1)} &= P(2 \text{ pupae, 1 female adult}) \\ &= P(2 \text{ female pupae, 1 female adult}) + P(1 \text{ female pupa and 1 male pupa, 1 female adult}) \\ &= \binom{2}{1} \beta^2 \rho (1 - \rho) + \binom{2}{1} \beta \rho (1 - \beta) \\ &= 2\beta^2 \rho (1 - \rho) + 2\beta \rho (1 - \beta) \\ &= 2\rho \beta (\beta - \beta \rho + 1 - \beta) \\ &= 2\rho \beta (1 - \beta \rho) \\ &= 2\rho \beta^2 \left( \frac{1}{\beta} - \rho \right) \\ &= 2\rho \beta^2 \gamma \\ &= \binom{2}{1} \rho \beta^2 \gamma^{2-1}. \end{aligned}$$

Thus, in general

$$q_{(n,1)} = \binom{n}{1} \beta^n \rho \gamma^{n-1}. \quad (3.5)$$

If we assume that equation (3.5) is true for all  $i \leq n$ , then we can show that it is also true for  $(n + 1)$  by assuming that either the single female survivor arrives before the last pupa or it does



not. If we assume the latter case, the last one must survive, that is

$$\begin{aligned}
 q_{(n+1,1)} &= q_{(n,1)} \cdot q_{(1,0)} + q_{(n,0)} \cdot q_{(1,1)} \\
 &= \binom{n}{1} \beta^n \rho \gamma^{n-1} \beta \gamma + (\beta \gamma)^n \binom{1}{1} \beta \rho \gamma^{1-1} \\
 &= \binom{n+1}{1} \beta^{n+1} \rho \gamma^n,
 \end{aligned}$$

which is true for all  $(n+1)$ .

Also, if we assume that equation (3.4) is true for all  $l \leq k$ , and we fix the value of  $n$ , then we can show that it is true for  $(k+1)$  by making an assumption similar to the one we had previously.

$$\begin{aligned}
 q_{(n,k+1)} &= q_{(n-1,k+1)} \cdot q_{(1,0)} + q_{(n-1,k)} \cdot q_{(1,1)} \\
 &= \binom{n-1}{k+1} \beta^{n-1} \rho^{k+1} \gamma^{n-k-2} \beta \gamma + \binom{n-1}{k} \beta^{n-1} \rho^k \gamma^{n-k-1} \binom{1}{1} \beta \rho \gamma^{1-1} \\
 &= \left[ \binom{n-1}{k+1} + \binom{n-1}{k} \right] \beta^n \rho^{k+1} \gamma^{n-(k+1)} \\
 &= \left[ \frac{(n-1)!}{(k+1)!(n-(k+2))!} + \frac{(n-1)!}{k!(n-(k+1))!} \right] \beta^n \rho^{k+1} \gamma^{n-(k+1)} \\
 &= \left[ \frac{(n-1)!}{(k+1)!(n-(k+1))!} \right] ((n-(k+1)) + (k+1)) \beta^n \rho^{k+1} \gamma^{n-(k+1)} \\
 &= \left[ \frac{n!}{(k+1)!(n-(k+1))!} \right] \beta^n \rho^{k+1} \gamma^{n-(k+1)} \\
 &= \binom{n}{k+1} \beta^n \rho^{k+1} \gamma^{n-(k+1)},
 \end{aligned}$$

which is true for all  $n > 0$  and  $1 < k+1 < n$ .

#### Remarks:

1. It was actually observed that there was no need to prove equation (3.2) by induction, as we had earlier thought. From equation (3.3), we can notice that for each pupa there are two possibilities; either it becomes an adult female or it does not. The probability that it becomes an adult female is  $\beta \varphi^T$ , and the probability that it does not is then clearly  $(1 - \beta \varphi^T)$ . Since the probabilities are the same for all pupae and these outcomes for different pupae are independent, the probability that there are  $k$  adult females from  $n$  pupae is given by a binomial distribution as

$$\begin{aligned}
 q_{n,k} &= \binom{n}{k} (\beta \varphi^T)^k (1 - \beta \varphi^T)^{n-k} \\
 &= \binom{n}{k} \beta^k \varphi^{Tk} \beta^{n-k} \left( \frac{1}{\beta} - \varphi^T \right)^{n-k} \\
 &= \binom{n}{k} \beta^n \varphi^{Tk} \left( \frac{1}{\beta} - \varphi^T \right)^{n-k}
 \end{aligned}$$

Thus, from equation (3.3), we obtain the expression for  $p_{n,k}$  as

$$\begin{aligned} p_{n,k} &= M_n \cdot q_{n,k} \\ &= \epsilon \lambda^{(\nu+n\tau)} (1 - \lambda^\tau) \binom{n}{k} \beta^n \varphi^{Tk} \left( \frac{1}{\beta} - \varphi^T \right)^{n-k}, \end{aligned} \quad (3.6)$$

which simply reduces to equation (3.2) when  $\beta = 0.5$ .

2. Hargrove's heuristic explanation for equation (3.2) in [Har05] is misleading because it terms a number greater than 1 a probability. Nonetheless, the formula is correct for the case he considered, and is also correct more generally with the adjustment of that term, as the proof shows.
3. Equation (3.2) works only when  $\beta=0.5$ . After making the correction, it can be observed that equation (3.6) works for all values of  $\beta$ .

Summing equation (3.2) over  $n$  leads us to the probability  $p_k$  that a female tsetse fly produces  $k$  surviving female offspring before she dies. Thus

$$p_k = \sum_{n=k}^{\infty} \epsilon \lambda^{(\nu+n\tau)} (1 - \lambda^\tau) \binom{n}{k} \beta^n \varphi^{kT} (1 + (1 - \varphi^T))^{n-k} \quad (3.7)$$

$$= \epsilon \lambda^\nu (1 - \lambda^\tau) \varphi^{kT} \sum_{n=k}^{\infty} \binom{n}{k} (\lambda^\tau \beta)^n (1 + (1 - \varphi^T))^{n-k}. \quad (3.8)$$

We start by finding the sum for integer values of  $k$  increasing from 0, until we are able to finally write the general formula for  $p_k$ .

When  $k = 0$ , we obtain

$$\begin{aligned} p_0 &= \epsilon \lambda^\nu (1 - \lambda^\tau) \sum_{n=0}^{\infty} \binom{n}{0} (\lambda^\tau \beta)^n (1 + (1 - \varphi^T))^n \\ &= \epsilon \lambda^\nu (1 - \lambda^\tau) \sum_{n=0}^{\infty} [\lambda^\tau \beta (1 + (1 - \varphi^T))]^n \\ &= \epsilon \lambda^\nu (1 - \lambda^\tau) \left[ \frac{1}{(1 - \lambda^\tau \beta (1 + (1 - \varphi^T)))} \right] \\ &= \frac{\epsilon \lambda^\nu (1 - \lambda^\tau)}{(1 - \lambda^\tau \beta (1 + (1 - \varphi^T)))}. \end{aligned}$$

When  $k=1$ , we obtain

$$\begin{aligned} p_1 &= \epsilon \lambda^\nu (1 - \lambda^\tau) \varphi^T \sum_{n=1}^{\infty} \binom{n}{1} (\lambda^\tau \beta)^n (1 + (1 - \varphi^T))^{n-1} \\ &= \epsilon \lambda^\nu (1 - \lambda^\tau) \varphi^T \sum_{n=1}^{\infty} n (\lambda^\tau \beta)^n (1 + (1 - \varphi^T))^{n-1}. \end{aligned}$$

If we let  $a = \lambda^\tau \beta, b = (1 + (1 - \varphi^T))$  and  $F = \sum_{n=1}^{\infty} n a^n b^{n-1}$ , this implies that

$$\begin{aligned} F &= ab^0 + 2a^2b + 3a^3b^2 + \dots \\ abF &= a^2b + 2a^3b^2 + \dots \\ (1-ab)F &= ab^0 + a^2b + a^3b^2 + \dots \\ ab(1-ab)F &= a^2b + a^3b^2 + a^4b^3 + \dots = \frac{a^2b}{(1-ab)} \\ F &= \frac{a}{(1-ab)^2} = \frac{\lambda^\tau \beta}{(1 - \lambda^\tau \beta(1 + (1 - \varphi^T)))^2}. \end{aligned}$$

Thus, the final solution for  $p_1$  becomes

$$\begin{aligned} p_1 &= \epsilon \lambda^\nu (1 - \lambda^\tau) \varphi^T F \\ &= \epsilon \lambda^\nu (1 - \lambda^\tau) \varphi^T \left[ \frac{\lambda^\tau \beta}{(1 - \beta \lambda^\tau (1 + (1 - \varphi^T)))^2} \right] \\ &= \frac{\epsilon \lambda^{\nu+\tau} (1 - \lambda^\tau) \beta \varphi^T}{(1 - \beta \lambda^\tau (1 + (1 - \varphi^T)))^2}. \end{aligned}$$

When  $k=2$ , we obtain

$$\begin{aligned} p_2 &= \epsilon \lambda^\nu (1 - \lambda^\tau) \varphi^{2T} \sum_{n=2}^{\infty} \binom{n}{2} (\lambda^\tau \beta)^n (1 + (1 - \varphi^T))^{n-2} \\ &= \epsilon \lambda^\nu (1 - \lambda^\tau) \varphi^{2T} \sum_{n=2}^{\infty} \left[ \frac{n(n-1)}{2} (\lambda^\tau \beta)^n (1 + (1 - \varphi^T))^{n-2} \right]. \end{aligned}$$

Also letting  $a = \lambda^\tau \beta, b = (1 + (1 - \varphi^T))$  and  $G = \sum_{n=2}^{\infty} \left[ \frac{n(n-1)}{2} a^n b^{n-2} \right]$ , we have

$$\begin{aligned} G &= a^2 b^0 + 3a^3 b + 6a^4 b^2 + 10a^5 b^3 + \dots \\ abG &= a^3 b + 3a^4 b^2 + 6a^5 b^3 + \dots \\ (1-ab)G &= a^2 b^0 + 2a^3 b + 3a^4 b^2 + 4a^5 b^3 + \dots \\ ab(1-ab)G &= a^3 b + 2a^4 b^2 + 3a^5 b^3 + 4a^6 b^4 + \dots \\ ((1-ab) - ab(1-ab))G &= (1-ab)^2 G = a^2 b^0 + a^3 b + a^4 b^2 + a^5 b^3 + \dots \\ ab(1-ab)^2 G &= a^3 b + a^4 b^2 + a^5 b^3 + a^6 b^4 + \dots = \frac{a^3 b}{(1-ab)} \\ G &= \frac{a^2}{(1-ab)^3} = \frac{(\lambda^\tau \beta)^2}{(1 - \lambda^\tau \beta(1 + (1 - \varphi^T)))^3}. \end{aligned}$$

Thus, the final solution for  $p_2$  becomes

$$\begin{aligned} p_2 &= \epsilon \lambda^\nu (1 - \lambda^\tau) \varphi^{2T} G \\ &= \epsilon \lambda^\nu (1 - \lambda^\tau) \varphi^{2T} \left[ \frac{(\lambda^\tau \beta)^2}{(1 - \beta \lambda^\tau (1 + (1 - \varphi^T)))^3} \right] \\ &= \frac{\epsilon \lambda^{\nu+2\tau} (1 - \lambda^\tau) \beta^2 \varphi^{2T}}{(1 - \beta \lambda^\tau (1 + (1 - \varphi^T)))^3}. \end{aligned}$$

Thus, in general

$$p_k = \frac{\epsilon\lambda^{\nu+k\tau}(1-\lambda^\tau)\beta^k\varphi^{kT}}{(1-\beta\lambda^\tau(1+(1-\varphi^T)))^{k+1}} \quad \text{for } k > 0. \quad (3.9)$$

The probability that a female tsetse fly produces at least one surviving daughter before she dies can be obtained by summing equation (3.9) over  $k$ . This is done as follows:

$$\begin{aligned} p_{(k>0)} &= \sum_{k=0}^{\infty} \frac{\epsilon\lambda^{\nu+k\tau}(1-\lambda^\tau)\beta^k\varphi^{kT}}{(1-\beta\lambda^\tau(1+(1-\varphi^T)))^{k+1}} \\ &= \frac{\epsilon\lambda^\nu(1-\lambda^\tau)}{1-\beta\lambda^\tau(1+(1-\varphi^T))} \sum_{k=0}^{\infty} \left[ \frac{\lambda^\tau\beta\varphi^T}{1-\beta\lambda^\tau(1+(1-\varphi^T))} \right]^k \\ &= \frac{\epsilon\lambda^\nu(1-\lambda^\tau)}{1-\beta\lambda^\tau(1+(1-\varphi^T))} \left[ \frac{\frac{\lambda^\tau\beta\varphi^T}{1-\beta\lambda^\tau(1+(1-\varphi^T))}}{1-\frac{\lambda^\tau\beta\varphi^T}{1-\beta\lambda^\tau(1+(1-\varphi^T))}} \right] \\ &= \frac{\epsilon\lambda^\nu(1-\lambda^\tau)}{1-\beta\lambda^\tau(1+(1-\varphi^T))} \left[ \frac{\lambda^\tau\beta\varphi^T}{1-\beta\lambda^\tau(1+(1-\varphi^T))-\lambda^\tau\beta\varphi^T} \right] \\ &= \frac{\epsilon\lambda^\nu(1-\lambda^\tau)}{1-\beta\lambda^\tau(1+(1-\varphi^T))} \left[ \frac{\lambda^\tau\beta\varphi^T}{(1-2\beta\lambda^\tau)} \right]. \end{aligned}$$

Substituting for  $\beta = 0.5$ , we obtain

$$p_{(k>0)} = \frac{\epsilon\lambda^{\nu+\tau}\beta\varphi^T}{1-\beta\lambda^\tau(1+(1-\varphi^T))}.$$

Thus, the probability that a female tsetse fly does not produce any surviving female offspring before she dies is given by

$$p_0 = 1 - p_{(k>0)} = 1 - \frac{\epsilon\lambda^{\nu+\tau}\beta\varphi^T}{1-\beta\lambda^\tau(1+(1-\varphi^T))}. \quad (3.10)$$

Assuming that we start with one female tsetse fly in the initial generation, which produces  $k$  surviving offspring, we can write that the moment generating function of the next generation is

$$\phi(\theta) = \sum_{k=0}^{\infty} p_k\theta^k = p_0 + \sum_{k=1}^{\infty} p_k\theta^k.$$

Substituting for  $p_0$  and  $p_k$  and putting the terms without  $k$  outside the summation sign we get

$$\begin{aligned} \phi(\theta) &= 1 - \frac{\epsilon\lambda^{\nu+\tau}\beta\varphi^T}{1-\beta\lambda^\tau(1+(1-\varphi^T))} + \frac{\epsilon\lambda^\nu(1-\lambda^\tau)}{1-\beta\lambda^\tau(1+(1-\varphi^T))} \sum_{k=1}^{\infty} \left[ \frac{\lambda^\tau\beta\varphi^T\theta}{1-\beta\lambda^\tau(1+(1-\varphi^T))} \right]^k \\ &= 1 - \frac{\epsilon\lambda^{\nu+\tau}\beta\varphi^T}{1-\beta\lambda^\tau(1+(1-\varphi^T))} + \frac{\epsilon\lambda^\nu(1-\lambda^\tau)}{1-\beta\lambda^\tau(1+(1-\varphi^T))} \left[ \frac{\frac{\lambda^\tau\beta\varphi^T\theta}{1-\beta\lambda^\tau(1+(1-\varphi^T))}}{1-\frac{\lambda^\tau\beta\varphi^T\theta}{1-\beta\lambda^\tau(1+(1-\varphi^T))}} \right] \\ &= 1 - \frac{\epsilon\lambda^{\nu+\tau}\beta\varphi^T}{1-2\beta\lambda^\tau+\beta\lambda^\tau\varphi^T} + \frac{\epsilon\lambda^\nu(1-\lambda^\tau)}{1-2\beta\lambda^\tau+\beta\lambda^\tau\varphi^T} \left[ \frac{\lambda^\tau\beta\varphi^T\theta}{1-2\beta\lambda^\tau+\beta\lambda^\tau\varphi^T-\beta\lambda^\tau\varphi^T\theta} \right]. \end{aligned}$$

Letting  $A = 1 - \lambda^\tau$ ,  $B = \beta\lambda^\tau\varphi^T$  and substituting for  $\beta = 0.5$  where convenient, we obtain

$$\begin{aligned}
\phi(\theta) &= 1 - \frac{\epsilon\lambda^\nu B}{A+B} + \frac{\epsilon\lambda^\nu A}{A+B} \left[ \frac{B\theta}{A+B-B\theta} \right] \\
&= \frac{(A+B)(A+B-B\theta) - \epsilon\lambda^\nu B(A+B-B\theta) + \epsilon AB\lambda^\nu\theta}{(A+B)(A+B-B\theta)} \\
&= \frac{(A+B)(A+B-B\theta) - \epsilon\lambda^\nu B(A+B) + \epsilon\lambda^\nu B^2\theta + \epsilon\lambda^\nu AB\theta}{(A+B)(A+B-B\theta)} \\
&= \frac{(A+B)(A+B-B\theta) - (A+B)(\epsilon\lambda^\nu B) + (A+B)\epsilon\lambda^\nu B\theta}{(A+B)(A+B-B\theta)} \\
&= \frac{(A+B)(A+B-B\theta - \epsilon\lambda^\nu B + \epsilon\lambda^\nu B\theta)}{(A+B)(A+B-B\theta)} \\
&= \frac{A+B(1-\theta - \epsilon\lambda^\nu + \epsilon\lambda^\nu\theta)}{A+B(1-\theta)} \\
&= \frac{A+B(1-\theta)(1-\epsilon\lambda^\nu)}{A+B(1-\theta)}.
\end{aligned}$$

Thus, we have

$$\phi(\theta) = \frac{A + BC(1-\theta)}{A + B(1-\theta)}, \quad (3.11)$$

where  $C = 1 - \epsilon\lambda^\nu$ .

As we have already seen in chapter 3, the extinction probability can be found by solving the quadratic equation  $\phi(\theta) = \theta$ , and it will be the smallest non-negative root. This is done as shown below.

$$\begin{aligned}
\frac{A + BC(1-\theta)}{A + B(1-\theta)} &= \theta, \\
\Rightarrow A + BC(1-\theta) &= A\theta + B\theta - B\theta^2, \\
\Rightarrow B\theta^2 - (BC + A + B)\theta + A + BC &= 0.
\end{aligned}$$

Thus the extinction probability is

$$\theta = \frac{BC + A + B - \sqrt{(BC + A + B)^2 - 4B(A + BC)}}{2B}. \quad (3.12)$$

This is the probability that a female tsetse population, resulting from an initial population of one fly, goes to extinction. On the other hand, if the initial population consists of  $N$  flies, then we say that the probability of extinction is  $\theta^N$ .

## 3.2 Mean and variance of the female tsetse population at generation $n$

We will use the method of moments to find the mean and variance of the offspring. From these variables we can then derive the mean and variance of the female tsetse population at a given

generation  $n$ .

By definition, the  $m^{\text{th}}$  moment of  $p_k$  is given by

$$M_m = \sum_{k=0}^{\infty} k^m p_k.$$

When  $m = 1$ , we obtain the first moment as

$$\begin{aligned} M_1 &= \sum_{k=0}^{\infty} k p_k \\ &= \sum_{k=0}^{\infty} \frac{k \epsilon \lambda^{\nu+k\tau} (1 - \lambda^\tau) \beta^k \varphi^{kT}}{(1 - \beta \lambda^\tau (1 + (1 - \varphi^T)))^{k+1}} \\ &= \frac{\epsilon \lambda^\nu (1 - \lambda^\tau)}{1 - \beta \lambda^\tau (1 + (1 - \varphi^T))} \sum_{k=0}^{\infty} k \left[ \frac{\lambda^\tau \beta \varphi^T}{1 - \beta \lambda^\tau (1 + (1 - \varphi^T))} \right]^k. \end{aligned}$$

Using the sum of power series, that is  $\sum_{n=0}^{\infty} n x^n = \frac{x}{(1-x)^2}$  to simplify the terms in front of the summation sign, we obtain

$$\begin{aligned} M_1 &= \frac{\epsilon \lambda^\nu (1 - \lambda^\tau)}{1 - \beta \lambda^\tau (1 + (1 - \varphi^T))} \left[ \frac{\frac{\lambda^\tau \beta \varphi^T}{1 - \beta \lambda^\tau (1 + (1 - \varphi^T))}}{\left(1 - \frac{\lambda^\tau \beta \varphi^T}{1 - \beta \lambda^\tau (1 + (1 - \varphi^T))}\right)^2} \right] \\ &= \frac{\epsilon \lambda^\nu (1 - \lambda^\tau)}{1 - \beta \lambda^\tau (1 + (1 - \varphi^T))} \left[ \frac{\frac{\lambda^\tau \beta \varphi^T}{1 - \beta \lambda^\tau (1 + (1 - \varphi^T))}}{\frac{(1 - \beta \lambda^\tau (1 + (1 - \varphi^T))) + \lambda^\tau \beta \varphi^T}{(1 - \beta \lambda^\tau (1 + (1 - \varphi^T)))^2}} \right] \\ &= \frac{\epsilon \lambda^\nu (1 - \lambda^\tau)}{1 - \beta \lambda^\tau (1 + (1 - \varphi^T))} \left[ \frac{\lambda^\tau \beta \varphi^T (1 - \beta \lambda^\tau (1 + (1 - \varphi^T)))}{(1 - \beta \lambda^\tau (1 + (1 - \varphi^T))) - \lambda^\tau \beta \varphi^T} \right] \\ &= \frac{\epsilon \lambda^{\nu+\tau} (1 - \lambda^\tau) \beta \varphi^T}{(1 - 2\beta \lambda^\tau)^2}. \end{aligned}$$

Thus for  $\beta = 0.5$ , we obtain

$$M_1 = \frac{\epsilon \lambda^{\nu+\tau} \beta \varphi^T}{(1 - \lambda^\tau)}. \quad (3.13)$$

When  $m = 2$ , we obtain the second moment as

$$\begin{aligned} M_2 &= \sum_{k=0}^{\infty} k^2 p_k \\ &= \sum_{k=0}^{\infty} \frac{k^2 \epsilon \lambda^{\nu+k\tau} (1 - \lambda^\tau) \beta^k \varphi^{kT}}{(1 - \beta \lambda^\tau (1 + (1 - \varphi^T)))^{k+1}} \\ &= \frac{\epsilon \lambda^\nu (1 - \lambda^\tau)}{1 - \beta \lambda^\tau (1 + (1 - \varphi^T))} \sum_{k=0}^{\infty} k^2 \left[ \frac{\lambda^\tau \beta \varphi^T}{1 - \beta \lambda^\tau (1 + (1 - \varphi^T))} \right]^k. \end{aligned}$$

Using the sum of power series, that is  $\sum_{n=0}^{\infty} n^2 x^n = \frac{x+x^2}{(1-x)^3}$  to simplify the terms in front of the summation sign, we have

$$\begin{aligned}
M_2 &= \frac{\epsilon \lambda^\nu (1 - \lambda^\tau)}{1 - \beta \lambda^\tau (1 + (1 - \varphi^T))} \left[ \frac{\frac{\lambda^\tau \beta \varphi^T}{1 - \beta \lambda^\tau (1 + (1 - \varphi^T))} + \left( \frac{\lambda^\tau \beta \varphi^T}{1 - \beta \lambda^\tau (1 + (1 - \varphi^T))} \right)^2}{\left( 1 - \frac{\lambda^\tau \beta \varphi^T}{1 - \beta \lambda^\tau (1 + (1 - \varphi^T))} \right)^3} \right] \\
&= \frac{\epsilon \lambda^\nu (1 - \lambda^\tau)}{1 - \beta \lambda^\tau (1 + (1 - \varphi^T))} \left[ \frac{\frac{\lambda^\tau \beta \varphi^T (1 - \beta \lambda^\tau (1 + (1 - \varphi^T))) + (\lambda^\tau \beta \varphi^T)^2}{(1 - \beta \lambda^\tau (1 + (1 - \varphi^T)))^2}}{\frac{(1 - \beta \lambda^\tau (1 + (1 - \varphi^T))) - \lambda^\tau \beta \varphi^T}{(1 - \beta \lambda^\tau (1 + (1 - \varphi^T)))^3}} \right] \\
&= \epsilon \lambda^\nu (1 - \lambda^\tau) \left[ \frac{\lambda^\tau \beta \varphi^T (1 - \beta \lambda^\tau (1 + (1 - \varphi^T))) + \lambda^\tau \beta \varphi^T}{(1 - 2\beta \lambda^\tau)^3} \right] \\
&= \epsilon \lambda^\nu (1 - \lambda^\tau) \left[ \frac{\lambda^\tau \beta \varphi^T (1 - 2\beta \lambda^\tau + 2\beta \lambda^\tau \varphi^T)}{(1 - 2\beta \lambda^\tau)^3} \right].
\end{aligned}$$

Thus for  $\beta = 0.5$ , we obtain

$$M_2 = \frac{\epsilon \lambda^{\nu+\tau} \beta \varphi^T (1 - \lambda^\tau (1 - \varphi^T))}{(1 - \lambda^\tau)^2}. \quad (3.14)$$

The mean or the expected number of surviving daughters a female tsetse fly is expected to have is given by  $\mu = M_1$  and the variance is given by  $\sigma^2 = M_2 - (M_1)^2$ . Thus, the mean  $E(X_n)$  and variance  $\text{Var}(X_n)$  of the surviving daughters at generation  $n$  are the same as the ones given in equations (2.5) and (2.6).

### 3.3 Time for the population of the female tsetse flies to become extinct

From equation (2.16), we derived the extinction probability at generation  $n$  in terms of a moment generating function as

$$\theta_n = \phi(\theta_{n-1}). \quad (3.15)$$

We also derived the first moments of  $T$  in equations (2.19) and (2.20), where  $T$  is the extinction time. Thus, using equations (3.11) and (3.15) and taking  $\theta_0 = 0$ , we can calculate the values of  $\theta_n$  by iteration. The first two, for example, are given below.

$$\theta_1 = \phi(\theta_0) = \phi(0) = \frac{A + BC}{A + B}, \quad (3.16)$$

$$\theta_2 = \phi(\theta_1) = \phi\left(\frac{A + BC}{A + B}\right) = \frac{A + BC \left(1 - \frac{A+BC}{A+B}\right)}{A + B \left(1 - \frac{A+BC}{A+B}\right)}. \quad (3.17)$$

In a situation where there are  $N$  surviving females,  $N > 1$ , equations (2.19) and (2.20) can be generalised. We already know that the probability of extinction at or before generation  $n$  is  $\theta_n$ .

If we have  $N$  surviving females, then the probability that they all become extinct at generation  $n$  is  $(\theta_n)^N$ . Thus equations (2.19) and (2.20) can be re-written as

$$E(T) = \sum_{n=0}^{\infty} (1 - (\theta_n)^N) \quad \text{and} \quad (3.18)$$

$$E(T^2) = \sum_{n=0}^{\infty} (2n + 1)(1 - (\theta_n)^N). \quad (3.19)$$

## 3.4 Results and analysis

### 3.4.1 The relationship between extinction probabilities and adult female daily mortality

Our general results and analysis start by looking at the extinction probability as a function of adult female daily mortality. A simple piece of code was written in python to solve equation (3.12) at some specific values of its parameters. All the results were obtained by assuming that  $\beta$  is 0.5, the pupal duration is 27 days, the time to first ovulation is 7 days and the inter-larval period is 9 days. Figure (3.1) displays the results of the relationship between extinction probability and adult daily mortality ( $\psi$ ). These results were obtained by looking at different values of female pupal daily mortality ( $\chi$ ). From the upper graph, we can see that the extinction probability increases with any increase in adult mortality. Thus, the lower the adult mortality, the lower the chances of extinction occurring and vice versa. From the figure, we can still note that if the pupal mortality is high, then extinction is certain even if the adult mortality is low. For example if  $\chi=3\%$  and  $\psi=1\%$ , then we have a greater than 40% chance that extinction will happen.

The lower graph of figure (3.1) displays the results of the relationship between the extinction probability and adult female mortality for different initial female populations. From the graph, we can ascertain that, the adult female mortality increases with increase in the probability of extinction. When the mortality goes beyond 3%, the probability remains constant and is equal 1. All these results are based on the assumption that all female tsetse flies are inseminated by fertile males, that is  $\epsilon=1$ .

### 3.4.2 The relationship between extinction probabilities and the probability of insemination

Figure (3.2) shows the relationship between extinction probability and the probability that a female is inseminated. In this case we are looking at the extinction probability as a function of  $\epsilon$  (the probability that a female tsetse fly is inseminated by a fertile male). We are also looking at a situation when  $\epsilon$  is less than 1. We can assume that some females die without being inseminated or a group of sterile males are released to fertilise virgin females. The upper and lower graphs



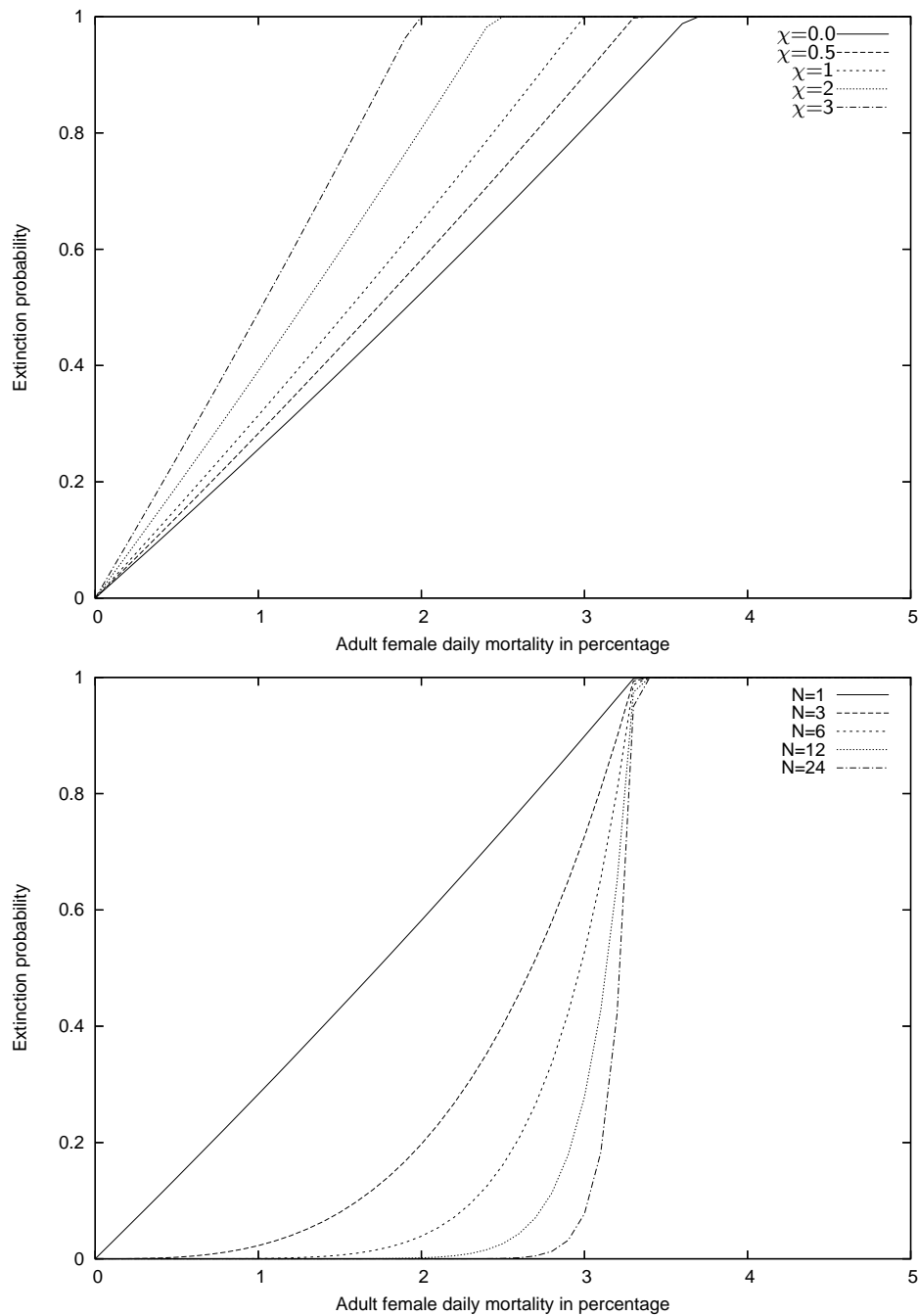


Figure 3.1: Upper graph: A graph of extinction probability against adult mortality for different values of pupal mortality. Lower graph: A graph of extinction probability against adult mortality for different values of initial population at constant pupal mortality ( $\chi = 0.5\%$ ).

show that extinction probabilities reduce with an increase in  $\epsilon$ , adult mortality and the number of the initial female population.

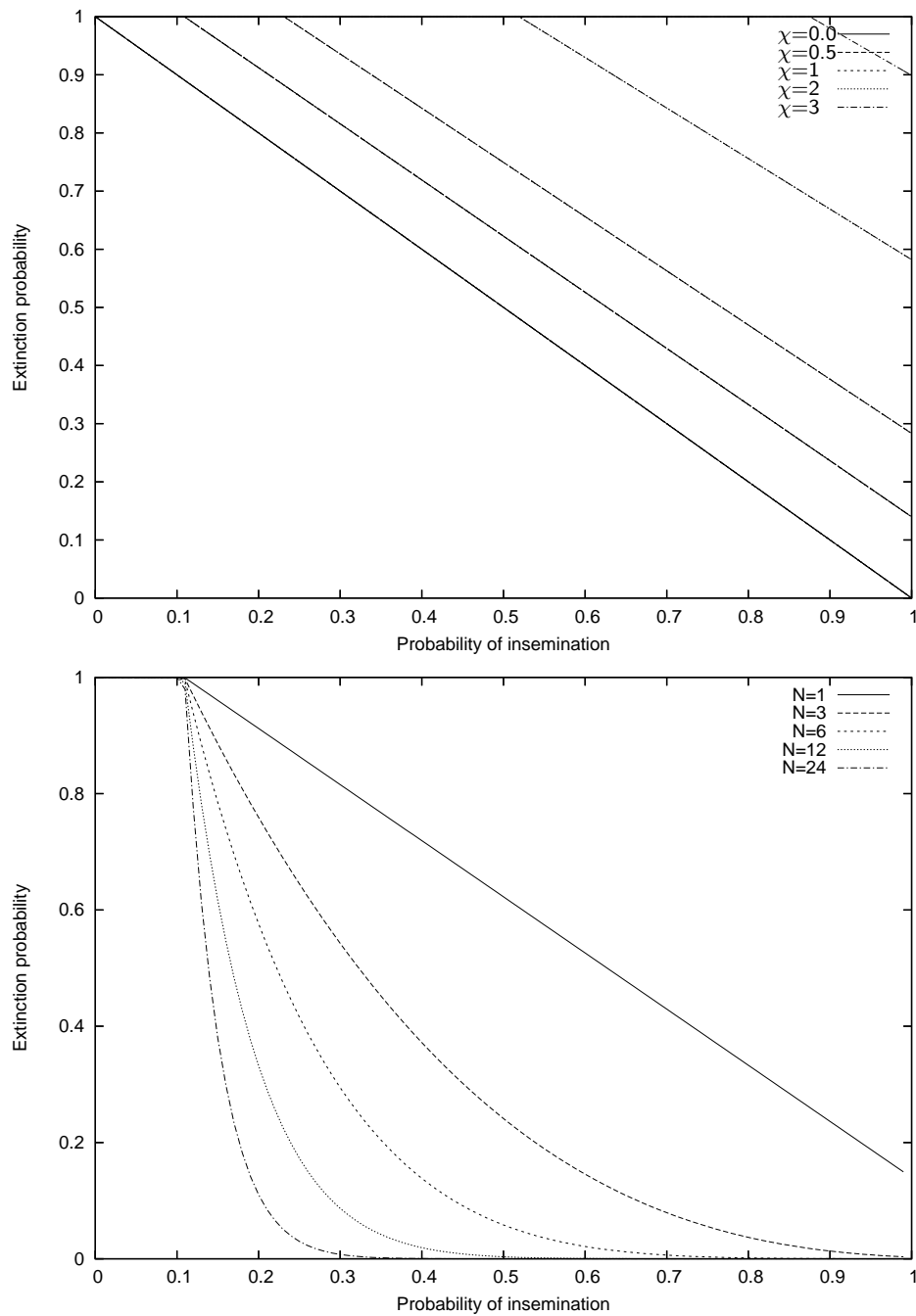


Figure 3.2: Upper graph: A graph of extinction probability against the probability of insemination for different values of adult mortality at constant pupal mortality ( $\chi = 0.5\%$ ). Lower graph: A graph of extinction probability against the probability of insemination for different values of initial female population;  $\psi = \chi = 0.5\%$ .

### 3.4.3 The mean and variance of the population growth

In order to estimate the size of the female population at any given generation, we need to look at the expected number of females and the variance. Equations (2.5) and (2.6) were solved using

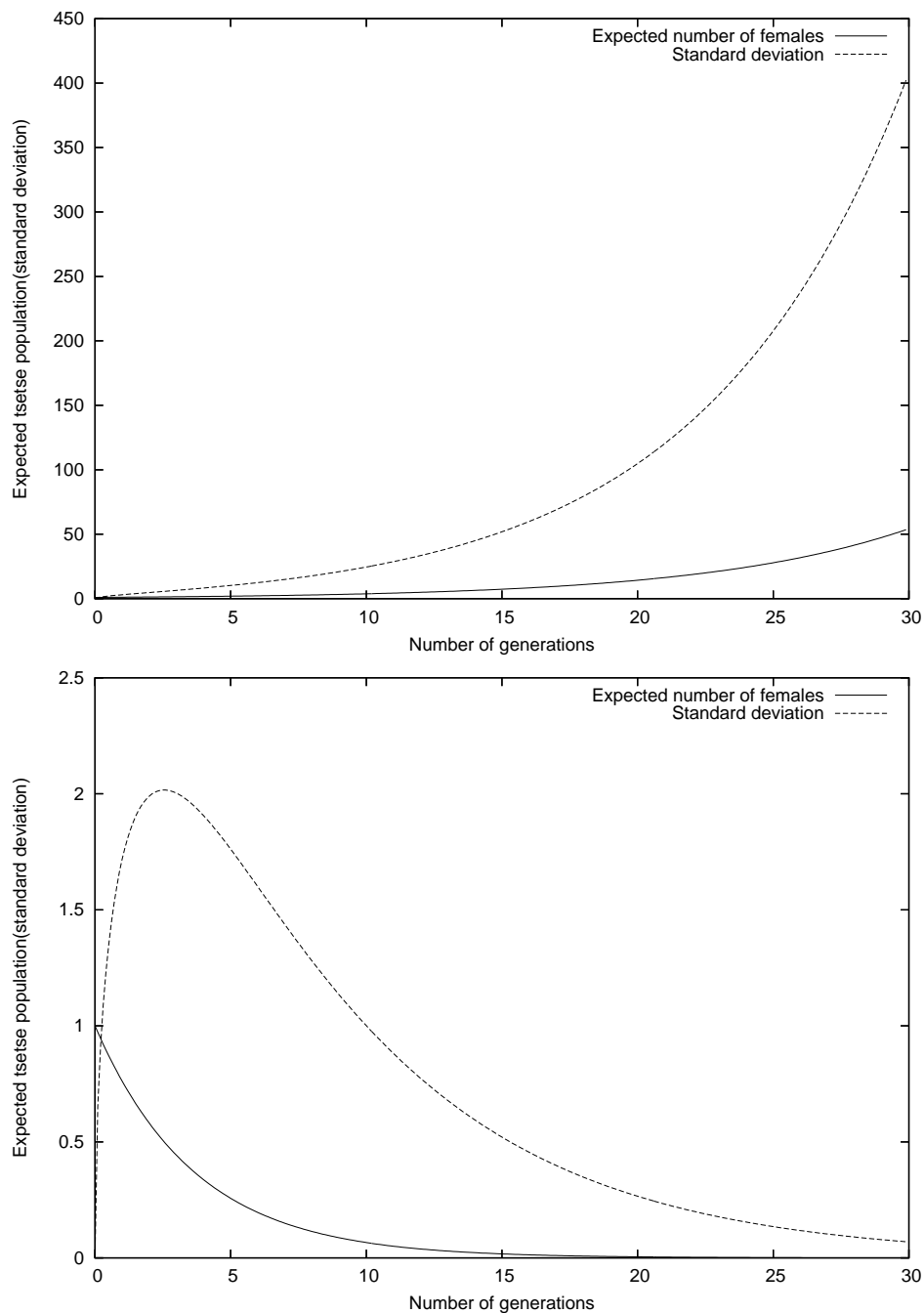


Figure 3.3: Upper graph: A graph of mean (standard deviation) against the number of generations;  $\psi=3\%$ ,  $\chi=0.5\%$ . Lower graph: A graph of mean (standard deviation) against the number of generations;  $\psi=4\%$ ,  $\chi=0.5\%$ .

python and figure (3.3) was obtained. Both graphs of figure (3.3) show the expected female population (standard deviation) against the number of generations. The results from the graphs show that, for low values of adult mortality, both the mean and standard deviation increase with increase in the number of generations if the pupal mortality is kept at 0.5%. So longer as  $\psi < 4\%$ ,

then we expect the mean and the standard deviation to grow, with the latter growing at a faster rate. When  $\psi > 4\%$ , still with the pupal mortality maintained at 0.5%, both the mean and the standard deviation reduce with any increase in the number of generations, with the latter reducing at a slower rate. Generally, in all the cases, the standard deviation is always above the mean.

### 3.4.4 Expected number of generations to extinction

We derived the general equation for the expected number of generations for  $N$  surviving females in (3.18). Equations (3.16) and (3.17) give the first two iterations of the probability of extinction. A simple piece of code was written in python to increase the number of iterations and solve equation (3.18) in order to find the expected number of generations to extinction. The upper graph of figure (3.4) shows that the expected number of generations to extinction decreases with any increase in pupal mortality. The lower graph of figure (3.4) gives the result of the expected number of generations to extinction against the probability of insemination. From the graph, we can see that the higher the probability of insemination, the greater the number of generations one would expect to result before the population becomes extinct.

The comparison between the expected number of generations to extinction and adult female mortality is given in figure (3.5). From the two graphs it is clear that the expected number of generations to extinction decreases with any increase in the adult female mortality. The decrease becomes slow when the probability of insemination is increased.

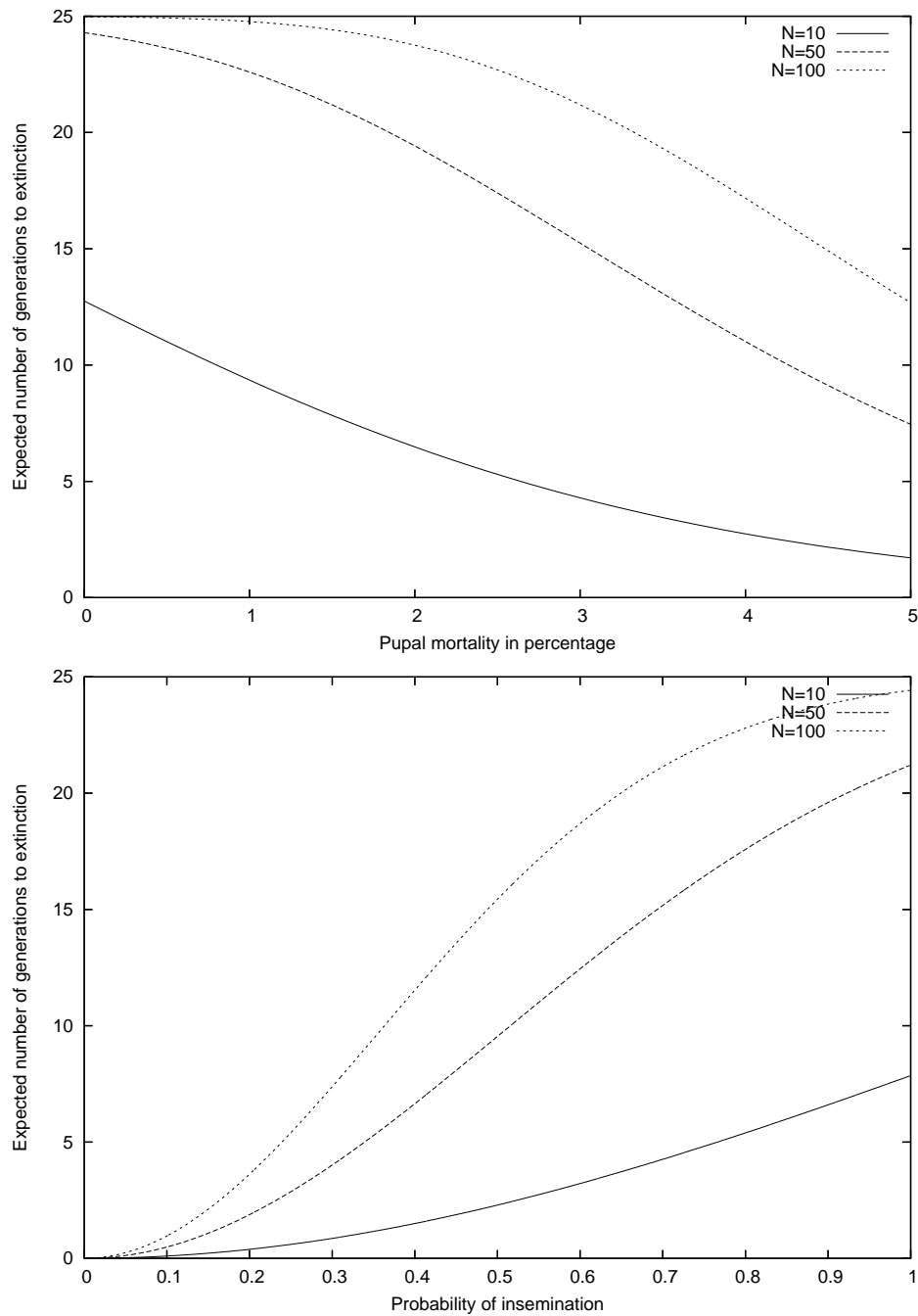


Figure 3.4: Upper graph: A graph of expected number of generations to extinction against pupal mortality in percentage;  $\psi=7\%$ ,  $\epsilon=1$ . Lower graph: A graph of expected number of generations to extinction against the probability of insemination;  $\chi=0.5\%$ ,  $\psi=8\%$ .

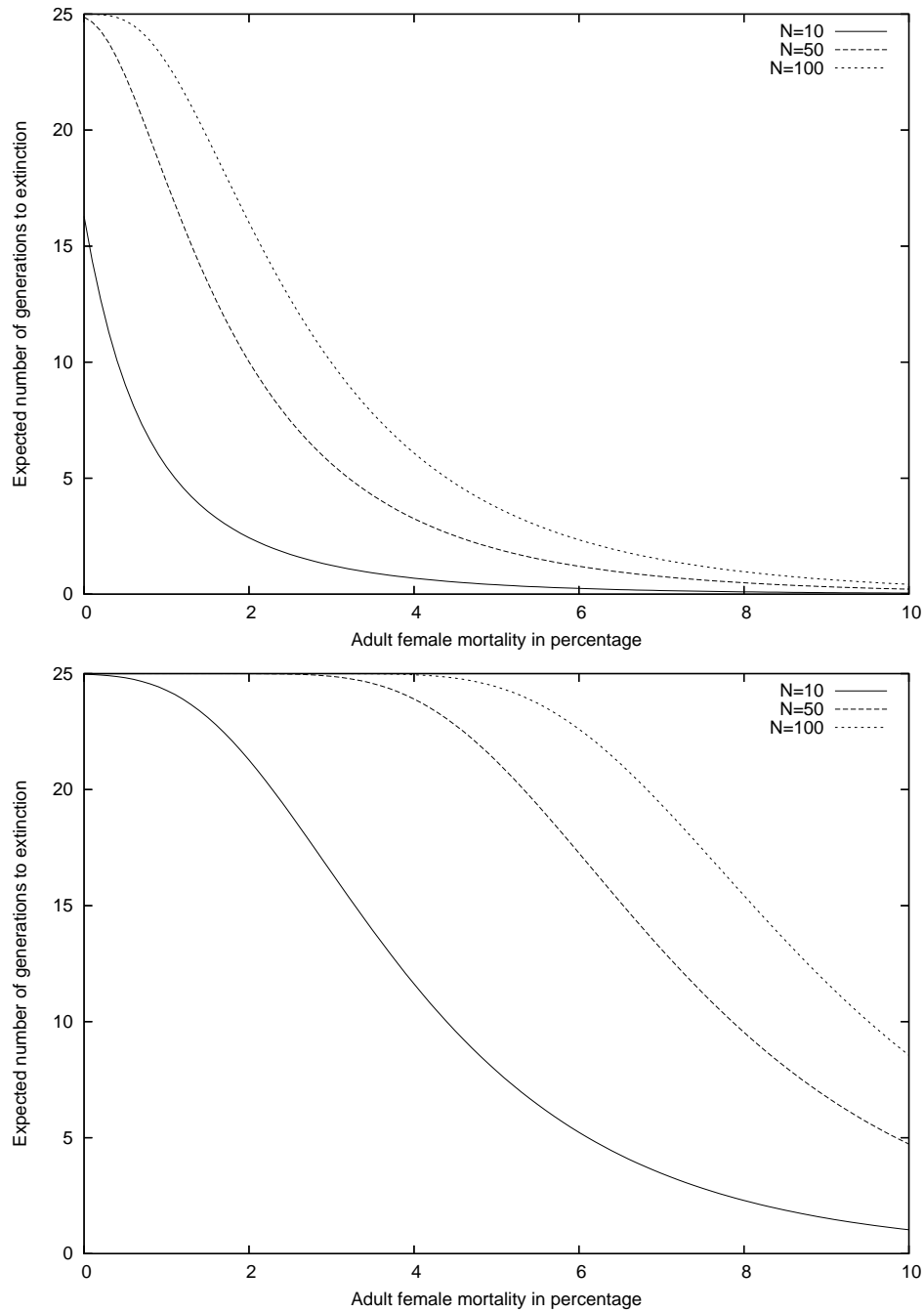


Figure 3.5: Upper graph: A graph of expected number of generations to extinction against adult female daily mortality;  $\epsilon=0.1$ ,  $\chi=0.5\%$ . Lower graph: Same graph as the upper graph but this case  $\epsilon=0.5$ .

## 4. Conclusion and future work

In this project, we presented a stochastic model which can be used to estimate the population number of tsetse flies and to describe their generations. We used the model to estimate each of the following dynamic variables:

1. expected number of generations and variance
2. expected tsetse population and variance
3. extinction probability
4. time to extinction by generation.

This model was based on the theory of discrete-time branching processes, which were presented in detail in chapter 2.

The major outcome of this project was presented in chapter 3, where the model is applied to pest eradication in the specific case of tsetse flies. The results obtained from the application show that it is not possible to eradicate all the tsetse flies without applying any control method. This could be done by using control methods such as sterile insemination technique (SIT) and insect-treated cattle or traps and targets to reduce the probability of insemination and adult female daily mortality respectively.

The fact that a tsetse fly produces one offspring at a time made the model both simple to construct and manageable. A possible future perspective would be to extend the model so that it can be used to describe the generations of species such as mosquitoes. These pests produce more than one offspring at a time, introducing a further level of complexity into our model. Given the time available for this essay however, this type of problem is left an open question.

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