Modelling the effects of temperature change on the dynamics of tsetse flies and trypanosomiasis disease transmission

by

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Thesis presented in partial fulfilment of the requirements for the degree of Master of Science in Mathematics in the Faculty of Science at Stellenbosch University

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Abstract

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Global temperatures have increased over recent decades. This is expected to have an impact on vector-borne diseases, raising questions such as: Will the increased temperature result in changing disease prevalence? How will vector populations be affected in terms of their density and distribution? It has been suggested that African trypanosomiasis, a zoonotic disease transmitted by tsetse flies, will exhibit increased incidence, and expand its geographical range, due to increasing temperatures. This project uses mathematical modelling to assess the impact of temperature change on tsetse fly population dynamics. Understanding these impacts could help us understand how trypanosomiasis transmission dynamics will be affected by global warming. We develop a temperature-dependent ordinary differential equations (ODE) model to model the growth in the numbers of pupal and adult tsetse. We fit the model to data on the number of tsetse flies (*Glossina pallidipes* Austen) on Antelope Island, Zimbabwe, between 5 February 1980 and 29 December 1981, estimated using mark recapture. The findings from this project concur with previous studies suggesting that temperature is the most important

factor determining the growth of tsetse populations. There appears, however, to be another factor, cycling annually, approximately in phase with the Normalised Difference Vegetation Index (NDVI), which also influences the survival of adult flies. Our findings show that minor changes in temperature have a big impact on tsetse population growth rates. In conclusion, our model suggests that high temperatures could give rise, at least, to local extinctions of tsetse populations.

Opsomming

Modellering van die effek van temperatuur verandering op die bevolkingsdinamika van tsetse vlieë en die oordrag van trypanosomiasis

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Temperature het wêreldwyd oor die afgelope dekades toegeneem. Dit sal na verwagting 'n impak op vektor-oordraagbare siektes hê, wat tot vrae lei soos: Sal die verhoogde temperature verandering in die voorkoms van siektes tot gevolg bring? Hoe sal vektorbevolkings geraak word in terme van hul digtheid en verspreiding? Daar is voorgestel dat die voorkoms van Afrika-trypanosomiasis, 'n zoönotiese siekte wat deur tsetsevlieë oorgedra word, sal toeneem en die geografiese omvang daarvan sal uitbrei as gevolg van toenemende temperature. Hierdie projek gebruik wiskundige modellering om die impak van temperatuurverandering op tsetsevlieg-bevolkingsdinamika te bepaal. Deur hierdie verband te verstaan, kan ons help om te beskryf hoe die oordrag-dinamika van trypanosomiasis deur globale verwarming beïnvloed sal word. Ons ontwikkel 'n temperatuurafhanklike gewone differensiaalvergelyking (ODE) model om die groei in die aantal pupale en volwasse tsetsevlieë te modelleer. Ons gebruik data van aantal tsetsevlieë om die model te pas. Hierdie data, van die spesie *Glossina pallidipes* Austen, is versamel op Antelope-eiland, Zimbabwe, tussen 5 Februarie 1980 en 29 Desember 1981,

deur gebruik te maak van die "mark recapture" metode. Die bevindinge van hierdie projek stem ooreen met vorige studies wat daarop dui dat temperatuur die belangrikste faktor is in die toename in tsetse populasies. Daar blyk egter nog ’n jaarlikse sikliese faktor te wees, ongeveer in fase met die genormaliseerde verskil in plantegroei indeks (NDVI), wat ook die oorlewing van volwasse vlieë beïnvloed. Ons bevindinge toon dat geringe temperatuurveranderinge ’n groot impak het op tsetse-bevolkingsgroeikoerse. Ten slotte stel ons model voor dat hoë temperature ten minste tot plaaslike uitwissings van tsetsebevolkings kan lei.

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Dedications

This work is dedicated to my mother S.T. Ngomane, my two sisters L.N. & B.P. Mthombothi and my niece S.M. Mawela.

Contents

List of Figures

List of Tables

Chapter 1

Introduction

1.1 Introduction

Recently there has been a growing interest in the effects of global warming on vector-borne diseases. Average global temperatures have increased by 0.7 °C during the past decade (IPCC, 2007) and are expected to increase by 1.5 °C to 6.0 °C by the year 2100 (Patz and Reisen, 2001). Researchers have identified that infectious vector-borne diseases are generally sensitive to climatic conditions; the survival and life cycle of insect vectors are driven by temperature, humidity and (sometimes) surface water (McMichael, 2003). Vector-borne disease transmission relies on the vector being present and being capable of transmitting the disease, and also on the presence of the relevant parasite (Martens *et al.*, 1995). Climate change must be in favour of the vector and parasite for the disease to persist, otherwise the disease will die out (Patz *et al.*, 1996). Change in climatic conditions is not the only factor determining the global emergence, resurgence, and redistribution of infectious disease: it is multi-factorial problem. One needs to focus not only on temperature change, but must also consider changes in land use, local biogeography, population migration, immunological history and control measures (Epstein, 1998).

Global warming will likely affect incidence, transmission dynamics and geographical distribution of the vector or host populations (Patz *et al.*, 2000; Patz and Reisen, 2001). Vector-borne pathogens may also be altered, which may lead to new strains of the vector-borne diseases. Change in geographical distribution may not be possible for hosts and vectors which are restricted to certain habitat types (Mills *et al.*, 2010). Change in vector density and geographic range could shift seasonal occurrence and result in the

vector spreading to more suitable areas (Khasnis and Nettleman, 2005). Vector migration is expected to happen at different rates depending on the vectors' dispersal capabilities, and climatic, and other environmental conditions. The newly occupied environment may lead to increases in population densities if the new area has less severe competition, and the environmental conditions are more favourable, or it may lead to decreased densities if new competitors threaten the survival of the vector (Mills *et al.*, 2010).

African trypanosomiasis is one of the vector-borne zoonotic diseases where increased incidence and expanded geographical range has been predicted, due to expected climate change (Moore *et al.*, 2012). Changes in temperature and precipitation directly impact the reproduction rate, development rate and longevity of tsetse (Martens *et al.*, 1995). Change in geographic distribution of vectors or hosts may bring these vectors or hosts in to contact with new human population (Mills *et al.*, 2010). Climate change may result in increasing or deceasing vector and / or host population densities. Increasing vector or host populations may potentially result in increased contact frequency and increased prevalence of infection (Mills *et al.*, 2010). Previous research established the importance of meteorological variables, particularly temperature, in determining the abundance and distribution of tsetse flies (Rogers, 1990; Rogers and Randolph, 1993). The distribution of tsetse flies in Zimbabwe was found to be sensitive to minor changes in environmental conditions. The difference in temperature between areas where tsetse flies were present and absent was 3.0 °C (Rogers and Randolph, 1993). To understand the transmission dynamics of trypanosomiasis and the impact of global warming on the disease transmission, it is essential to have a deeper understanding of tsetse fly population dynamics and how they are likely to change with increasing temperatures. Attempts have been made to investigate the relationship between tsetse fly populations and climate change (Hargrove, 2001; van der Linden, 1984). However, most of these studies did not use dynamic models to model the tsetse populations and did not incorporate seasonal temperature into their models. Existing literature on tsetse fly biology and population dynamics is reviewed in Chapter 2.

1.2 Reason for study

1.2.1 Motivation

This project is motivated by the growing interest in the effects of global warming on vector-borne diseases. We will validate our model using data from a mark-release-recapture study performed on Antelope Island, Zimbabwe by Vale *et al.* (1986). Refer

to Chapter 4, section 4.2 for the summary of the study, and for a full description refer to Vale *et al.* (1986).

1.2.2 Research question

How will climate change affect tsetse fly population dynamics and the transmission dynamics of African trypanosomiasis?

1.2.3 Problem statement

Global warming is predicted to increase disease incidence for trypanosomiasis and possibly widen geographic ranges for the vector population. It is essential to understand the dynamics of tsetse flies populations and the effect of temperature change, as this can assist in designing control programmes to eliminate tsetse flies and trypanosomiasis in different areas. Modelling the population estimates obtained for *G. pallidipes* from the Antelope Island study will help us understand how temperature change affects this species. We can use these results to project how temperature changes will affect the transmission dynamics of trypanosomiasis and use these results to inform policy.

1.2.4 Aim

The aim of this project is to investigate, using mathematical modelling, the impact of climate change on the dynamics of tsetse fly populations and how this impacts the transmission dynamics of trypanosomiasis.

1.2.5 Objectives

1. Develop mathematical model(s) to study the dynamics of tsetse flies living under constant climatic conditions (temperature, humidity etc.)
2. Extend the mathematical models to explore the impact of pupal density-dependent mortality on the population dynamics of tsetse flies
3. Extend the mathematical model(s) for real-life situations where temperatures change and where fly mortality is a function of temperature:
    a. fit the model outputs to the Antelope Island data
    b. and then use these models to project the impact of temperature change on tsetse fly population growth rates and distribution

4. Incorporate the proposed model(s) into existing vector-borne SIR models to investigate the impact of temperature change on the transmission dynamics of trypanosomiasis.

1.3 Thesis outline

This thesis is divided into six main sections. Chapter 2 reviews existing literature on tsetse flies: we begin with the tsetse life cycle, then review studies that investigated the effects of temperature on tsetse fly reproduction and mortality rates. To understand tsetse population dynamics better we look at their preferred hosts and investigate different control measures used to eliminate or control tsetse populations. Finally, we look at tsetse as a vector of sleeping sickness (Human African Trypanosomiasis, HAT) and the burden of HAT on the affected populations. In Chapter 3 we introduce the ODE model and state the model assumptions and model equations. We then define the different parameters that we will use in the temperature-dependent ODE model which will be introduced in Chapter 4. Pupal and adult mortality functions consist of unknown parameters. Using the temperature-dependent ODE model we fit the model output to the data and estimate values of the parameter which produce the best fit for the data. In addition to temperature, we included two extra factors in our model (specifically affecting the adult mortality rates): (i) an unknown factor with an annual cycle, which is out of phase with temperature and (ii) pupal density-dependent mortality. To investigate the effect of each of these factors, plus the effect of temperature, we create different model scenarios which are shown in Chapter 5. We also project how the population will behave in the next 10 years using recorded temperatures from 1980 to 1990. Our results are discussed in Chapter 6. Finally, we conclude and give recommendations in Chapter 7.

Chapter 2

Literature Review

2.1 Background of tsetse flies

Tsetse flies (genus *Glossina*) are blood-sucking insects found in about ten million square kilometres in sub-Saharan Africa, in about 36 countries (Leak, 1999). Their presence in an area is determined by factors such as climate, suitable vegetation, and host availability. Climate and soil type determine the type of vegetation; although tsetse feed only on blood, vegetation is an important factor as it provides suitable shelter for the tsetse species and also provides food for most of the hosts that tsetse feed on. Different tsetse species prefer different vegetation types. Temperatures below 17 °C and above 35 °C are not ideal for tsetse survival (Leak, 1999). Both sexes feed exclusively on blood, which provides both the nutrition and water content required for their survival (Hargrove, 2004).

Unlike most biting insects, a female tsetse needs only to mate once in her lifetime and produces only one larva at a time. The larva spends most of the time in the adult female fly's uterus, which is different to most biting flies that lay their eggs in a moist environment where the larvae obtain their nutrients and energy as they develop into adults (Hargrove, 2004). As a result, tsetse flies have a lower reproduction rate than almost all other insects (Leak, 1999). Tsetse flies generally mate near or on host animals. The mating process usually takes about an hour or two. The male settles at the back of the female and transfers sperm to the uterus of the female. The sperm is stored in the spermatophore which is formed during copulation (Leak, 1999). After mating it takes a few hours for the sperm to move to the spermathecae where it will be utilised by the adult female for the rest of her reproductive life (Leak, 1999; Pollock, 1982).

2.1.1 Life cycle

The tsetse life cycle has four major stages: egg, larva, pupa and adult. The female tsetse ovulates after insemination. The egg moves into the uterus where it is fertilised by the sperm stored in the spermatheca and it hatches after 3-4 days and produces a larva (Leak, 1999).

The larval stage consists of three instars (L1, L2 and L3). The larva is nourished via the uterine gland with milk, rich in fat and protein, produced from the bloodmeal (Pollock, 1982).

After the L3 stage, the female deposits the fully grown larva on the ground, generally on loose sandy soil (Hargrove, 2004; Pollock, 1982) or under an overhanging rock or branch (Pollock, 1982) to protect the pupa from predation and harsh weather conditions. A new egg ovulates immediately after the larva is deposited and the subsequent larvae are produced every seven to twelve days thereafter (Hargrove, 2004; Pollock, 1982). The larva usually weighs as much or more than the female which was carrying it (Hargrove, 2004). As soon as the larva is deposited it burrows into the ground and within an hour or two it develops into a pupa, forming a hard dark shell to form the puparium. The pupa does not feed: instead it utilises the reserved proteins and fat accumulated during larval development (Hargrove, 2004; Pollock, 1982).

The puparial period lasts at least three weeks depending on the ambient temperature (Hargrove, 2004; Pollock, 1982). Half of the tsetse population is represented by pupae (Leak, 1999). The organs of the adult fly begin to form and the fat and proteins reserves built up during the larval period are used up. After the pupal period, the adult fly emerges with a soft body and small crumpled wings. It was observed from female *G. pallidipes* that large amounts of fat and protein are transferred to the larva while it is in the uterus, leaving the female tsetse with low fat after the pregnancy (Hargrove, 1999). Consequently, the female tsetse then needs urgently to find a bloodmeal, in order to avoid starvation. Factors such as the mother not obtaining sufficient blood meals or coming in contact with insecticides, can likely result in the mother aborting the egg or the larva (Pollock, 1982).

2.1.2 Effects of climate on reproduction rates

The distribution of the flies across Africa is strongly influenced by climate. The rates at which all metabolic processes occur in tsetse flies are all dependent on temperature.

Interlarval period, pupal period, adult lifespan and the period between successive feeds are all shortened with increasing temperature (Hargrove, 2004; Rogers, 1990). Temperature plays a vital role in the survival of tsetse: not only does it affect the different developmental periods but it also plays a huge role in the fly's flight activity (Phelps and Lovemore, 1994).

Adult female tsetse ovulate for the first time at the age of about eight days and every eight to twelve days thereafter (Hargrove, 2004; Leak, 1999). The pupal period is between 20 and 90 days (Phelps and Burrows, 1969*b*). Both these periods are mainly dependent on temperature but also on the sex of the fly, tsetse species, and location (Hargrove, 2004; Leak, 1999). At 25 °C the pregnancy lasts for nine days (Hargrove, 2004). At 30 °C the pupal period is about 20 days and at 16 °C it is about 100 days. Females emerge about two to five days earlier than males depending on temperature (Phelps and Lovemore, 1994). At a fixed temperature of 25 °C females emerge after 27 days whilst males emerge after 30 days. Females emerge after 100 days and males after 105 days at a fixed temperature of 16 °C (Phelps and Burrows, 1969*b*). Temperatures above 32 °C and below 17 °C are problematic for tsetse populations. When temperatures are low below 17 °C tsetse sit in direct sunlight and when temperatures are high, above 32 °C tsetse are inactive and they seek artificial refuges, tsetse will seek shelter in cool shaded places (Vale, 1971). Leak (1999) found that for laboratory tsetse colonies the optimum temperature for reproduction is about 25 °C. Hargrove (2004) found it to be around 26 °C for an island population of tsetse, and laboratory studies performed by van der Linden (1984) found the optimum temperature of 25 °C for *G. pallidipes*.

The amount of fat reserve is proportional to size: smaller flies therefore have less fat than larger flies. This explains why low temperatures, below 16 °C, are not suitable for the development of smaller tsetse fies as the fat reserved during the larval period gets exhausted before the pupa is fully matured (Bursell, 1960). High temperatures, above 40 °C are fatal to both small and large flies and pupae (Phelps and Burrows, 1969*a*). Phelps and Clarke (1974) observed that extreme temperatures result in higher mortality in young flies, particularly in small male flies. The fly needs enough fat to complete development from pupa to adult and to survive long enough to obtain its first bloodmeal (Bursell, 1960).

Temperature is not the only factor that has been associated with tsetse survival; measures of dryness such as saturation deficit and humidity are among other factors that are usually considered. Hargrove (2001) found that survival of adult *G. m. morsitans*

was dependent only on temperature; whilst for *G. pallidipes* the author observed that the temperature and saturation deficit are equally important factors for the survival of the adult flies. (Rogers, 1990) also found a relationship between monthly changes in saturation deficit and density-independent mortality for *G. pallidipes*. *G. pallidipes* lose water faster than *G. m. morsitans* (Bursell, 1959): this may be due to the fact that *G. pallidipes* are more active than *G. m. moristans* in the field (Hargrove, 1991). High temperatures, high saturation deficit and frequent flight activity increase water loss (Bursell, 1959; Hargrove, 2001) which may explain why survival in the two species is affected by different factors.

2.1.3 Tsetse survival and mortality rates

The rates of larval production and development determine the reproduction rate and both will be determined by climatic variation and the availability of hosts for tsetse to feed on. Most insects produce more than one offspring at a time, they lay eggs in moist environment where the egg will develop into an adult (Hargrove, 2004). By contrast, female tsetse produces one larva at a time, the egg hatches in the uterus and the larva is retained in the uterus until it develops into an L3 instar. This reproductive method is known as adenotrophic viviparity. The larva is fed whilst in the uterus: once deposited it utilises the nutrients accumulated whilst in the uterus for development purposes until it is ready to emerge as a young adult (Hargrove, 2004; Leak, 1999; Pollock, 1982). Accordingly, tsetse have a low birth rate compared to other insects (Hargrove *et al.*, 1995; Leak, 1999), and the only way for tsetse species to survive is to maintain a low mortality rate. The larva spends most of its time in the uterus and as soon as it is deposited it burrows into the ground: this makes the immature stages less susceptible to predation. Both larval and pupal stages carry small risks compared to other insects, resulting in smaller losses than in most other insects. Previous studies such as the ones carried out by Turner and Snow (1984) and Hargrove (1999) supports that in utero losses, mostly due to abortion, are minimal within the tsetse populations. Ovarian dissection of *G. pallidipes* indicated reproductive losses of one or two percent which was mainly due to abortion (Turner and Snow, 1984). In Zimbabwe at Rekomitjie Research Station less than one percent loss due to abortion were observed in *G. pallidipes* Austen and *G. m. moristans* Westwood (Hargrove, 1999). It was suggested, however, that abortion rates are higher than average during hot-dry seasons (Hargrove, 1999).

Obtaining bloodmeals involves flight activity: then on the fly identifying its host and feeding on it (Hargrove, 2004). Flight activity involves an order of magnitude increase

in the rate of energy consumption and feeding carries its own risks (Bursell *et al.*, 1974). Tsetse generally feed at intervals of two to five days as estimated by mark-recapture studies (Rogers, 1977; Rogers and Randolph, 1986). The life of a female tsetse is a cycle of obtaining a bloodmeal, finding a secure shelter to convert the bloodmeal into a larva, depositing the larva and flying to search for next bloodmeal then repeating the whole process (Hargrove, 2004). Females have to find an optimal balance between obtaining sufficient blood for production of larvae whilst using minimum energy and avoiding dangerous feeding scenarios. By contrast, the routine for male tsetse consists entirely of feeding, and mating with as many female virgins as possible under the least dangerous conditions (Hargrove, 2004; Leak, 1999).

For a tsetse population to grow, each female must produce more than one surviving daughter (Phelps and Lovemore, 1994). That is, the female must live for more than 25 days (Hargrove, 1988). For a populaton to be stable, even if pupal losses are zero-daily mortality of the females must be less than four percent (Hargrove, 1988). Despite the fact that male and female tsetse flies emerge in equal numbers, tsetse populations generally consist of more female flies than male flies (Hargrove, 2004; Leak, 1999; Phelps and Lovemore, 1994). On average 70-80 % of the population represents females (Leak, 1999). Under laboratory conditions, one male fly can copulate with up to 15 female flies and one female fly can produce at least 10 offsprings. In the wild, however, female flies are likely to produce fewer offspring (Leak, 1999). Female tsetse generally survive longer than males. Under laboratory conditions females generally have a lifespan of up to about eight to twelve weeks, whilst male flies survive for about four to six weeks (Jackson, 1949; Leak, 1999). In the wild, tsetse have a shorter lifespan: on average females survive for 20-40 days, whilst males survive for an average of 14-21 days Glasgow (1963), though this varies from place to place influenced by temperature and environmental factors (Phelps and Lovemore, 1994). Relatively small changes in the survival probabilities of female flies have significant effect on population levels (Hargrove and Williams, 1998).

High temperatures require increased metabolic rates, which in turn requires more frequent feeding (Hargrove and Coates, 1990). Females can either feed more frequently and/or reduce body temperature by limiting flight activity, to ensure they produce larvae of a viable size (Hargrove, 2004). High temperatures reduce the energy required to process the bloodmeal and the duration required for blood meal digestion (McCue *et al.*, 2016).

Teneral flies are at risk of starvation given their low-fat levels and incompletely developed flight muscle. Consequently, many young teneral flies die due to starvation or attempting to feed in high-risk situations (Hargrove, 1975*a*). Teneral flies generally have higher mortality rates after emergence but the mortality rates decrease after flies take their first blood meal (Hargrove *et al.*, 2011). Ovarian dissection at Rekomitjie Research Station showed that during the hot-dry seasons female teneral *G. pallidipes* experienced severe mortality (Hargrove, 1999). Smaller flies have relatively lower fat levels at emergence as compared to larger flies (Phelps, 1973). The high losses experienced by teneral flies during the hottest seasons can be attributed to small pupal sizes which produce flies with low-fat levels at emergence (Phelps and Clarke, 1974). Smaller flies also have limited mobility and hence are ineffective in locating hosts (Vale *et al.*, 2014). Low temperatures usually have the same effect (Phelps and Clarke, 1974). Extremely high or extremely low temperatures are observed to result in increased mortality in small young flies (Phelps and Clarke, 1974).

Mortality can be indirectly measured by physical factors (size or weight). Flies that have low-fat levels are likely to produce smaller puparia, smaller puparia develop into smaller adults which are more likely to die of starvation since they have low levels of fat and they have poorly developed flight muscle. Flies with low fat levels are also more likely to feed at high-risk situations with high chances of feeding mortality, whilst nourished flies tend to avoid high-risk feeding situations. For example feeding on humans is relatively high-risk for tsetse (Vale, 1974). It was observed that *G.m.morsitans* males that fed on humans had 50% less fat than the ones that fed on an ox (Vale, 1974). Larger flies are less likely to die from starvation as compared to smaller flies because larger flies have bigger reserves of fat (Phelps and Clarke, 1974).

2.1.4 Host preference

The availability of different hosts strongly influences the distribution and abundance of tsetse fly species (Robertson, 1983). Tsetse flies use vision and odour detection to locate their preferred hosts (Gibson and Torr, 1999; Torr and Solano, 2010; Vale, 1974). Shape, colour, movement, shade and light are important factors for visual location (Buxton, 1955). Odour is of great importance when locating hosts from greater distances (Vale, 1982*b*). Tsetse could either search for hosts to feed on or wait for the hosts to pass by (Vale, 1980): the choice is highly determined by the number of days that have passed since the tsetse's last bloodmeal and the ambient temperature (Hargrove and Williams, 1995). Mature tsetse and recently fed tsetse are less likely to feed compared to newly

emerged flies and flies that haven't fed in days (Vale, 1974). Previous studies deduced that, in general, savannah tsetse (i.e. *G. pallidipes*, *G. m. morsitans*) prefer to feed on the following wild animals: warthog, bushpig, kudu and bushbuck; and on the following domestic animals: cattle and donkeys (Robertson, 1983). Tsetse will occasionally feed on less preferred hosts if favoured hosts are unavailable (Phelps and Lovemore, 1994). The defensive behaviour of the hosts poses a risk to feeding tsetse (Randolph *et al.*, 1992). The host's mass and defensive behaviour play a huge role when tsetse select its hosts. Tsetse prefer big and less defensive hosts (Hargrove *et al.*, 1995; Vale, 1977). Savannah tsetse find human odour and visual effect repellent, hence only the young tsetse with very low fat reserves attempt to feed on humans (Hargrove, 1976; Vale, 1974).

2.1.5 Control measures of tsetse flies

Over the years different tsetse control methods have been used. The first tsetse elimination technique to be implemented was the removal of tsetse's food source which was thought to be all wild animals. The hunting experiment was successful in eliminating tsetse flies in parts of Zimbabwe and Zululand but not as successful in Zambia and Botswana (Phelps and Lovemore, 1994). Observations and experiments later showed that it was not necessary to eliminate all wild animals but only those that tsetse preferred to feed on. This observations gave rise to the Nagupande experiment in Zimbabwe, in the 1960s, where the was selective shooting of mammals that were tsetse's preferred hosts (Cockbill, 1967). The tsetse population decreased when the shooting started (Lord *et al.*, 2017). The hunting experiment was stopped due to the introduction of insecticides, insecticide-treated cattle, insecticide applied to traps and targets, and aerial and ground spraying.

The growth of human population has resulted in unplanned control of tsetse, particularly in Southern Africa. As the human population grows the area of unoccupied land decreases, which in turn means less habitat for tsetse and it also leads to increased farming and hunting activities which reduces food supply for the tsetse. Modifying vegetation by fire or clearing woodlands to produce grasslands is another tsetse control technique that has been used before but came to a stop due to high costs and its long-term effect on the environment (Phelps and Lovemore, 1994).

Insecticides can be applied either by ground spraying or aerial spraying as means of eliminating tsetse flies. The effectiveness of the use of insecticides requires knowledge of tsetse's resting habitat. These methods require careful environmental monitoring

(Phelps and Lovemore, 1994). Aerial spraying was used first in Zululand against tsetse: tsetse habitats were sprayed from a low flying aircraft. The spraying was done in the early mornings and late afternoon (du Toit, 1954). Ground spraying involved identifying vegetation types and locations that tsetse preferred to shelter in during the hot-dry season. These habitats were sprayed with insecticides and tsetse died when they rested in these habitats. The spraying of insecticides was done during the cool-dry season, just before the beginning of the hot-dry season. Insecticides were found to be harmful to the environment, and some animals, when applied directly to the environment either by aerial or ground spraying (Phelps and Lovemore, 1994). Applying insecticides to targets or baits, did not raise any environmental concerns and it was more effective (Phelps and Lovemore, 1994). As a consequence, the use of insecticide such as DDT have been replaced with odour-baited and insecticide-treated targets and traps (Phelps and Lovemore, 1994).

In 1930 the use of traps was introduced in Zululand as a way to control tsetse, which led to the death of many *G. pallidipes* but did not eliminate them (Harris, 1930). Attempts were made to improve the traps, and to make them more attractive to the tsetse flies (Vale, 1982*a*). Studies carried out in West Africa found that tsetse are attracted to the colour blue, the inclusion of a blue cloth in their traps increased the effectiveness of the traps for catching *palpalis* group tsetse (Phelps and Lovemore, 1994). Torr *et al.* (1995) and Green and Flint (1986) found that *G. m. morsitans* and *G. pallidipes* are attracted to royal blue and black cloths and to the natural odour of ox (Vale, 1974), whilst studies in Zululand found that the royal blue colour was attractive to *G. austen* but not the black colour (Kappmeier, 1997). All tsetse species were found to be attracted to carbon dioxide, but using carbon dioxide with traps in the field as a way to attract tsetse is impractically expensive for anything other than research purposes (Phelps and Lovemore, 1994). The chemicals 3-n-propyl phenol, octenol and 4-methylphenol are used to attract tsetse to baits used in Zimbabwe for *G. m. morsitans* and *G. pallidipes* (Vale *et al.*, 1986, 1988). This bait was found to be ineffective against the *palpalis* group in West Africa (Späth, 1995). Studies have shown that not all tsetse species are attracted to the same odour or colour: identifying each species' preference and designing traps accordingly will make the use of traps as a tsetse control measure more effective (Torr, 1990; Torr *et al.*, 1995).

The use of insecticide-treated cattle (ITC) has been found to be an efficient, affordable and environmentally friendly method for controlling tsetse and trypanosomiasis. Cattle can either be dipped in the solution containing insecticides or the solution can be applied

to the cattle by the farmer (Thomson, 1987). Though this was one of the affordable methods it was still costly for many farmers (Kajunguri *et al.*, 2014). This method proved to be efficient, since the flies don't find the insecticide repellent. The fly cannot therefore differentiate between treated and untreated cattle and flies die following contact with treated cattle (Baylis *et al.*, 1994).

Other methods that were found to be environmentally friendly include the use of insect hormones that caused the female tsetse to produce larvae which will not form a puparia, or hormones that increase abortion rates and the use of sterilising chemicals to sterilise males often referred to as the sterile insect technique (SIT) (Phelps and Lovemore, 1994). Using SIT and insect hormones was found to be more effective if used together with traps. The success of SIT depends on the majority of female flies mating with sterile males instead of fertile male. The populations must consist at least ten times as many sterile as fertile males (Phelps and Lovemore, 1994), and the sterile male flies must inseminate at least 10% of the female flies and to ensure this happens, about 80% of the male flies must be sterile (Williams *et al.*, 1990). Female flies inseminated by a sterile male will not produce any offspring and will lead to the population dying out provided there is no immigration onto the treated area (Phelps and Lovemore, 1994).

2.1.6 Human African Trypanosomiasis

Human African Trypanosomiasis (HAT), also known as sleeping sickness, is a vector-borne disease transmitted by tsetse flies (*Glossina spp.*). HAT has two known forms of infection: *Trypanosoma brucei gambiense* (*T. b. gambiense*) which is responsible for about 97% of all reported HAT cases. *T. b. gambiense* causes a chronic infection, an infected person can survive for months or years without showing any symptoms. Usually by the time symptoms become evident the disease has already invaded the central nervous system (WHO, 2017). *Trypanosom brucei rhodesiense* (*T. b. rhodesiense*) accounts for the remaining cases of HAT and causes an acute infection. Distinct symptoms generally emerge after a few months or weeks of infection. *T. b. rhodesiense* develops faster than *T. b. gambiense* and quickly spreads to the central nervous system (WHO, 2017). WHO (2017) recorded only 2804 cases of HAT in 2015, though it is estimated that actual cases are about 20 000 with an estimated population of 65 million people at risk. Diagnosis and treatment of HAT is expensive. Administering the drugs to treat HAT requires trained personnel. HAT is hard to treat in stage two and the treatment is toxic with undesirable side-effects. HAT can be fatal if untreated. Treating stage one is easy and affordable but symptoms of stage one are not distinct, making it harder to diagnose (WHO, 2017).

Considerable progress has been made in using mathematical modelling to study the transmission dynamics of trypanosomiasis (Hargrove *et al.*, 2012; Moore *et al.*, 2012), so it is only fair we also design a study focusing on tsetse population dynamics to get more information out of disease models, which will incorporate tsetse population dynamics, and the biological and meteorological factors which impact the dynamics. Understanding tsetse fly population dynamics will help to decide how and when to implement vector-control strategies.

2.2 Chapter overview

A number of studies have been preformed to investigate the effect of temperature on larval and adult tsetse flies. Temperatures between 16 °C and 32 °C have been found to be conducive for tsetse populations to survive. Some of the studies looked at the effects of temperature under laboratory conditions, where the temperature was kept constant, which is obviously not the case in the field. In our modelling we will be using daily average temperatures observed in the field. Previous studies established that tsetse don't feed on all mammals; they feed on preferred hosts and on average feed every two to five days. We discussed different control strategies used. Traps and targets proved to be both affordable and environmentally friendly. Finally, we looked at the two forms of trypanosomiasis found in Africa. Our study is similar to the one done by Hargrove and Williams (1998) but we will use ordinary differential equations (ODE) models instead of optimised simulation and we are modelling the *G.pallidipes* species using data from Antelope Island, Lake Kariba, Zimbabwe.

Chapter 3

Mathematical Modelling: Model Introduction

3.1 Introduction

Mathematical modelling can be used to explain the dynamics of infectious diseases, compare different control strategies (Luz *et al.*, 2010), calculate what proportion needs to be vaccinated and to determine which factors are important in the transmission dynamics of the disease. Scientific hypotheses can be generated and tested using mathematical modelling (Grassly and Fraser, 2008). Ross (1916) was the first person to use ordinary differential equations (ODEs) to model infectious diseases. He used mathematical modelling to investigate factors that influenced disease dynamics. For a realistic model, one must identify all the factors that are important in the transmission dynamics of the disease. Only then can the information be translated into equations (Luz *et al.*, 2010). Essential factors include biological processes, climate, other environmental factors and the biology of the vector (where applicable). When dealing with a vector-borne disease, vector control measures may also need to be in place; it is not realistic to consider only interventions that focus on the human population: one must also acknowledge the role of the vector in disease transmission. Consequently, understanding the population dynamics of the vector may help with the development of effective vector control strategies and understanding transmission dynamics of the disease will increase the chances of eliminating and/or controlling the vector-borne disease (Hollingsworth *et al.*, 2015). The understanding of tsetse population dynamics will aid the development of effective and economical control strategies for trypanosomiasis.

In this chapter, we present the model variables, model parameters, and the ODE model that we propose for modelling our tsetse fly study population and explain the different model parameters obtained from literature. Initially we want to show how tsetse populations will behave when parameters are kept constant and are not dependent on temperature.

3.2 Model development

In our model we include, explicitly, only the pupal and adult stages. The egg and first three larval instar stages all occur in utero and it is thus unnecessary to model their numbers explicitly. Losses during the in utero stages are implicitly incorporated into pupal losses.

The state variables and model parameters are defined in the table below.

Table 3.1: Definition of state variables model parameters

State variable	**Definition**
P	pupae
F	adult female flies
M	adult male flies
Parameter	**Definition**
r	emergence rate
b	birth rate
μ_p	pupal mortality rate
μ_f	female adult mortality rate
μ_m	male adult mortality rate
k_p	density-dependent mortality for pupae

ODE model

In this subsection, we introduce the model and discuss the model assumptions and model equations.

3.2.1 Model assumptions

We begin with a simple and biologically plausible ODE-model which considers change over time for the population of pupae and adult flies. The model as shown in Figure 3.1 assumes that female adults produce pupae at a fixed rate b, and pupae emerge as adults at a fixed rate r. It is known that female and male tsetse flies emerge in approximately

equal numbers (Buxton, 1955). In our model, we therefore, assume pupae emerges at rate $\frac{r}{2}$ as female flies and the other half as male flies.

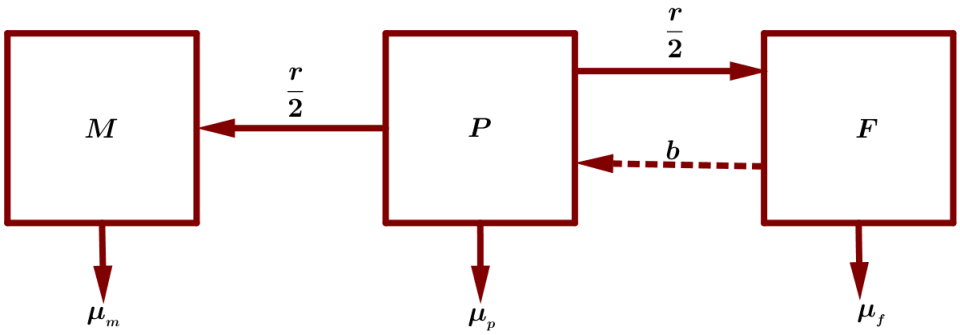


Figure 3.1: Schematic diagram of the ODE model

For simplicity, we will assume the population has a fixed natural mortality of μ_p for pupae, μ_f for female adult flies and μ_m for male adults. All parameters have units of days. Initially we have P_0 pupae, F_0 female adults and M_0 male adults.

3.2.2 Model equations

The mathematical equations show how the pupae (P), female adult flies (F), and male adult flies (M) populations change with time.

ODE model without density dependent mortality

The mathematical equations of the ODE model that does not include pupal density-dependent mortality is:

$$\frac{dP}{dt} = bF - rP - \mu_p P \tag{3.2.1}$$

$$\frac{dF}{dt} = \frac{r}{2}P - \mu_f F \tag{3.2.2}$$

$$\frac{dM}{dt} = \frac{r}{2}P - \mu_m M \tag{3.2.3}$$

Figure 3.2 shows a model population for tsetse flies, with initial conditions $P(0) = P_0$, $F(0) = F_0$ and $M(0) = M_0$. Initially, we assume we have 150 pupae, and no adult flies (i.e. $P(0) = 150$, $F(0) = 0$ and $M(0) = 0$). We assumed females produce larva every 10 days, and pupae emerge as adult flies after 30 days. Pupal mortality rate is 0.02, female mortality rate is 0.02 and male mortality is 0.04. Parameters are not temperature dependent. The population grows exponentially with time with no finite upper limit to population size, which is not realistic.

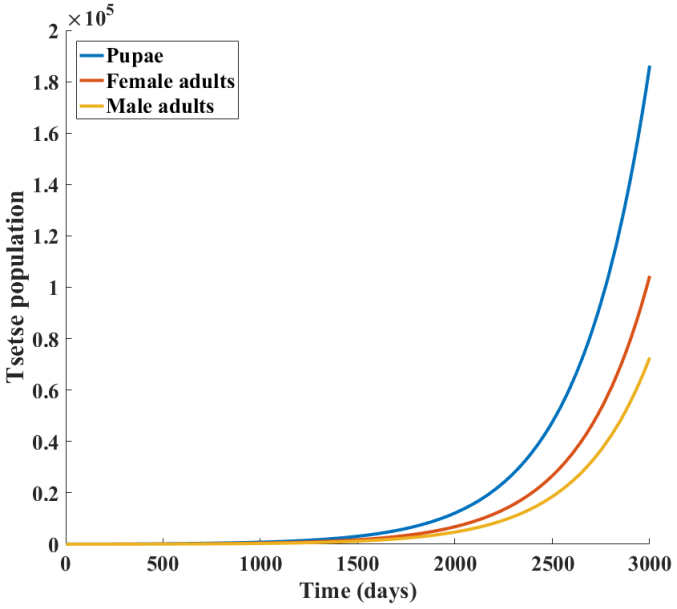


Figure 3.2: Model tsetse population without any density dependent mortality.

ODE model including density dependent mortality

The mathematical equations of the ODE model with pupal density-dependent mortality (k_p) is given by:

$$\frac{dP}{dt} = bF - rP - (\mu_p + k_p P)P \tag{3.2.4}$$

$$\frac{dF}{dt} = \frac{r}{2}P - \mu_f F \tag{3.2.5}$$

$$\frac{dM}{dt} = \frac{r}{2}P - \mu_m M \tag{3.2.6}$$

In figure 3.3 we show how the tsetse population changes when we add pupal density-dependent mortality (k_p) to the model, with initial conditions as above. The other parameters are the same as used in equations 3.2.1 - 3.2.3. The introduction of pupal density-dependent mortality slows down the population growth. Instead of growing exponentially the population reached equilibrium. This implies that pupal density-dependent mortality is important for tsetse population dynamics.

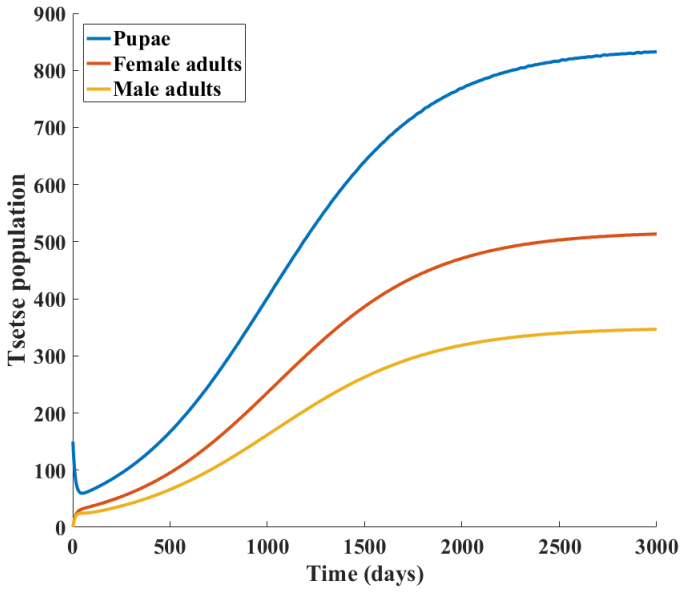


Figure 3.3: Model tsetse population with pupal density dependent mortality

3.3 Model parameter definition

Larval production, pupal period, adult lifespan and mortality are all dependent on temperature. Temperatures below 17 °C and above 35 °C are likely to lead to extinction of tsetse populations (Vale, 1971). Previous studies showed that if tsetse flies were exposed to moderately high temperatures for a long period of time, substantial mortality rates

were recorded. It was also observed that even reducing temperatures to 20 °C already led to tsetse flies experiencing increased mortality and/or resulted in adult flies becoming inactive (Terblanche *et al.*, 2008). Further reductions in temperature will clearly exacerbate such effects.

In this section we use parameters from Hargrove (2004) to parameterise relationship in our model for (i) larval production by adult female flies (ii) pupal duration (iii) pupal mortality and (iv) adult mortality. These relationships between various rates and temperatures were used to calculate the rates in our model. We used temperatures recorded using a Stevenson screen at Kariba airport approximately five kilometres from Antelope Island.

3.3.1 Model assumptions

As already mentioned, the birth and mortality rates of tsetse flies have also been shown to be dependent on temperature. With that, we need to incorporate temperature into the ODE model, which is the model we will use to fit the Antelope Island data and also use it to project future tsetse population dynamics. The model assumptions and model equations are discussed below for the temperature-dependent model.

3.3.2 Larval production by adult flies (birth rate)

Hargrove (2004) using results from Hargrove (1994) showed the relationship between larval production and temperature (Figure 3.4). The duration of larval production for the first pupa, (I_0) with $k_1 = 0.061$, $k_2 = 0.0020$ (Hargrove, 2004) is given by equation 3.3.1. The inter-larval period for the subsequent pupa, (I) is also given by equation 3.3.1 with $k_1 = 0.1046$, $k_2 = 0.0052$ (Hargrove, 2004) where T is the average temperature.

$$I = \frac{1}{k_1 + k_2 \cdot (T - 24)} \tag{3.3.1}$$

In Figure 3.4, as temperature increases, time to production of subsequent larva is shortened. At 25 °C the first larva (I_0) is produced by day 16 and subsequent larvae (I) are produced every 9 days. As expected, at 32 °C the periods are shorter with I_0 about 13 days and I about 6 days, whilst at lower temperatures (16 °C), the first larva is produced around day 22, and the subsequent larva is produced 15 days later.

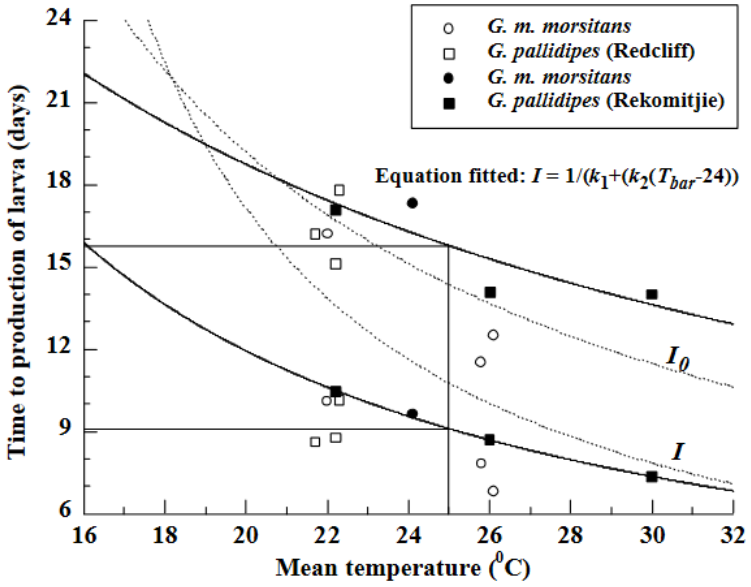


Figure 3.4: The relationship between temperature and the time (I_0), it takes to produce the first larva and the time (I) it takes to produce subsequent larvae for *G. m. morsitans* and *G. pallidipes* tsetse species (Hargrove, 2004).Both I_0 and I decreases with increasing temperature.

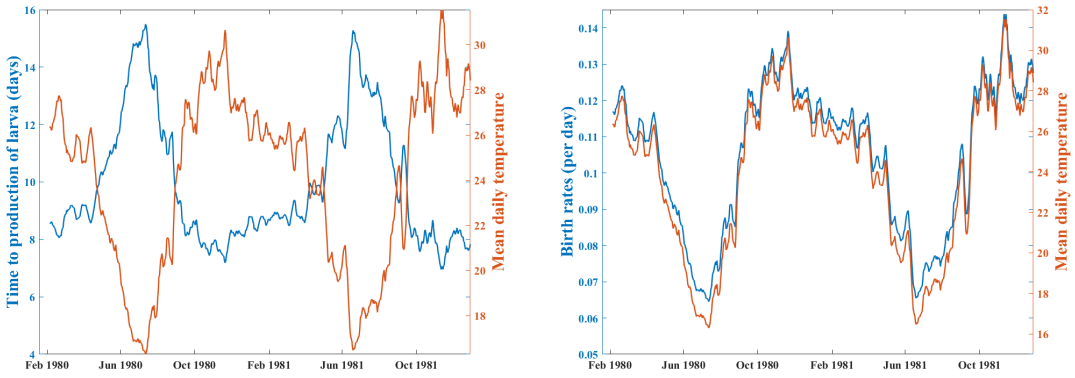
From the definition of time to larval production of subsequent pupa, we define the birth rate ($b(T)$) as the reciprocal of I:

$$b(T) = \frac{1}{I} = k_1 + k_2 \cdot (T(t) - 24) \tag{3.3.2}$$

where k_1, k_2 are as mentioned above and $T(t)$ is temperature as a function of time.

In Figure 3.5 we show how the duration of larva production changes in days and we also show how emergence rate changes (during the period of our study at Antelope Island) with changing temperature, using the same parameters as those defined by Hargrove (2004). In our model, we assume tsetse flies take about 15 days to produce larva around July at temperatures of 16.2 °C, whilst it takes about 7 days in November (with temperatures of up to 31.5 °C). Consequently, birth rates were higher in November and lower in

July; July 1980 recorded the lowest birth rates and November 1981 had the highest birth rates.



(a) larva production (b) birth rates

Figure 3.5: Graph showing how (a) larva production period and (b) birth rates, vary with temperature. The higher the temperature the shorter the larva production period, hence the higher the birth rates.

3.3.3 Pupal duration (emergence rate)

The number of days it takes for pupae to emerge as adults is determined by temperature and this can be seen in Figure 3.6 (Phelps and Burrows, 1969*c*).
The pupal duration (I_p) is defined as:

$$I_p = \frac{1 + \exp(a + b \cdot T)}{k} \tag{3.3.3}$$

.

where $a = 5.5$, $b = -0.25$, $k = 0.057$ for females and $a = 5.3$, $b = -0.24$, $k = 0.053$ for males and T is the average temperature (Hargrove, 2004).

From Figure 3.6 we see that the pupal duration gets shorter with increasing temperature. At 25 °C pupal duration is about 30 days. Female tsetse flies have a slightly shorter period than the males at every temperature. At 16 °C the pupal duration is about 100 days, whilst at 32 °C it is about 20 days.

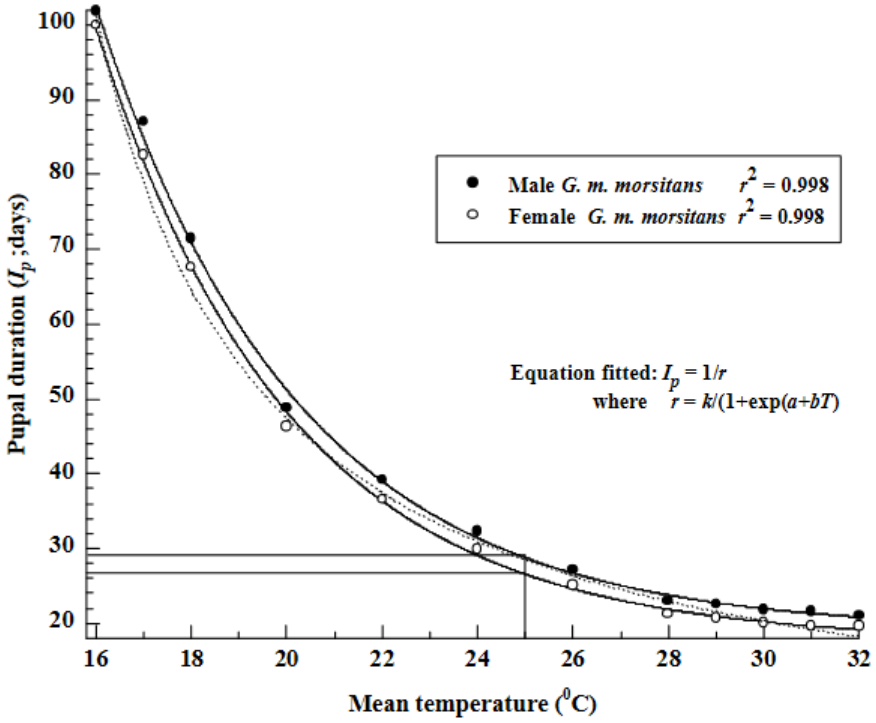


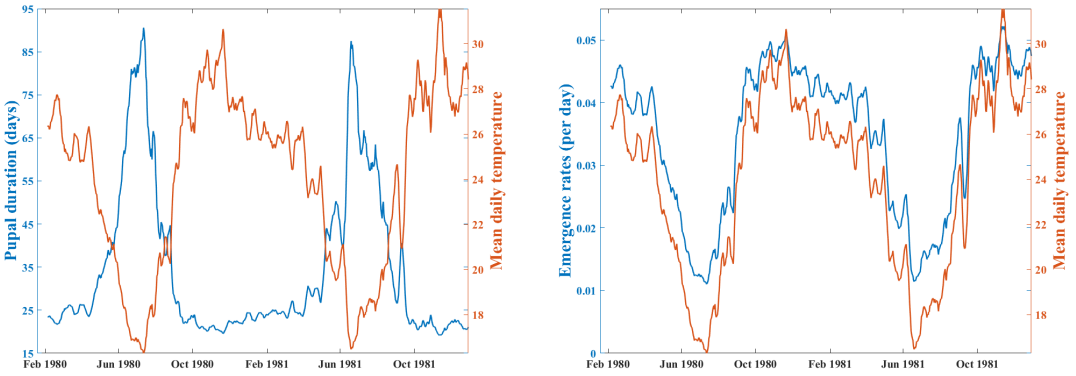
Figure 3.6: The relationship between temperature and pupal duration (I_p) (Hargrove, 2004). Increasing temperature shortens pupal durations and female flies emerge at least a day earlier than male flies. Data from Phelps and Burrows (1969*c*).

From the definition of pupal duration we will define the emergence rate ($r(T)$) as the reciprocal of I_p :

$$r(T) = \frac{1}{I_p} = \frac{k}{1 + \exp(a + b \cdot T(t))} \tag{3.3.4}$$

with a, b, k parameter values same as for I_p.

Figure 3.7 was obtained using the same parameters as those defined by Hargrove (2004). Lowest emergence rates (about 0.01 per day) and longer pupal periods (about 90 days) were observed around July with temperatures as low as 16 °C, whilst shorter pupal periods (about 19 days) and higher emergence rates (about 0.05 per day) were observed in November which is the hottest month of the year.



(a) Pupal duration (b) Emergence rate

Figure 3.7: Graph showing how (a) pupal duration in days and (b) emergence rates (per day) vary with temperature. Emergence rate increases with temperature, whilst pupal periods get shorter with increasing temperature.

3.3.4 Pupal mortality

Phelps and Burrows (1969*c*) and Phelps (1973) performed a laboratory study to investigate the effects of temperature on pupal mortality. The authors observed that for temperatures between 16 °C and 32 °C the overall pupal mortality was a U-shaped curve. With highest mortality observed at 16 °C and 32 °C (Fig. 3.8).

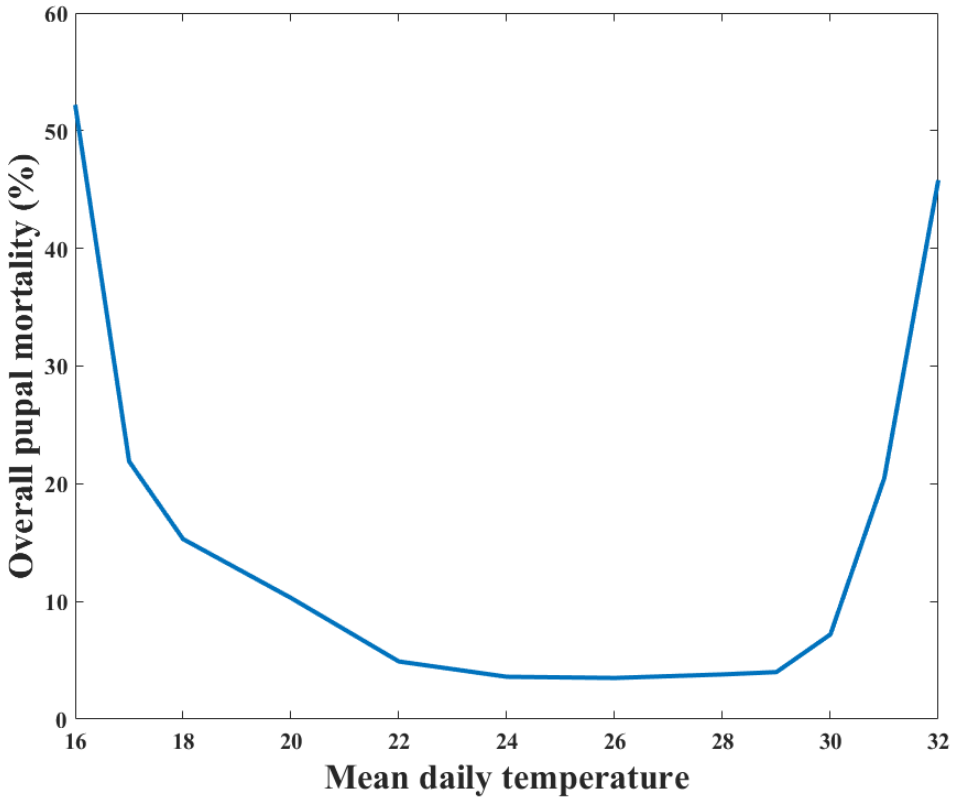


Figure 3.8: The relationship between temperature and pupal mortality. Highest mortality rates are recorded at 16 °C and 32 °C.

The pupal mortality function (equation 3.3.5) we will use is defined by Hargrove (unpublished).

$$\mu_p(T) = p_0 + p_1 \exp(-p_2(T-16)) + p_3 \exp(p_4(T-30)) \tag{3.3.5}$$

Rogers (1974) performed field experiments that showed that tsetse populations can be affected by density-dependent mortality. These studies showed evidence of density-dependent mortality on pupae. It has also been shown that, weather may affect mortality but can not determine population density (Rogers, 1979). Accordingly, our model only considers pupal density-dependent mortality (k_p), which is independent of temperature.

3.3.5 Adult mortality

Hargrove (2004) modelled the relationship between adult mortality and temperature as defined by equation 3.3.6 and 3.3.7 for female and male flies, respectively. For our model, we will use these equations to define female and male mortality rates.

Female and male adult mortality rates ($\mu_F(T)$ and $\mu_M(T)$) are given by (Hargrove, 2004):

$$\mu_F(T) = \frac{exp(f_0 + f_1 \cdot T(t))}{100} \tag{3.3.6}$$

$$\mu_M(T) = \frac{exp(m_0 + m_1 \cdot T(t))}{100} \tag{3.3.7}$$

The mortality rate for *G. pallidipes* is rather unusual, Figure 3.9. For temperatures between 16 °C and 24 °C the mortality appears to be approximately constant, with an average daily mortality rate of 0.029 per day for male flies and 0.025 per day for females. For temperatures of more than 25 °C the daily mortality rate increases with temperature, reaching a maximum of 0.1 per day and 0.07 per day for male and female flies, respectively.

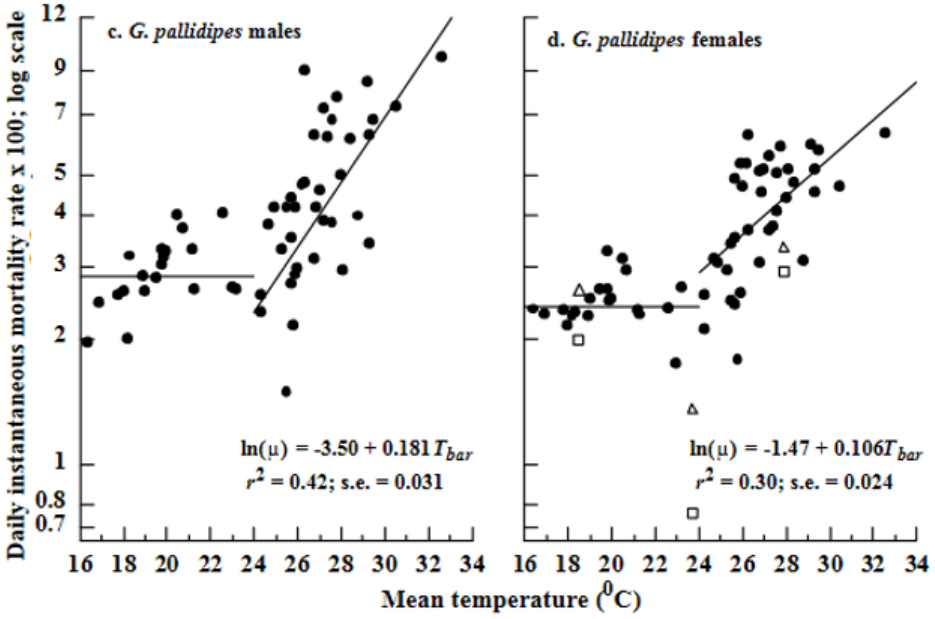
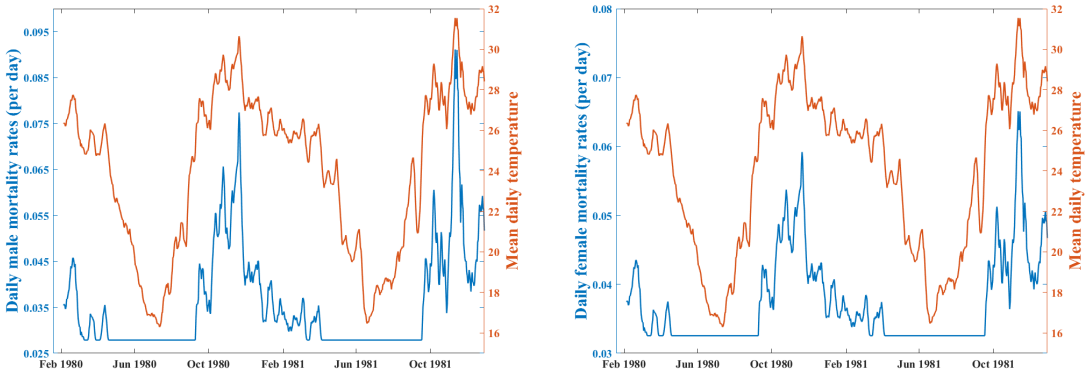


Figure 3.9: Adult mortality rates for (a) *G. pallidipes* male and (b) *G. pallidipes* female flies. Mortality rates increase exponentially with temperature for temperatures exceeding 25 °C. Figures from (Hargrove, 2004)

Figure 3.10 was also obtained using parameters defined by Hargrove (2004). For temperature between 16 °C and 25 °C, male mortality rate is constant at 0.027 per day and female daily mortality rate is constant at 0.0325. Mortality rates increase with temperature when temperatures are greater than 25 °C, with male mortality reaching a maximum of 0.0911 per day and females reaching 0.065 per day in November 1981. Male flies have a lower mortality rate at low temperatures.



(a) Male mortality rates

(b) Female mortality rates

Figure 3.10: The effect of temperature on (a) male and (b) female adult mortality rates. For temperatures below 25 °C mortality rates are constant, but for temperatures exceeding 25 °C mortality rates increase with increasing temperature.

3.4 Chapter overview

In this chapter, we introduced the ODE model that will be used to model tsetse fly populations. We reviewed Hargrove (2004), explained the parameters and showed how we will use these parameters in our ODE model. We then reviewed Phelps and Burrows (1969*c*) to investigate the effects of temperature on pupal mortality.

Chapter 4

Model Development and Parameter Estimation

4.1 Introduction

In this chapter, we give a summary of the study area and methods used during the Antelope Island experiment. We adapt the ODE model introduced in chapter 3.2 to make it temperature-dependent by modifying the parameters from Hargrove (2004) with the pupal mortality adapted from Phelps and Burrows (1969*c*). We estimate the unknown parameters for μ_P, μ_F and μ_M by fitting the model output to the Antelope Island data. Simple models are preferred, but if a model is too simple it will exclude necessary factors that influence the population dynamics. Conversely, complicated models can make it more difficult to explain the role of each parameter in the population dynamics (Grassly and Fraser, 2008). A model should be flexible enough to allow for parameters to be added if necessary and should represent the population of interest as realistically as possible (Grassly and Fraser, 2008).

4.2 Antelope Island data

4.2.1 Study area

Vale *et al.* (1986) performed the study on Antelope Island in Lake Kariba Zimbabwe. The area of Antelope Island is about 4.5 km^2 with thin and rocky soil and sparse grass cover but an abundance of deciduous trees.

4.2.2 Methods

In August 1979 33 cattle were placed on the island. The cattle were introduced to provide hosts for tsetse to be imported onto the island. Prior to the study 13 lions invaded the island and killed most of the warthog and kudu which resulted in a decrease in tsetse populations. When the study began the island had five warthogs, a bushbuck, five kudus, two troops of baboons and about 100 impala. The cattle were injected with Samorin every three months to prevent them from being infected with trypanosomiasis.

Puparia of *G. m. morsitans* and *G. pallidipes* were obtained from Rekomitjie, Research Station, Zimbabwe. Between August and October 1979, about 2000 puparia of each species were placed on natural breeding sites on the island which were identified to be the sandy floors of empty antbear tunnels. About 80% of the pupae of each species emerged and since female and male tsetse are known to emerge in roughly equal numbers (Buxton, 1955), by the end of November approximately 800 male flies and 800 female flies of each species had emerged.

Vale *et al.* (1986) wanted to test different field baits as potential methods for controlling tsetse populations. To assess the effectiveness of these baits on population levels, he needed a healthy tsetse population. This experiment was performed for the purpose of studying the impact of different control strategies.

The authors considered four different control strategies where each treatment took about eight to nine months. Prior to the control phase, however, the tsetse population was allowed to grow without interference-between August 1979 and April 1981. The first control stage began around April 1981 and ended around December 1981. The treatment involved the use of six traps to sterilise and release the flies. The traps were baited with carbon dioxide and acetone. The traps proved to be more effective for *G. pallidipes* than for *G.m.morsitans*. In the second stage the sterilizers were removed and the traps were now fitted with retaining cages. This stage took place between December 1981 and September 1982. The third stage was between December 1981 and May 1982 which was similar to the second stage. To improve the catch of *G. m. morsitans* traps were also operated 3 hours after sunrise. The final stage, stage four was from 29 May 1983, the traps previously used were replaced with 20 odour-baited insecticide treated targets. All targets were operated daily until they were removed on the 17th of April 1984 by which time it was not possible to catch any flies on the island. Vale *et al.* (1986) provide a more detailed description of the study and exact quantities of the chemicals used for

treatment.

The mark-release-recapture method described by Jolly (1965) and Seber (1965) was used to estimate adult population parameters. Flies were caught on ox fly rounds operated daily during the first three and last three hours of the day. Flies were marked using a colour and marking position corresponding to the week of capture, and then released again. The monitoring team caught tsetse with hand nets, each fly was recorded, marked distinctively with oil paint and released.

We use population data from the period 5 February 1980 to 29 December 1981 for *G. pallidipes* as shown in Figure 4.1 for the female flies and in Figure 4.2 for the male flies. The data consists of weekly estimates of the tsetse population. At the beginning of the study tsetse flies were caught and given daily markings. During the course of the experiment, however, the marking system changed from daily to weekly. Flies were now caught, given weekly markings and then released. During the period between the daily and weekly marking phases, in order to allow the population to adapt to the new marking system, flies were not marked for 18 weeks to allow all flies with daily marks to die naturally. Accordingly, the MRR estimates for this period are missing. We are developing a model for tsetse populations that does not include any methods for controlling tsetse populations. Using this data is justified because the sterilising traps had little impact on the tsetse population on the island, therefore we can ignore the impact of the sterilising traps on the tsetse population. In addition to the data on *G. pallidipes*, daily minimum and maximum temperatures were recorded using the Stevenson screen at Kariba airport. We use mean daily temperatures (the average of the minimum and maximum daily temperatures) in our model.

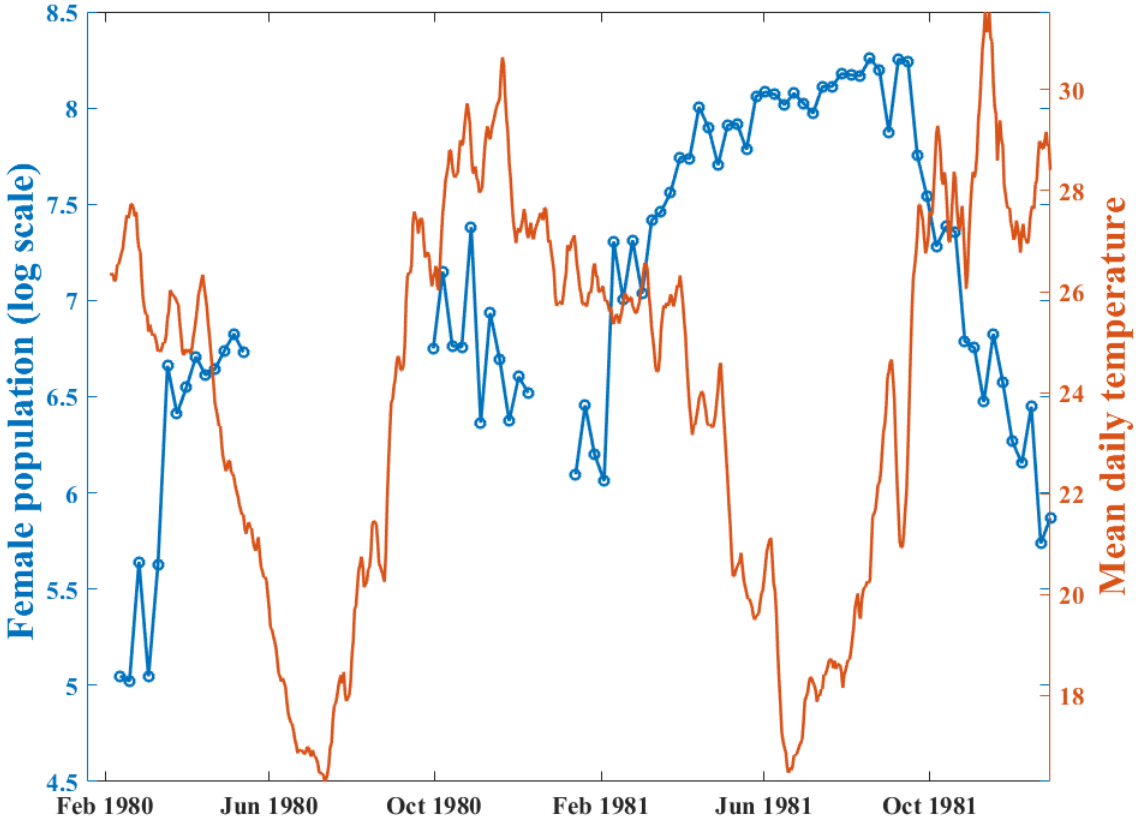


Figure 4.1: Changes in tsetse fly *G. pallidipes* female population and mean daily temperature on Antelope Island, between 5 February 1980 and 29 December 1981.

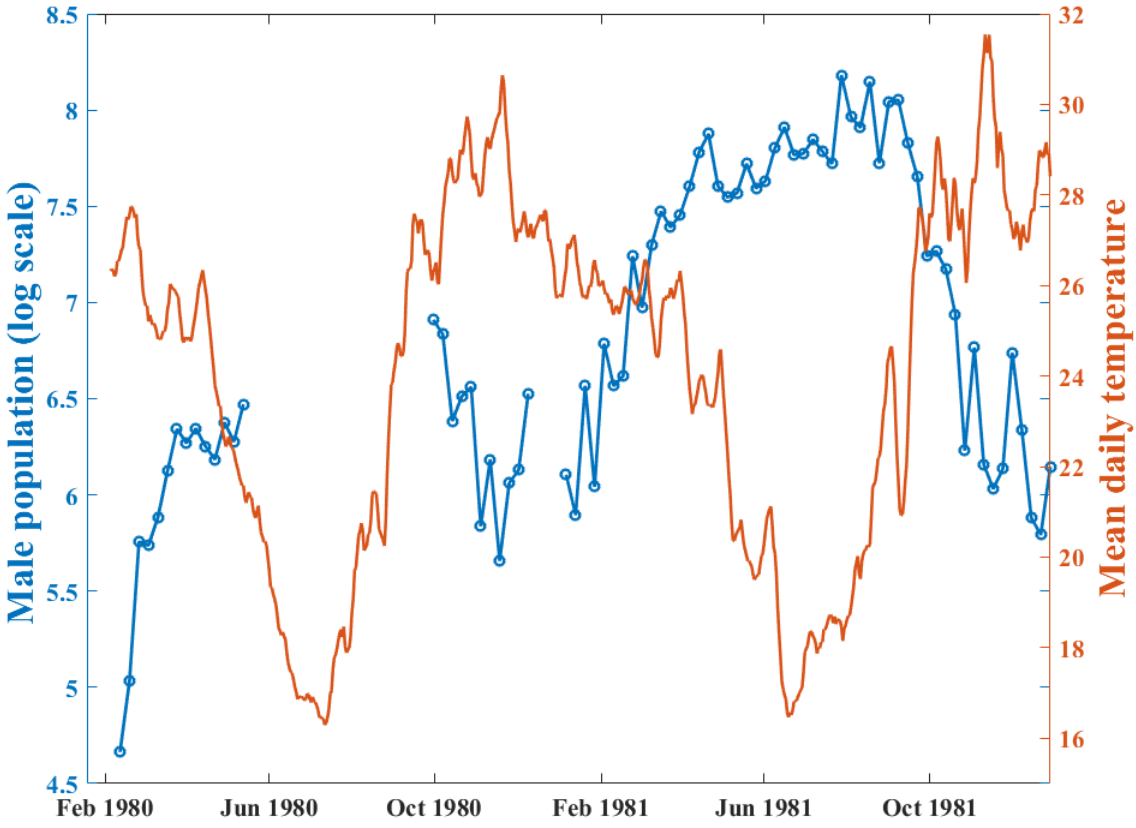


Figure 4.2: Changes in *G. pallidipes* adult male population and mean daily temperatures between 5 February 1980 and 29 December 1981 on Antelope Island.

The female population is higher than the male population. At high temperatures, the *G. pallidipes* population decreased, whilst at low temperatures, the population increased. The population of *G. pallidipes* reached its maximum around August 1981. We have missing data entries from 20 May 1981 to 23 September 1981 and again from 16 December 1981 to 13 January 1982. Missing data is as a result of changing the tsetse marking system from the daily to the weekly system-as described above.

4.3 Temperature-dependent ODE model

For the model shown in figure 4.3 we assume that the birth rate, emergence rate, pupal mortality and female and male adult mortality rates are all dependent on temperature. We also assume that there is pupal density-dependent mortality, independent of temperature or any other climatic effect. We assume female flies produce pupae at rate $b(T)$ and the pupae emerge at rate $r(T)$. Note that in our model adult flies consist of both immature (teneral) and mature flies. The pupae die at rate $\mu_P(T)$ with additional density-dependent mortality at rate $k_P P(t)$, whilst the female and male adult flies mortality rates are $\mu_F(T)$ and $\mu_M(T)$, respectively.

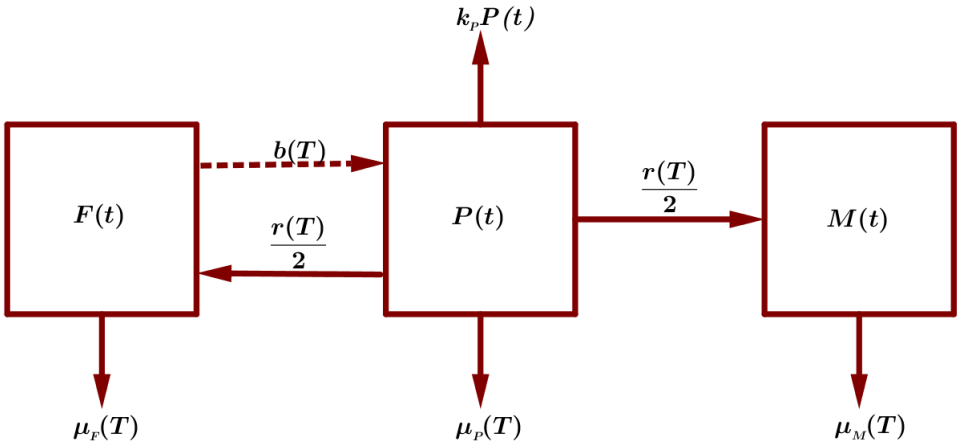


Figure 4.3: Schematic diagram of the temperature-dependent ODE model

As a recap, we define the birth, $b(T)$ and emergence rates, $r(T)$ in the following equations (Hargrove, 2004) where $k_1 = 0.1046$, $k_2 = 0.0052$ and $T(t)$ is temperature as a function of time

$$b(T) = k_1 + k_2 \cdot (T(t) - 24) \tag{4.3.1}$$

and

$$r(T) = \frac{k}{1 + \exp(a + b \cdot T(t))} \tag{4.3.2}$$

wit $a = 5.5$, $b = -0.25$, $k = 0.057$ for the female adult flies and and $a = 5.3$, $b = -0.24$, $k = 0.053$ for the male adult flies, and $T(t)$ is temperature as function of time.

The adult mortality rates now also incorporate extra parameters f_c and m_c, which are the parameters for the annual cycle. Hargrove and Williams (1998) observed that there were seasonal fluctuations in adult mortality other than those due to temperature, humidity and saturation deficit. The authors observed a residual effect which was not related to any meteorological factors, though it showed a strong annual cycle. The annual cycle is defined as a factor with a sinusoidal wave with a one-year period, with range $[-1.0\ 1.0]$ (Hargrove and Williams, 1998). The annual cycle parameters are f_c and m_c for the female and male populations, respectively.

Figure 4.4 shows how the annual cycle changes with changing temperature during the course of our study at Antelope Island.

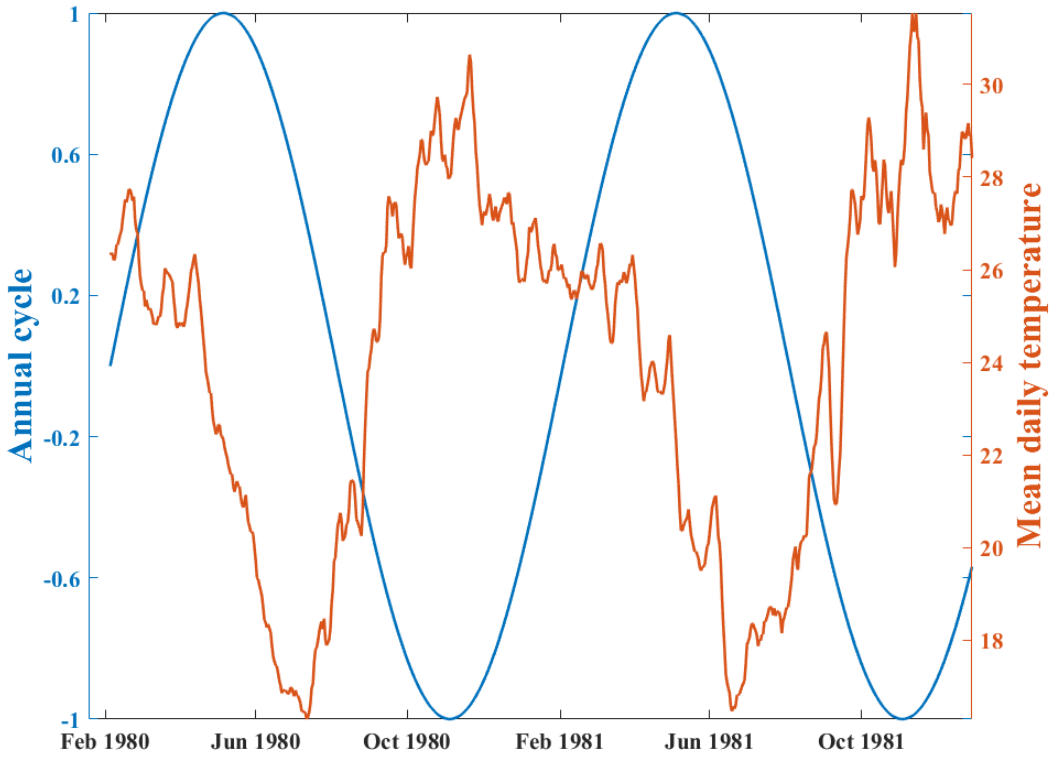


Figure 4.4: Change in annual cycle values on Antelope Island with changing temperature during the period of our study.

During the study on Antelope island, there were no records of normalised difference of vegetation index (NDVI) collected prior to October 1981. Looking at the recorded NDVI from October 1981, and annual cycle observed by (Hargrove and Williams, 1998) in figure 4.5. It is observed that the annual cycle is in phase with NDVI. It is therefore, possible that the annual cycle observed by the authors was in fact the NDVI. NDVI and temperature are out of phase. NDVI reaches its maximum peak before the lowest temperature is recorded. This is also true for minimum NDVI and maximum temperature. High NDVI is associated with greener vegetation-high temperature results in dry vegetation. Greener vegetation provides better habitat for tsetse flies.

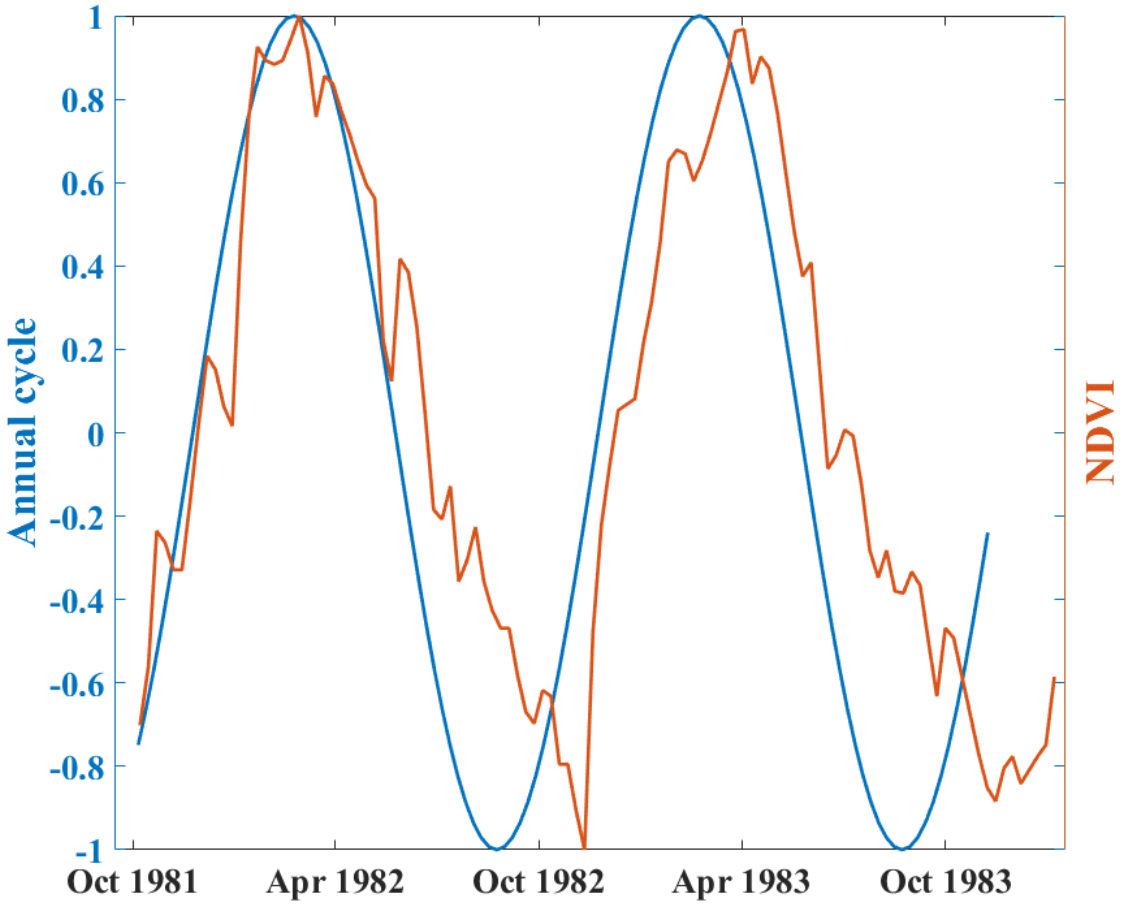


Figure 4.5: Change in annual cycle and NDVI values.

Female adult mortality rate, $\mu_F(T)$ is given by:

$$\mu_F(T) = \frac{exp(f_0 + f_1 \cdot 25 + f_c \cdot cycle(t))}{100}, \ for\ T \leq 25 \tag{4.3.3}$$

$$\mu_F(T) = \frac{exp(f_0 + f_1 \cdot T(t) + f_c \cdot cycle(t))}{100}, for\ T > 25 \tag{4.3.4}$$

Male adult mortality rate, $\mu_M(T)$ is given by:

$$\mu_M(T) = \frac{exp(m_0 + m_1 \cdot 25 + m_c \cdot cycle(t))}{100}, \; for\; T \leq 25 \tag{4.3.5}$$

$$\mu_M(T) = \frac{exp(m_0 + m_1 \cdot T(t) + m_c \cdot cycle(t))}{100}, \; for\; T > 25 \tag{4.3.6}$$

where the parameters values for f_0, f_1, f_c, m_0, m_1 and m_c will be estimated by fitting the ODE temperature-dependent model output to the Antelope Island data set for the adult tsetse fly population.

Phelps and Burrows (1969*c*) performed laboratory studies to investigate the relationship between pupal mortality and temperature. The authors considered temperatures between 16 °C and 32 °C. Hargrove (unpublished) fitted the data of Phelps and Burrows (1969*c*) (Fig. 3.8) and obtained the function describing the relationship between pupal mortality and temperature. The pupal mortality, $\mu_P(T)$ is defined as:

$$\mu_P(T) = p_0 + p_1 \exp(-p_2(T - 16)) + p_3 \exp(p_4(T - 30)) \tag{4.3.7}$$

where the parameters p_0, p_1, p_2, p_3 and p_4 will be estimated by fitting the ODE model output to Antelope Island data.

4.3.1 Model equations

Figure 4.3 shows the schematic diagram of our temperature-dependent model. We will use the following equations to model the pupae (P), female adult (F) and male adult (M) populations and estimate parameters for $\mu_P(T)$, $\mu_F(T)$, $\mu_M(T)$ and k_P.

$$\frac{dP}{dt} = b(T) \cdot F(t) - (\mu_P(T) + k_P \cdot P(t)) \cdot P(t) - r(T) \cdot P(t) \tag{4.3.8}$$

$$\frac{dF}{dt} = \frac{r(T)}{2} \cdot P(t) - \mu_F(T) \cdot F(t) \tag{4.3.9}$$

$$\frac{dM}{dt} = \frac{r(T)}{2} \cdot P(t) - \mu_M(T) \cdot M(t) \tag{4.3.10}$$

4.4 Parameter estimation

In this section, we estimate the parameters for μ_P, μ_F and μ_M by fitting the model output to the Antelope Island data. As a preliminary step, we did manual parameter optimization using ODE45 solver in Matlab. We changed each parameter until we obtained a first approximation fit to the data, using parameter values from Hargrove (2004) for μ_F (f_0, f_1, f_c) and μ_M (m_0, m_1, m_c) and Hargrove (unpublished) for μ_P (p_0, p_1, p_2, p_3 and p_4) as initial values. After obtaining our first approximation, we imported the newly found parameter values to the Optimization Toolkit and used simulated annealing, iterated descent and iterated local search optimization techniques to provide optimal estimates of the unknown parameters.

4.4.1 Parameter optimization techniques

We used the Optimization Toolkit to do parameter estimation. We define the ODE function and solve the model using ODE45. We set the parameter values with their respective lower and upper bounds. The chosen methods minimise the residual sum of squares (RSS) as defined in section 4.4.2. The Optimization Toolkit comes with a manual that explains all the different techniques used. We list below the definitions of the techniques we have used.

Simulated Annealing

Simulated Annealing is a method that finds a good solution to an optimization problem. It is best used when the model has many local optima. The simulated annealing algorithm generates an initial solution then explores the nearby area. If a neighbouring solution proves to be better than the current solution, it moves to it, if not, algorithm stays. This continues until the solution no longer improves. At the beginning the algorithm chooses the parameters randomly to avoid being stuck at a local maxima. This is why it is a good method regardless of the starting points. This method is good at finding an approximate global minimum. It can find a very good solution even in noisy data.

Iterative Descent

Iterative descent is a method that minimizes functions. Initial conditions are provided, and the algorithm calculates the gradient at that point. The solution moves to the negative direction of the gradient and the process repeats. The algorithm changes parameter values so as to minimize the function. The algorithm converges when the gradient is

zero (at the local minimum). The step size must be chosen with caution. If the step size is too large, the algorithm will diverge, whilst if it is too small the algorithm will take a long time to converge. It's the best method to use if good initial solutions are provided.

Iterated Local Search

Iterative local search is an improved version of local search methods. Local search methods are known to get stuck at the local minimum, if nearby points are not better. Iterated local search starts the routine at different points each time. A parameter is chosen at random, changes it until it reaches a minimum, then starts searching from the new minimum until no new minimum is obtained. It works well for arbitrary quality solution.

4.4.2 Estimated parameter values

Table 4.2 shows the parameter values that gave the best fit according to the values of R-squared (R^2). For each method, after each run we took the resulting parameter values as initial values for the next run. We did this until the values of R^2 and RSS no longer improved, whilst keeping track of the pupal and adult mortality rates to ensure the model mortality rates are within accepted ranges as reported in the literature.

RSS is the residual sum of squares and TSS is the total sum of squares, calculated as shown below (StackExchange, 2015),

$$RSS = \sum (observed\ data - model\ output)^2 \tag{4.4.1}$$

$$TSS = \sum (observed\ data - mean(observed\ data))^2 \tag{4.4.2}$$

$$R^2 = 1 - \frac{RSS}{TSS} \tag{4.4.3}$$

Three optimization techniques were used initially to fit the data; the best method is the one that returns the highest R^2 value. Table 4.1 shows the different optimization techniques we used with their respective R^2 values for both female and male adult flies. From table 4.1, we observe that iterated local search gave the highest R^2 value. We then used the iterated local search method to estimate the parameter values.

Table 4.1: Parameter estimation methods and their respective R^2 values

Method	R^2(female flies)	R^2 (male flies)
Simulated annealing	0.56	0.54
Iterated local search	0.60	0.55
Iterated descent	0.59	0.53

The estimated parameter values are shown in table 4.2; these values were obtained by fitting the model output to the Antelope Island data using the iterated local search method.

Table 4.2: Unknown parameters with their estimated values.

Parameter	values
f_0	-3.35
f_1	0.1799
f_c	0.88
p_0	0.0014
p_1	0.450
p_2	2.7
p_3	0.089
p_4	0.99
k_p	9e-7
m_0	-3.1010
m_1	0.18
m_c	-0.219

Using the values from table 4.2 and the iterated local search method we obtain best fits to the data shown in figure 4.6 and figure 4.7 for female and male *G. pallidipes*, respectively. The iterated local search, with R^2 of 0.60 for female flies and R^2 of 0.55 for the male flies, gave the better fit for both populations than the other methods.

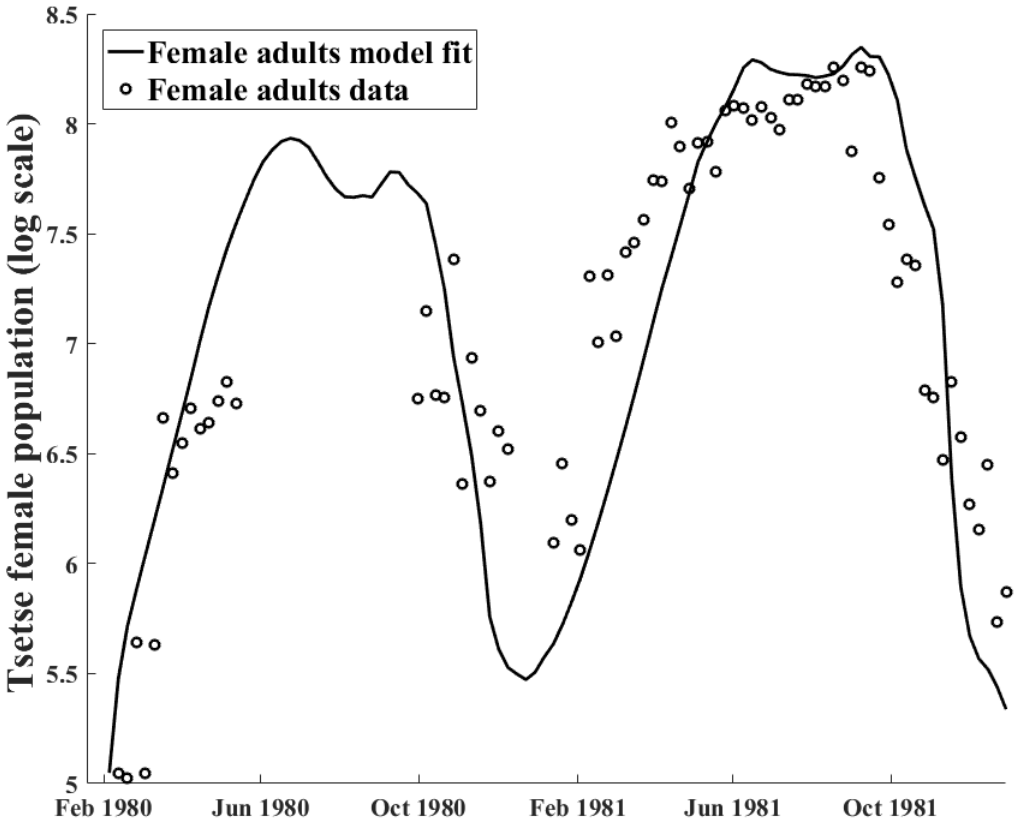


Figure 4.6: Antelope Island data with the best fit obtained using the iterated local search method for female adult flies. The model fit has an R^2 of 0.60.

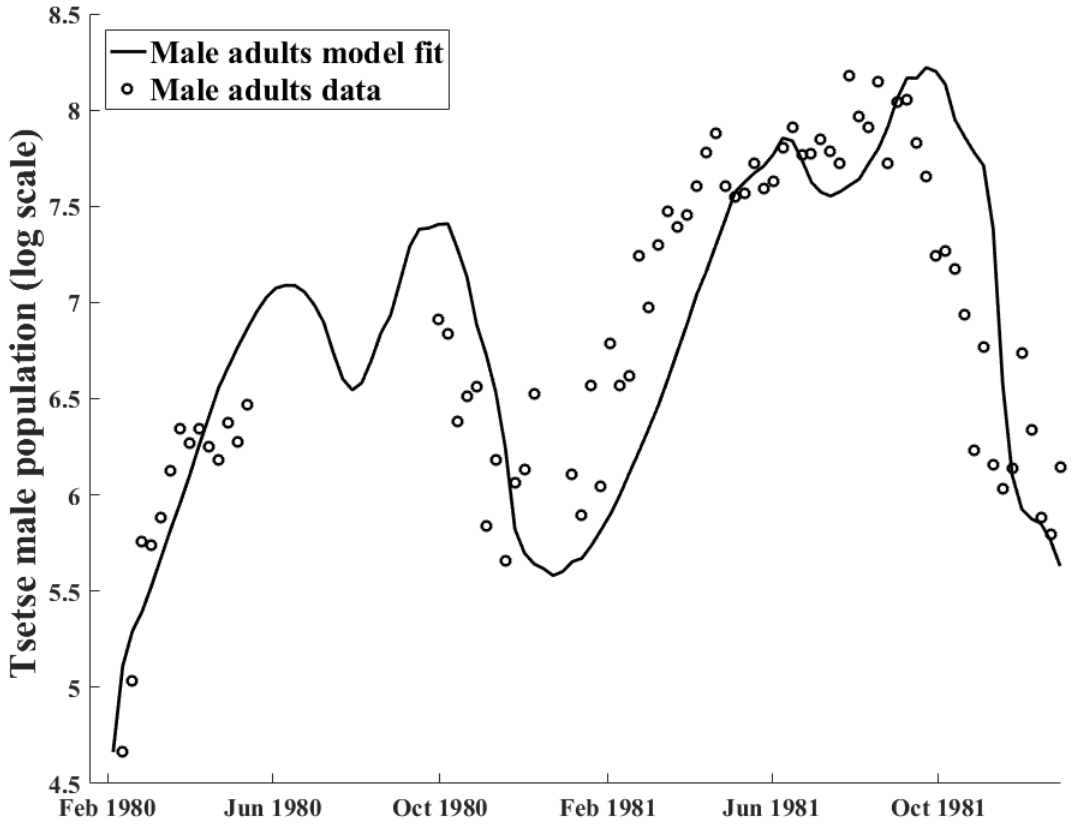


Figure 4.7: Antelope Island data with the best fit obtained using the iterated local search method for the male adult flies with an R^2 value of 0.55.

It is important to note that to fit the model to the female population data and to estimate the unknown parameters for μ_P andμ_F, we restrict the model to $\frac{dP}{dt}$ (equation 4.3.8) and $\frac{dF}{dt}$ (equation 4.3.9). Excluding male flies from our model did not change the population dynamics of the female flies. We only need to assume that there are always sufficient numbers of male flies to inseminate female flies. Fitting the model to the male data we used the full model and estimated the unknown parameters for μ_M.

The chosen estimated parameter values were confirmed by keeping track of how the pupae, adult female and adult male mortality rates changed over time with changing

temperature. We ensured that the mortality rates are within accepted ranges reported in the literature.

Figure 4.8 shows how the modelled pupal mortality, $\mu_P(T)$ changes with changing temperature during the period of the study at Antelope Island. The pupal mortality rates show the same trend as those predicted by Phelps (1973). Our model predicts high mortality rates during the coldest and hottest time of the year. During the coldest time of the year, July 1980 at 16.3 °C $\mu_P(T)$ was 0.21 per day, whilst in July 1981 with temperatures as low as 16.5 °C, $\mu_P(T)$ was 0.13 per day. November, the hottest month of the year at Antelope Island, November 1980 had $\mu_P(T)$ of 0.17 per day with temperatures as high as 30.5 °C, whilst November 1981 had the highest daily $\mu_P(T)$ of 0.41 at 31.5 °C. November 1981 recorded the highest μ_P followed by July 1980, whilst the lowest $\mu_P(T)$ was observed throughout the year with $\mu_P(T)$as low as 0.0014 per day.

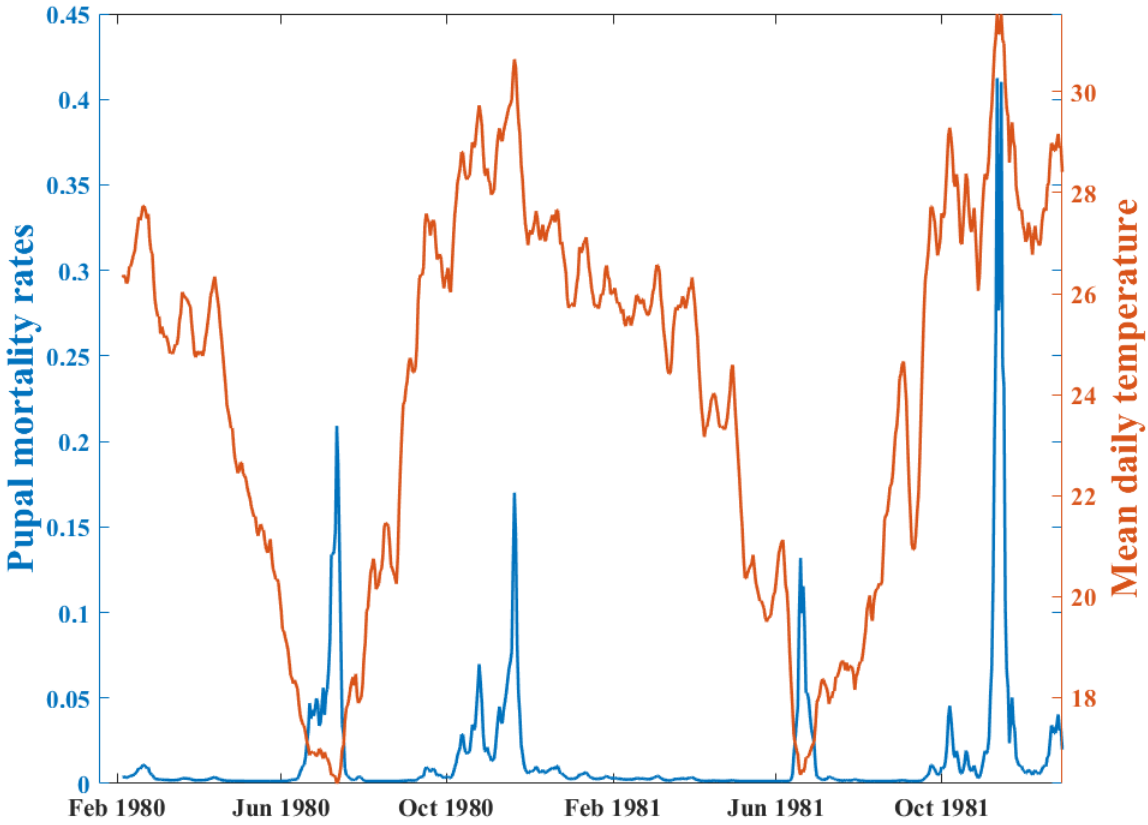


Figure 4.8: Change in pupal mortality at Antelope Island with changing temperature. Highest mortality occur during the hottest and the coldest time of the year.

Female adult mortality rates $\mu_F(T)$, increases with temperature for temperatures greater than 25 °C (Fig. 4.9). Lowest $\mu_F(T)$ are observed in May 1980 with $\mu_F(T)$ of about 0.0086 per day and maximum temperature of 22.5 °C, whilst highest μ_F of 0.15 per day was observed around November with temperatures reaching a maximum of 31.5 °C. As a consequence of including the annual cycle factor, $\mu_F(T)$ is not constant between 16 °C and 24 °C as assumed by (Hargrove, 2004). This is because the adult mortality rates are now influenced by both temperature and annual cycle.

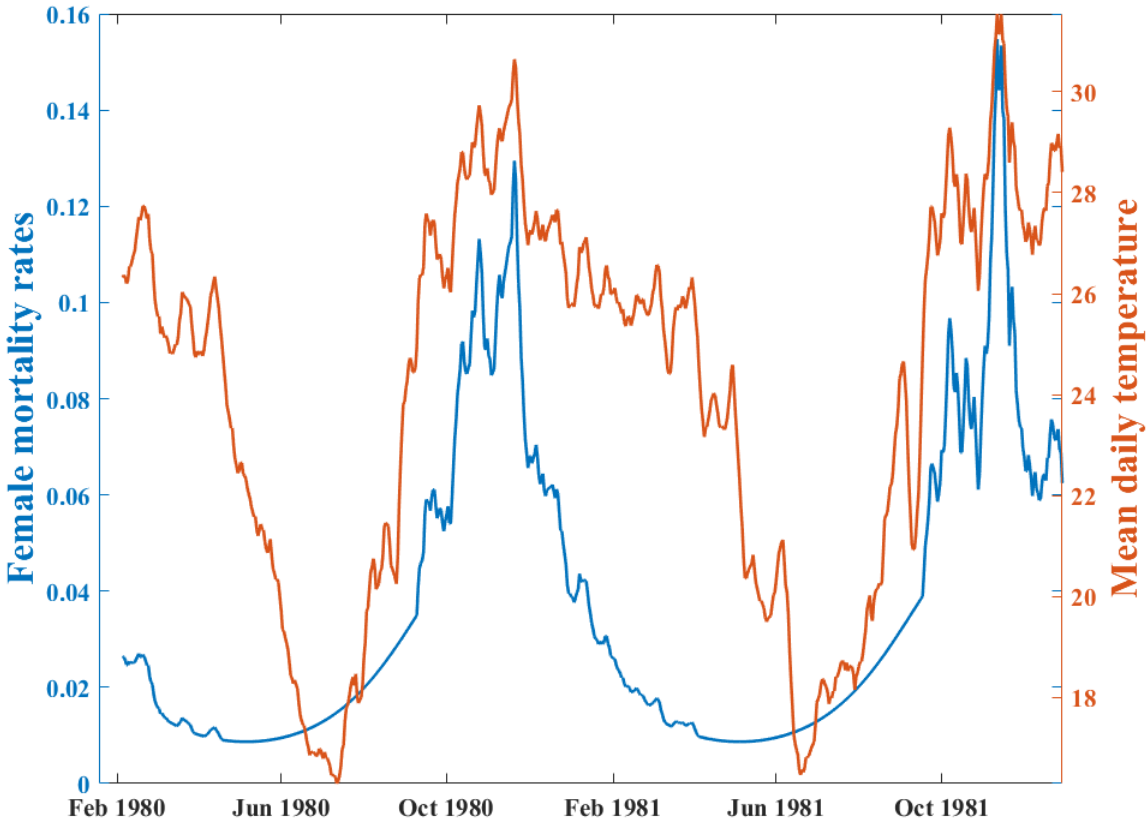


Figure 4.9: Changes in female adult mortality rates at Antelope Island with changing temperature during the period of our study. The highest mortality occurs during the hottest time of the year.

In May male flies had the lowest adult mortality rates, μ_M of about 0.035 per day (Fig. 4.10) whilst, male mortality rates were higher in November. November 1980 recorded maximum temperatures of 30.6 °C with μ_M of about 0.12 per day, whilst November 1981 had μ_M of about 0.16 per day at maximum temperatures of 31.5 °C.

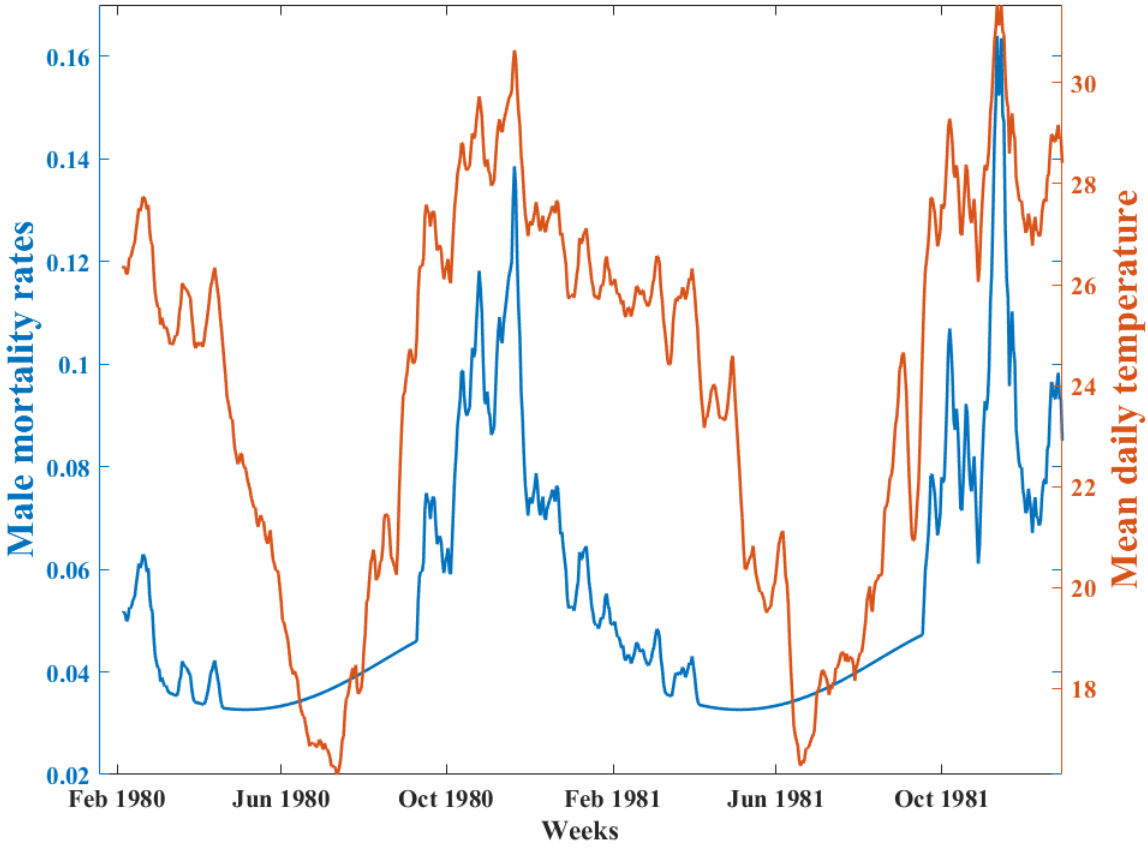


Figure 4.10: Effects of temperature on male adult mortality rates on Antelope Island.

For temperatures around 23 °C (around May), female adults had the lowest mortality rates of about 0.009 per day compared to the male flies that had daily mortality rates of about 0.035 per day, whilst at higher temperatures male flies have daily mortality rates of 0.16 and female flies have mortality rates as high as 0.15 per day.

4.5 Chapter overview

In this chapter, we briefly described the Antelope Island study which provided the data used in the present modelling exercise. We introduced the ODE temperature-dependent model which we used to model the observed changes in the numbers of female and male *G. pallidipes* during the study on Antelope Island. The different optimization tech-

niques we used to estimate the unknown parameters for μ_P, μ_F and μ_M were explained. The method that provided the highest R^2 value was chosen as the preferred method. Mortality rates for pupae, female and male adult flies were used to validate our model. The chosen parameter values gave mortality rates which are within the range of values as defined by literature. The parameter values estimated in the models will be used in the next chapter to investigate the importance of temperature, annual cycle and pupal density-dependent mortality in our ODE model.

Chapter 5

Model Scenarios and Model Projections

5.1 Introduction

It has previously been observed that tsetse population survival is highly dependent on temperature, though there are other factors such as population-density, host availability, control measures and other environmental and climate factors that also influence population survival. In our model, we included pupal density-dependent mortality (k_p) and annual cycle as extra factors driving the pupal and adult mortality, respectively. In this chapter we aim to assess how the different factors (temperature, annual cycle and k_p) affect tsetse population dynamics.

To carry out the investigation we created seven restricted models for each sex, in addition to the full model. We vary the three factors of interest and obtain different model scenarios as one or more parameter is omitted. The best model will be selected using the R^2 and Akaike Information Criterion (AIC) values. AIC compares the quality of the set of established models relative to each other. It is a method used to determine which model fits the data best, without being influenced by the number of model parameters (Burnham and Anderson, 2004). For $\frac{n}{K} < 40$ (where n is the sample size and K is the number of parameters) AICc is recommended. In our case, we calculate AICc due to our small sample size. The model with the lowest AIC/AICc value is the best model.

$$AIC = 2K + n\, log(RSS/n) \tag{5.1.1}$$

where n is the sample size (number of data points), K is the number of parameters and RSS is the residual sum of squares.

$$AICc = AIC + \frac{2K(K+1)}{n-K-1} \tag{5.1.2}$$

5.2 Model scenarios

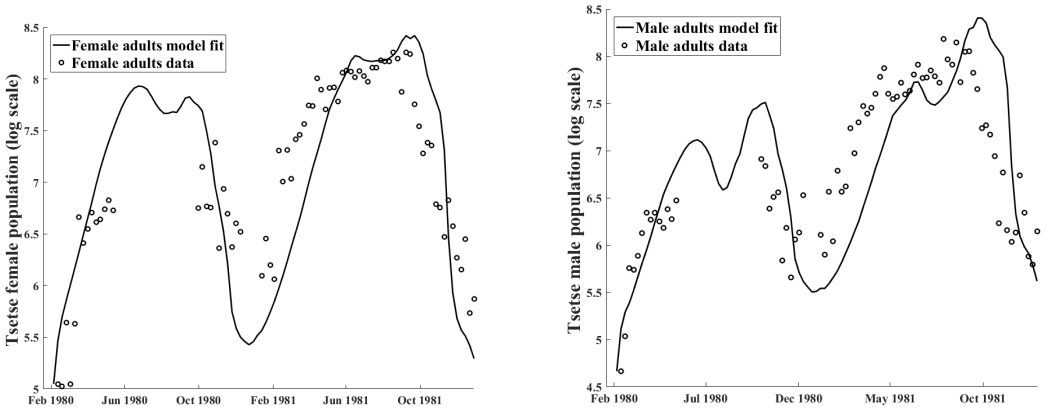
In total, we have seven restricted models plus the full model. If a parameter is excluded in a model it is represented by 0, otherwise, it is 1. When temperature is set to 0, temperature is set equal to 24.0 °C which is the average temperature calculated from the temperature recorded from 5 February 1980 to 29 December 1981. Table 5.1 shows the different restricted models with their respective AICc and R^2 values obtained for each model. A preferred model is the one with the lowest AICc value (Burnham and Anderson, 2004) and the highest R^2 value.

Table 5.1: The different models with their respective AICc and R^2 values. Model 1 (full model) gives the best fit to the data.

Model	Temperature	Annual Cycle	Density-dependence Mortality	Females		Males	
				AICc	R^2	AICc	R^2
1	1	1	1	-72.89	0.60	-69.97	0.55
2	1	1	0	-58.98	0.51	-64.95	0.52
3	1	0	1	-54.39	0.50	-47.24	0.39
4	1	0	0	-51.02	0.46	-50.68	0.42
5	0	1	1	-43.51	0.40	-40.37	0.33
6	0	1	0	-36.04	0.34	-28.77	0.22
7	0	0	1	167.01	-	133.3	-
8	0	0	0	205.89	-	166.82	-

Model 7 and model 8 had negative R^2 values. A negative R^2 value simply means that a horizontal line will fit our data better than the model output, that is RSS is greater than TSS (Burnham and Anderson, 2004). Mathematically a negative R^2 does not make sense, hence we used the AICc value to judge the goodness of the model.

Model 2 (Fig. 5.1) includes the annual cycle and temperature, with the pupal density-dependent mortality term excluded. The model gives a good fit with an R^2 value of 0.51 (AICc of -58.98) for the female population and R^2 of 0.52 (AICc of -64.95) for the male population.

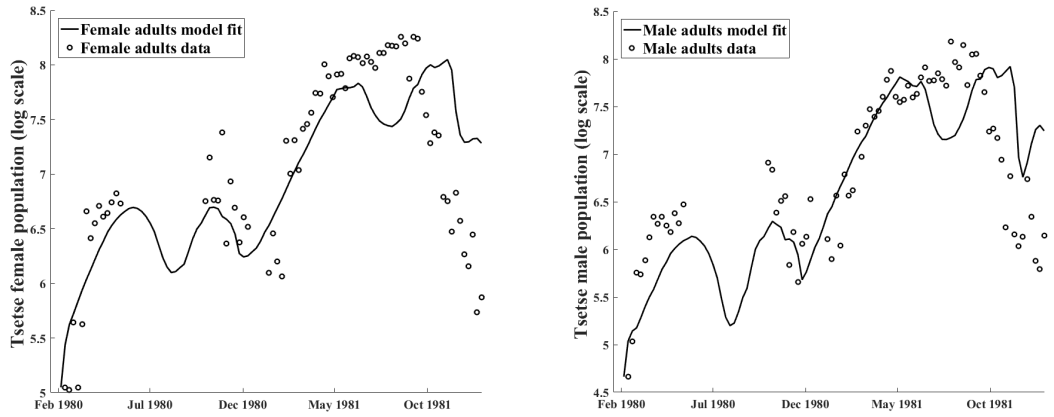


(a) Female adult flies

(b) Male adult flies

Figure 5.1: Model fits obtained for model 2 for (a) female and (b) male adult flies. Model 2 gave the second best fits to the data.

Model 3 excludes only the annual cycle term. In figure 5.2 we observe that the model output fits the female data relatively well, with an R^2 of 0.50 (AICc of -54.39) and gave a relatively poor fit for the male adult flies with an R^2 of 0.39 (AICc of -47.24). The model population does not decrease towards the end of the study, the model population is significantly higher than the observed population. The observed population increases from February until August 1982, yet the model output decreases significantly around July only to increase around September when the observed population decreases.

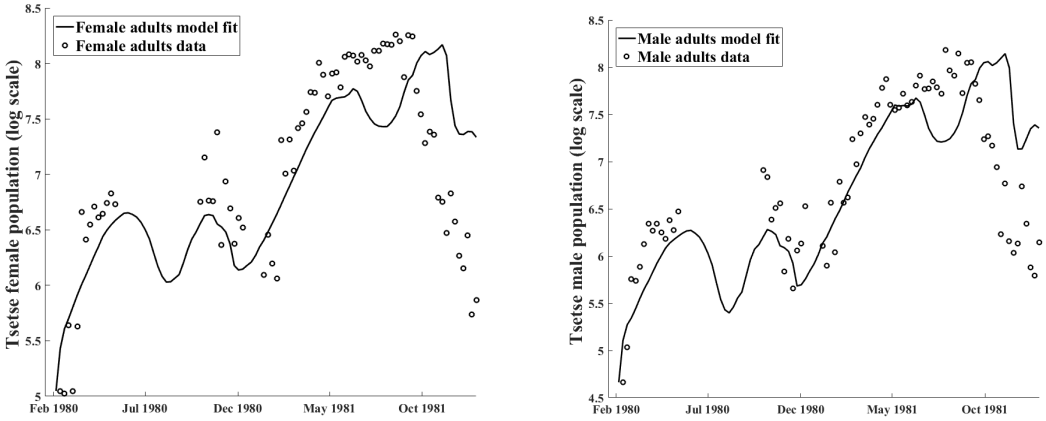


(a) Female adult flies

(b) Male adult flies

Figure 5.2: Model fits obtained when the annual cycle factor is excluded for (a) female and (b) male adult flies. Model outputs fits the female population better than the male population.

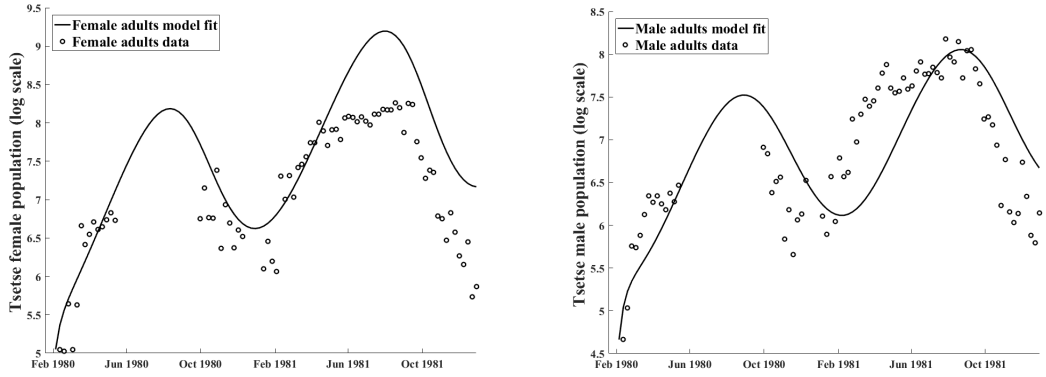
Model 4 only considers temperature as a meteorological factor. Model outputs for figure 5.3 are similar to outputs for model 3 (Figure 5.2) which considered two factors, temperature and the density-dependent mortality. For the female flies model 4 has an R^2 of 0.46 (AICc of -51.02) whilst model 3 had an R^2 of 0.50 (AICc of -54.39). For the male flies model 4 has an R^2 of 0.42 (AICc of -50.68) whilst model 3 has an R^2 of 0.39 (AICc of -47.24). Clearly, model 3 fits the population data slightly better than model 4 for the female adult flies, whilst model 4 fits the male population data better than model 3. This suggests that including pupal density-dependent mortality to our model improves the model fit for the female adult, whilst for the male flies considering temperature only explains the male population dynamics better than including both pupal density-dependent mortality and temperature.



(a) Female adult flies (b) Male adult flies

Figure 5.3: Model fits obtained for model 4, where the model only included temperature for (a) female flies and (b) male adult flies. Model 4 fits are similar to the fits obtained from model 3.

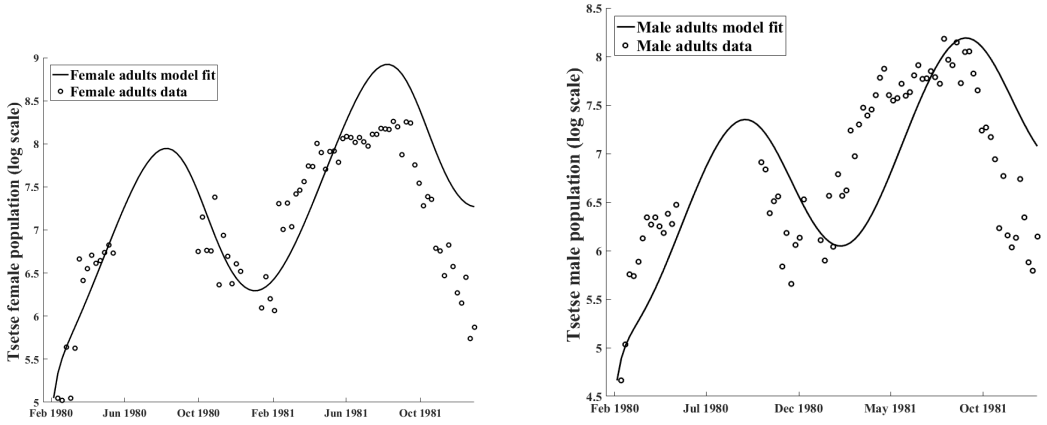
Figure 5.4 shows the results of model 5, where temperature is fixed at 24.0 °C and only includes the annual cycle and k_P factors. The annual cycle produces a model output that mimics the data well, though the model fits are not the best. The female adult flies have an R^2 of 0.40(AICc of -43.51) and R^2 of 0.33 (AICc value of -40.37) for male adults.



(a) Female adult flies (b) Male adult flies

Figure 5.4: Model outputs for model 5 (a) female (b) male adult flies.

For model 6 (Fig. 5.5) we only include the annual cycle term, meaning temperature is fixed at 24.0 °C and $k_p = 0$. Model 6 produced poor fits for the adult flies with R^2 of 0.34 (AICc of -36.04) and R^2 of 0.22 (AICc of -28.77) for female and male adult flies, respectively. Model 5 and model 6 produced similar fits, with model 5 producing better fits than model 6.

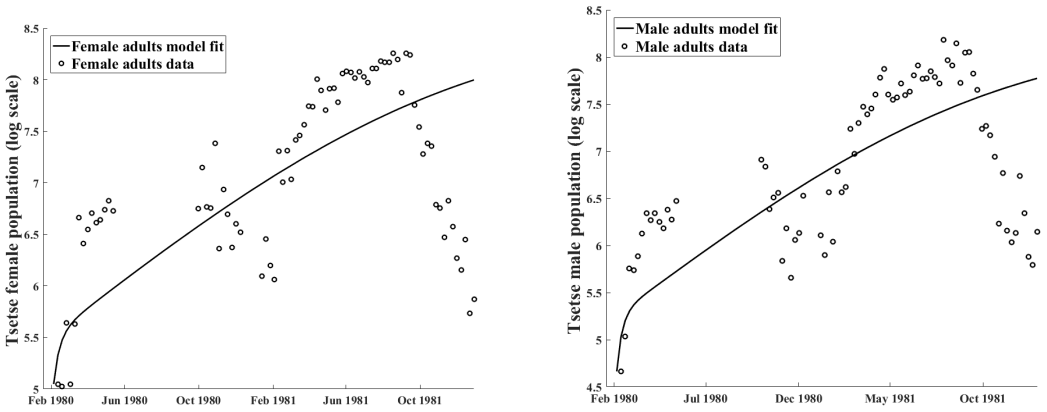


(a) Female adult flies

(b) Male adult flies

Figure 5.5: Model fits from model 6 which only includes the annual cycle factor. Model 6 fits (a) female adult flies better than (b) male adult flies.

Model 7 has fixed temperature, the annual cycle is excluded and only k_p is included. Model outputs for model 7, Figure 5.6 are similar to Figure 5.7 (model 8). For the female flies, model 8 has an AICc of 205.89 and model 7 has an AICc of 167.01, whilst for the male adult flies, model 8 has an AICc of 166.82 and model 7 has an AICc of 133.30. Model 7 gives the second worst model fit for our data.

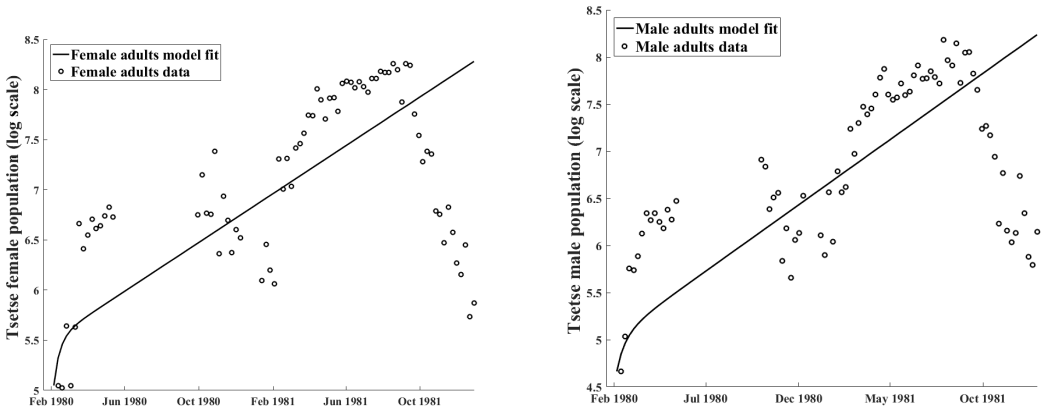


(a) Female adult flies

(b) Male adult flies

Figure 5.6: Model fits obtained when fitting model 7 to the (a) female and (b) male adult flies. Excluding temperature and annual cycle gave the second worst fit.

The R^2 values obtained for both the female and male model fits are negative for model 8 (Fig. 5.7), showing that a horizontal line will fit our data better than the model fit obtained (Burnham and Anderson, 2004). This is a consequence of excluding the annual cycle & k_p factors and keeping the temperature constant at 24.0 °C. The model output increases linearly with time though it grows slower than the observed population. Figure 5.7a, the female flies have an AICc of 205.89 and the male flies (Fig. 5.7b) have an AICc value of 166.82, which is the highest obtained for all models, making it the worst model for both sexes.



(a) Female adult flies

(b) Male adult flies

Figure 5.7: Resulting model fit when excluding all 3 factors for (a) female and (b) male adult flies. The model populations grow linearly with time, though they grow slower than the observed populations.

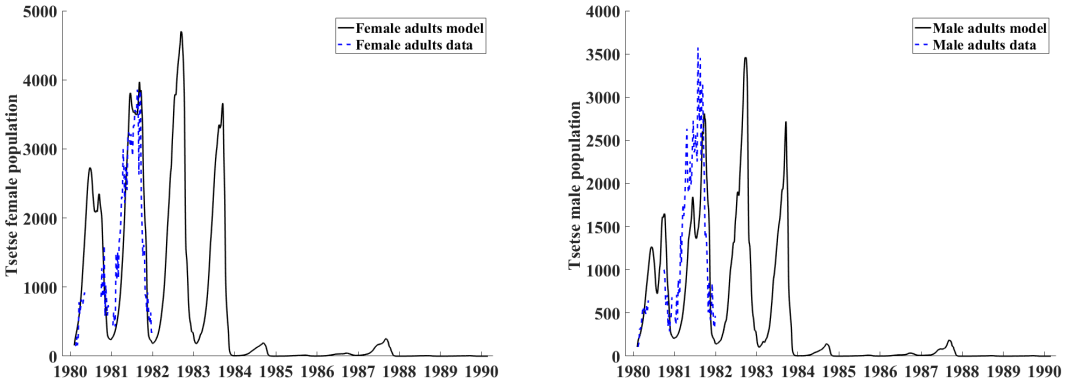
The different restricted models showed that the survival of both the female and male adult flies is influenced by different climatological factors. Our study found temperature to be the most important factor influencing population dynamics of adult tsetse flies on Antelope Island.

5.3 Model projections

In this section, we use the ODE temperature-dependent model calibrated with population estimates data from 5 February 1980 to 29 December 1981. We use this model to predict how the population dynamics would have changed if temperatures were to either stay constant, increase or decrease. Temperatures were recorded using a Stevenson screen, the screen recorded daily minimum and maximum temperatures at Kariba airport approximately five kilometres from Antelope Island. In our model we use the the average daily temperatures. Firstly, we use the recorded temperature and observe how the adult population changes during this period. Then we change the temperature by adding and subtracting up to two degrees and use the ODE model to predict the population dynamics.

For the female adult flies (Fig. 5.8a), the first few years the model population keeps the

same trend with population numbers remaining more or less constant. A rapid decline in population numbers was observed in September 1983, then recovered by December 1983, although the population never reached its initial numbers. Female adult population numbers were nearing zero in November 1984, November 1987 and November 1988 and recovered by March 1985, April 1988 and April 1989. Male adult flies (Fig. 5.8b) experienced a rapid decline in population growth in September 1983, October 1984 and September 1987, and recovered in March 1984, January 1985 and January 1988, respectively. Our model predicts that the adult population went extinct by November 1989 without any control strategies.

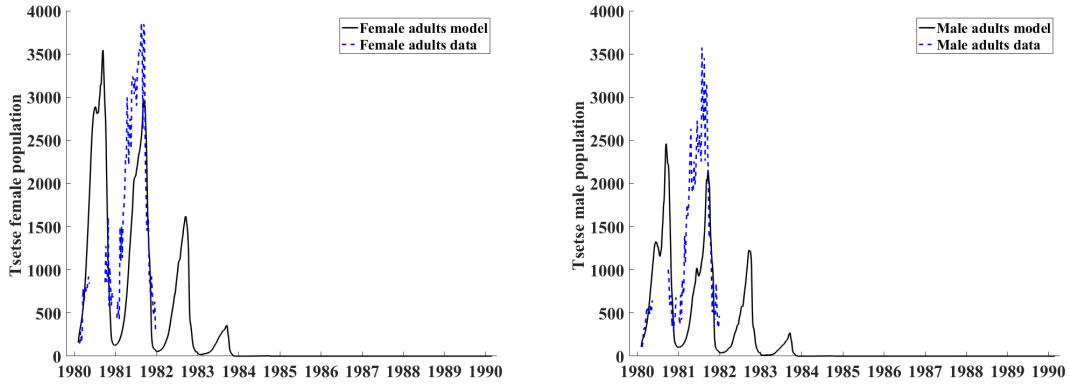


(a) Female adult flies

(b) Male adult flies

Figure 5.8: Model projections for (a) female and (b) male adult flies. The model predicts population dynamics from 1980 to 1990 for tsetse adult population on Antelope Island. According to our model, we expect the adult population to have gone extinct by November 1989.

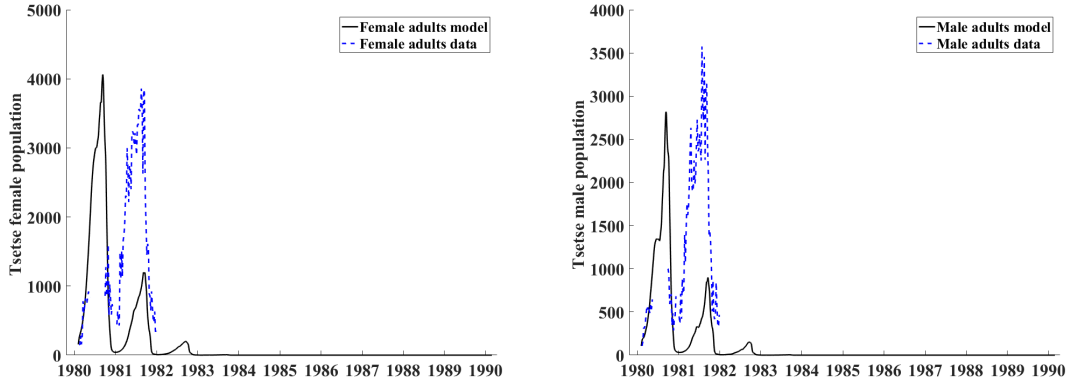
In figure 5.9, we used the ODE model to predict how soon the population would have changed if the temperature increased by 0.5 °C. The model population grows more slowly than the observed population after the first population decrease. In September 1983 the population growth decreased sharply, by November 1983 the population was close to zero but recovered in January 1984. The adult population became extinct in October 1984. If temperature increased by half a degree the population will be extinct 5 years earlier than if the temperature had stayed constant.



(a) Female adult flies (b) Male adult flies

Figure 5.9: Model projections for (a) female and (b) male adult flies if the temperature increases by 0.5 °C . The predicted population went extinct in October 1984.

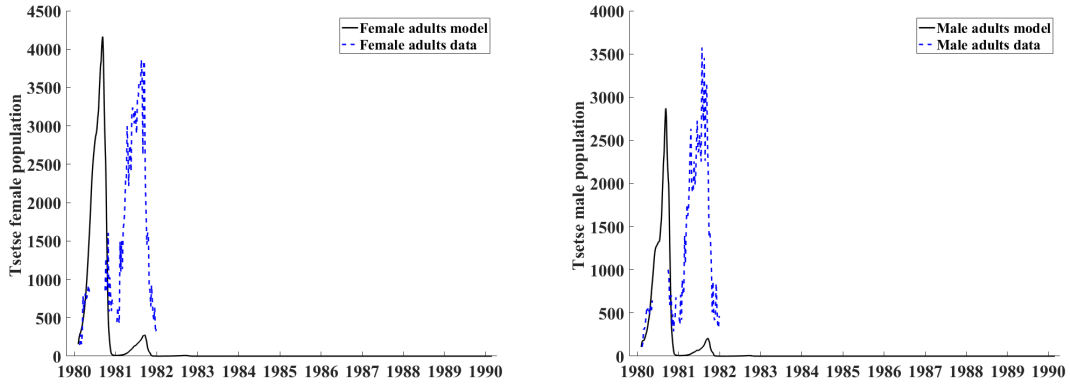
The tsetse fly population decreased and never recovered to its initial numbers for both the female (Fig. 5.10a) and male (Fig. 5.10b) adult flies. By December 1982 the population's numbers nearly reached zero, then population growth increased by June 1983. Both the male and female adult populations went extinct by October 1983.



(a) Female adult flies (b) Male adult flies

Figure 5.10: Model projections for (a) female and (b) male adult flies if the temperature increased by one degree. The female and male populations decreased every year, and died out by October 1983.

The higher we increased the temperature, the faster the population became extinct. In figure 5.11 and figure 5.12 there is a clear trend of decreasing tsetse population when the temperature is increased by 1.5 °C and 2.0 °C, respectively. From these results, we found that as we increased temperature, the sooner the tsetse population went extinct. As expected, the model populations are lower than the observed populations (after November 1980). In figure 5.11, increasing temperature by 1.5 °C resulted in both the female (Fig. 5.11a) and male (Fig. 5.11b) going extinct by October 1982.

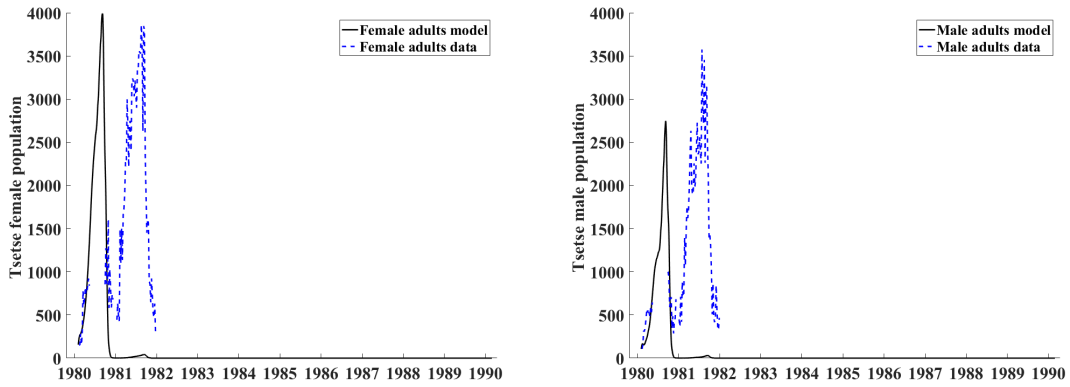


(a) Female adult flies

(b) Male adult flies

Figure 5.11: Model projections for (a) female and (b) male adult flies if the temperature increased by 1.5 °C. The predicted population shows a decreasing trend every year and died out as early as October 1982 for both female and male adult populations.

When we increased temperature by 2.0 °C, the model population fits the observed data significantly better during the first year. The model population went extinct as early as November 1981.

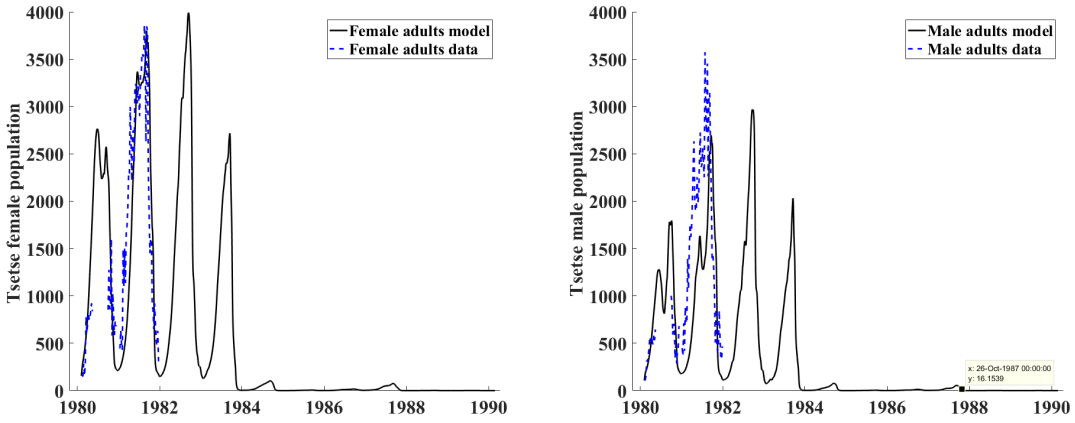


(a) Female adult flies

(b) Male adult flies

Figure 5.12: Model projections for (a) female and (b) male adult flies if the temperature increased by 2.0 °C . An increase of 2.0 °C results in the tsetse population going extinct population within a year of the beginning of the study (November 1981).

The previous results indicate that increasing temperatures resulted in the Antelope Island population going extinct sooner. If the temperature stayed constant, the adult population would have gone extinct by October 1989. If temperature increased by 1.0 °C, the population would have gone extinct by October 1983. We observe that increasing the temperature by as little as 0.1 °C (Fig. 5.13) resulted in the population dying out in October 1988.

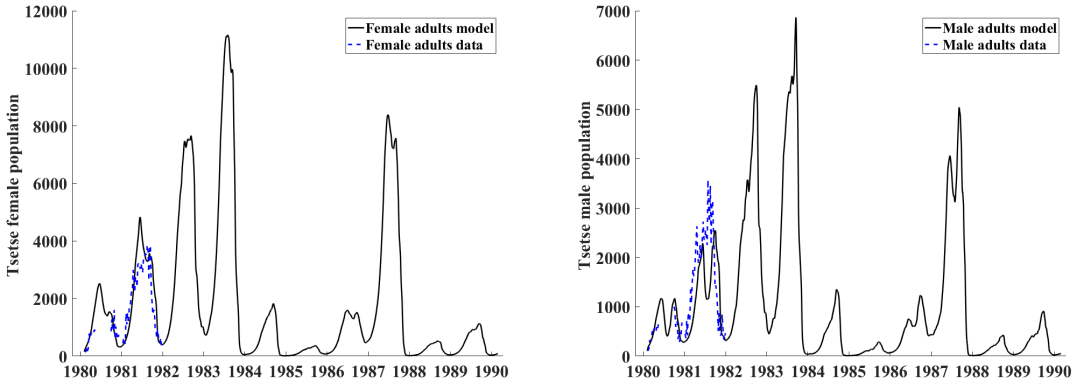


(a) Female adult flies

(b) Male adult flies

Figure 5.13: Model projections for (a) female and (b) male adult flies if the temperature increased by 0.1 °C

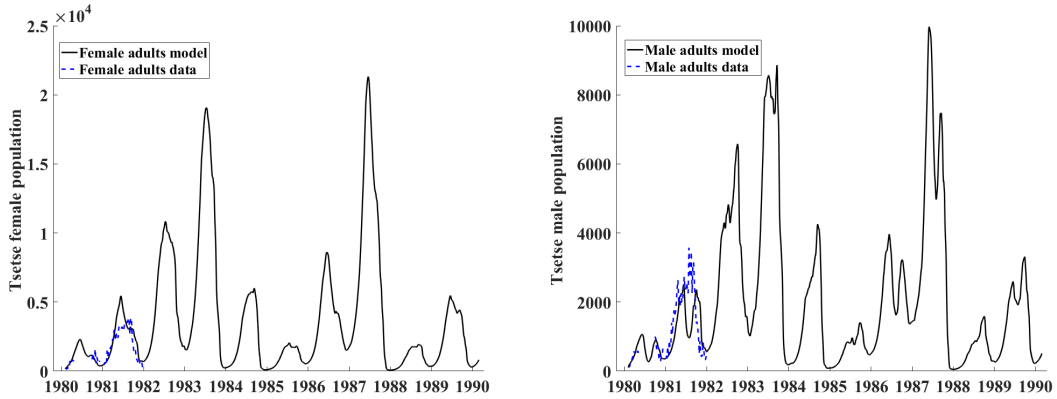
If we decreased the recorded temperature we observe that the population continued growing, as shown in figures 5.14 - 5.17. Firstly, we consider a scenario where the model temperature was 0.5 °C lower than observed as shown in figure 5.14. The female tsetse adult flies reached their maximum population in August 1983 and male adult reached their maximum population in September 1983. From February 1980 the female adult population increased, then suddenly decreased in August 1983, where the population went from 11147 to 93 by December 1983. Male adult flies display the same trend until the population declined in September 1983 (from 6865 to 43 by January 1984).



(a) Female adult flies (b) Male adult flies

Figure 5.14: Model projections for (a) female and (b) male adult flies if the temperature decreased by 0.5 °C . Female population fits the data relatively better than the male population.

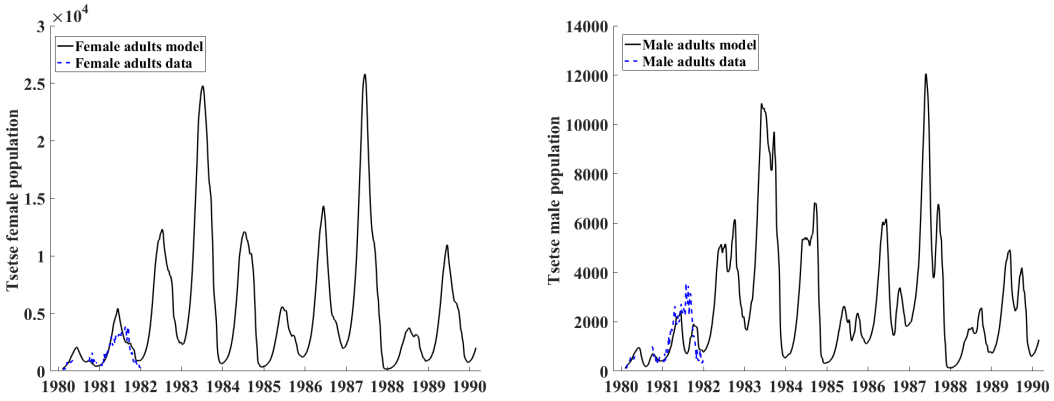
The female population (Fig. 5.15a) is observed to be significantly higher than the male population (Fig. 5.15b) when temperature was decreased by 1.0 °C . July 1983 (19060) and June 1987 (21323) recorded the highest number of female flies, whilst September 1983 (8858) and June 1987 (9971) recorded the highest number of male adult flies.



(a) Female adult flies (b) Male adult flies

Figure 5.15: Model projections for (a) female and (b) male adult flies if the temperature decreased by 1.0 °C . The female and male model populations were five and three times higher than the observed female and male populations, respectively.

Figure 5.16 shows how the adult population changes if the observed temperature is decreased by 1.5 °C. The biggest population loss was experienced in July 1983 and June 1987 where the female adult population (Fig. 5.16a) went from 24690 in July 1983 to 656 in December 1983 and went from 25757 in June 1987 to 175 by January 1988. The male adult population decreased from 9680 in September 1983 to 533 in December 1983, and in May 1987 it went from 12060 to 3777 by August 1987.

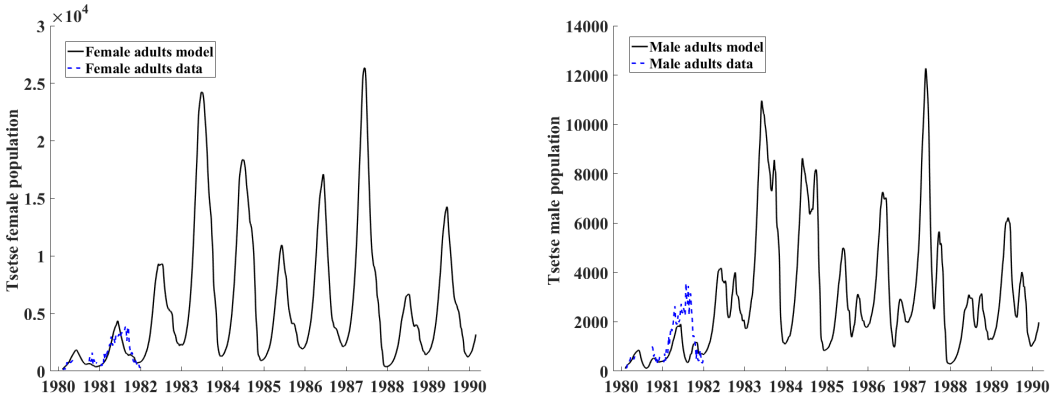


(a) Female adult flies

(b) Male adult flies

Figure 5.16: Model projections for (a) female and (b) male adult flies if the temperature decreased by 1.5 °C . The female population is double that of the male population.

Finally, we decreased the recorded temperature by 2.0 °C as shown in figure 5.17. Population growth persisted. When the temperature was decreased by two degrees, female population grew to a maximum of 26340 in June 1987 and male population to a maximum of 12194 in May 1987.



(a) Female adult flies

(b) Male adult flies

Figure 5.17: Model projections for (a) female and (b) male adult flies if the temperature decreased by 2.0 °C .

The results of this section suggest that if temperatures increased at all above this observed level on Antelope Island tsetse populations would have reached extinction very quickly, whilst if temperatures had decreased tsetse populations would persist. When temperatures decreased by 2.0 °C, the model population reached its highest population, whilst when temperature increased by 2.0 °C the population went extinct within a year of the beginning of the study.

5.4 Chapter overview

In this chapter, we investigated the effect of the following factors: temperature, annual cycle and pupal density-dependent mortality. We created eight models to carry out the analysis. The different model scenarios showed that the female and male adult fly populations are influenced by different climatological factors. Temperature is the most important factor, although, the annual cycle also influenced the population dynamics. Finally, we projected the model population for a period of 10 years, from 1980 to 1990. From the model projections we observe that if the observed temperature is increased by as little as 0.5 °C , the adult population died out by October 1984. On the other hand, if the recorded temperature decreased tsetse population growth rates increased.

Chapter 6

Discussion

The original aim of this study was to investigate the impact of temperature change on tsetse fly population dynamics and on the transmission dynamics of trypanosomiasis. In practice, however, our study only focused on the effects of temperature on tsetse fly population dynamics: due to time constraints and lack of data on trypanosomiasis we did not work on the disease. We developed a temperature-dependent ODE model to model the growth of tsetse fly populations. We have data on *G. pallidipes* from the Antelope Island experiment, which was conducted between August 1979 and April 1984. We used population data from the 5^{th} of February 1980 to the 29^{th} of December 1981. During this period there were either no traps in place in the island or only sterilizing traps were present. We assume that there were no control measures present because the sterilising traps had little impact on the tsetse populations. In addition to the tsetse data, we have daily average temperatures from the Island that we use to parameterize the birth, emergence and mortality rates for our model. In our model, the pupal and adult mortality rate functions had parameters that were estimated by fitting the model population to the observed tsetse population from Antelope Island. The model fitting was performed using iterated local search optimization techniques in Matlab R2016a.

Three different techniques were used to fit the model output to the data, the chosen method was the one with the highest R^2 value for both the female and male adult flies. Fitting the ODE model output to the Antelope Island data gave an R^2 value of 0.60 for the female population and R^2 of 0.55 for the male population.

Pupal, female adult and male adult mortality rates helped us choose the estimated parameter values. Our model predicted daily pupal mortality, μ_p (Fig. 4.8) as high as 0.21

per day during the coldest time of the year (July 1981) and as high as 0.41 per day during the hottest time of the year (November 1980). These results concur with previous studies which observed that overall pupal mortality was highest at the lowest and highest temperatures (0.52 per day at 16 °C and 0.45 per day at 32 °C) (Phelps and Burrows, 1969*c*). The rest of the year, daily pupal mortality rates were as low as 0.0014 per day, which concur with Hargrove (2004), who stated that for tsetse populations to survive losses during their egg, larval and pupal stages must be minimal.

Adult mortality rates increased with temperature when temperatures exceeded 25 °C. Female adult mortality rates (μ_F) had a minimum of 0.0086 per day around May and a maximum of 0.15 per day around November (Fig. 4.9). Male adult mortality rates (μ_M) had a minimum of 0.0349 per day around May and a maximum of 0.16 per day around November (Fig. 4.10). Our model predicted that male adult flies have higher mortality rates than female adult flies, which is consistent with the observations of Hargrove (2004) and Pollock (1982). As already mentioned, female adult flies spend their lives obtaining meals, converting the meals to fat and protein which is fed to the developing larva, depositing the larva and repeating this cycle. Adult male flies spend their lives trying to mate with as many virgin female flies as possible (Hargrove, 2004; Leak, 1999). The different mortality rates are a result of the different roles played by the female and male adult flies. For tsetse populations to survive, female adult mortality rates must not exceed 0.04 per day (Hargrove, 1988). Previous studies observed that newly emerged flies (teneral, immature flies) have higher mortality rates than mature adult flies (Hargrove *et al.*, 1995, 2011). Our model predicts daily female adult mortality rates of up to 0.15 per day during hot-dry seasons. In our model we considered adult flies to consist of both immature and mature flies, this explains why our predicted mortality rates are so high. The predicted mortality rates for both pupae and adult flies is consistent with observations from previous studies.

This study has shown that our ODE model explains about 55-60% of the variance in the estimated population of adult flies (R^2 of 0.60 for female adult flies and R^2 of 0.55 for male adult flies). For both the female and male adult fly populations, our model fits the data relatively well (Fig. 4.6 and Fig 4.7, respectively) until December 1980; from January 1981 the model population grows more slower than the observed population. The model output mimics the data, suggesting that our model captures the tsetse fly population dynamics relatively well.

Our ODE model includes two extra factors in addition to temperature: annual cycle and

pupal density-dependent mortality (k_p) which are extra parameters for the pupal and adult mortality functions, respectively. Mortality rates defined by Hargrove (2004) did not include the annual cycle and k_p fctors. Hargrove (2001) reported that the survival of adult *G.pallidipes* flies was correlated with both temperature and saturation deficit. As already mentioned, Hargrove and Williams (1998) observed a residual effect on adult mortality which was not associated with temperature, humidity or saturation deficit. Although we used the annual cycle, our model still does not consider saturation deficit and humidity. We believe that as suggested by Hargrove (2001), incorporating humidity and saturation deficit to our model should improve the fit, hence explain the population dynamics even better. However, we did not include humidity and saturation deficit in our model because we are not certain how these factors impact tsetse population dynamics. Until we have a better understanding we cannot include these factors in our model. Investigating the role of humidity and saturation deficit in tsetse population dynamics is beyond the scope of this project. Further investigations are required to determine the effect of other meteorological and biological factors. Although our model was validated with data from Antelope Island for *G.pallidipes*, the ODE model could be used to model populations of other tsetse fly species.

The next step was to assess the relative impacts of temperature, annual cycle and k_p on our model population. As already discussed, excluding temperature means we are keeping temperature fixed at 24.0 °C, which is the average of the recorded temperature from 5 February 1980 to 29 December 1981. We created seven restricted models to carry out this investigation.

Model 1 gave the best fit. Model 2 (excluding k_p) gave the second best fit. For model 3, we excluded the annual cycle only. For both the female and male adult flies, the resultant model fit was slightly worse than the fit from the full model. Compared to the full model, model 3 captures the population recovery relatively well between December 1980 and June 1981. Unexpectedly, the model population decreases between June and September 1981, though the observed population continues to grow. The observed population decreases again in October 1981, and the model population decrease is delayed, though the observed population continues to decrease until the end of December 1981. However, the model population recovers and increases. This model output is similar to model 4, which excluded both the annual cycle and k_p.

Model 5 included both the annual cycle and k_p, whilst model 6 only included the annual cycle. The presence of the annual cycle shaped the model fit to mimic data though the

fits were bad, with R^2 values of less than 0.5.

Model 7 only includes k_p, whilst model 8 excludes all the factors. For both models, the resulting model fit is a straight line. Model populations grow slower than observed populations. It is somewhat surprising that having excluded all the factors (temperature, k_p and annual cycle), the model population grows slower than the observed population. We expected the model population to grow faster and be higher than the observed population. At 24.0 °C adult flies produce larvae at rate 0.1049 (after every 9.5 days) and pupae emerge at rate 0.0326 (after about 30 days). Adult daily mortality rate is 0.0216 for female flies and 0.0406 for male flies. This may be because 24.0 °C is not the the optimum reproductive temperature. Hargrove (2004) found the optimum temperature for reproduction of tsetse flies in an island to be 26.0 °C.

Model 1 to model 4, in that order, produced the top 4 best fits for the female adult flies. Model 2 and model 3 suggest that the annual cycle and k_p have roughly the same impact on female adult flies. The top 4 best fits for the male adult flies are model 1, 2, 4 and 3. This suggests that the pupal density-dependent mortality has little impact on the male adult flies, so little that the model including temperature only gives a better fit than the model with temperature and k_p. This is surprising since k_p acts on the pupae and we assumed pupae emerges in equal numbers as male and female adults. Considering the model with temperature (and without temperature), the top 2 best model fits are the model 1 and model 2 (model 5 and model 6), both these models include annual cycle. These results suggest that after temperature, the annual cycle is the second most important factor influencing the population dynamics of tsetse flies on Antelope Island.

Our model results concur with previous studies, which suggested that temperature was the most important factor influencing tsetse population growth rates. However, our model, suggest that the annual cycle which is in phase with NDVI also influences the survival of adult flies.

The aim of section 5.3 was to assess how changing temperature impacts tsetse population dynamics. We used the ODE model to project tsetse fly population dynamics from 1980 to 1990. We considered three possible scenarios where temperature either stayed constant, increased or decreased. We used temperatures recorded using a Stevenson screen between 1980 and 1990 at Kariba airport approximately five kilometres from Antelope Island . We predicted that the population on Antelope Island would have gone extinct by November 1989 with temperatures at the recorded levels, even in the absence

of any trapping pressure. Our model shows that if temperature increased by even half a degree, the adult population would have gone extinct by October 1984. When temperature increased by at least one degree the model population did not follow the same trend as the observed population. From November 1980, model population shows a decreasing trend. Increasing temperature resulted in the predicted tsetse population going extinct earlier than if temperature had stayed constant. Tsetse adult populations went extinct by October 1983, October 1982 and November 1981 when temperature was increased by 1.0 °C, 1.5 °C and 2.0 °C, respectively. These results are broadly consistent with previous research which state that high temperatures will likely result in tsetse populations dying out (Hargrove, 2004; Leak, 1999).

Our study showed that if temperature were to decrease on Antelope Island, the tsetse population would continue to grow in a healthy fashion. When considering lower temperatures, the predicted tsetse population grew and was significantly higher than the observed population. Decreasing the temperature by 0.5 °C does not result in the extinction of the population, however, increasing the temperature by 0.1 °C the population went extinct by October 1988. These findings suggest that temperatures on Antelope Island (when the study was performed) were already higher than the optimum temperatures for tsetse populations to thrive. It has been shown, however, that ambient temperatures are higher than the temperature experienced in deposition sites. Moreover, adult tsetse use cooler refuge sites when ambient temperatures exceed 32.0 °C (Hargrove, 2004). The temperatures experienced by all life stages of tsetse can therefore be lower than ambient at the hottest times of the year. Our use of ambient temperature in our models may thus over-estimate the mortality rates occurring in pupae and adult flies. If this is the case, populations might not have gone extinct as quickly as we predict. Further work is necessary to throw further light in this problem.

Chapter 7

Conclusion and Future Work

7.1 Conclusion

The aim of this project was to investigate the effects of temperature on tsetse fly population dynamics. We planned to do this by applying an ODE model to mark-recapture estimates of tsetse fly populations on Antelope Island. Results from the literature suggest that temperature was not the only factor that influenced tsetse population, hence we added two extra factors to our model, (i) the annual cycle, which is in phase with NDVI, and (ii) pupal density-dependent mortality, k_p. Our model explains about 55-60 % of the variance in the estimated populations of male and female *G. pallidipes*.

This study has shown that temperature is the most important factor influencing adult mortality rates and population growth rates for tsetse populations. The above result concurs with previous studies on the effects of temperature on tsetse populations. However, our study suggests that the annual cycle is another factor influencing the survival of adult tsetse flies. The results indicate that female and male adult flies are influenced by different meteorological factors; which is not surprising since female and male adult flies have different roles within the tsetse population.

There is, therefore, a need to investigate the annual cycle factor and find out how exactly it influences tsetse populations. It would be interesting to assess the effects of humidity and saturation deficit and observe how these factors might change our current results.

Part of the third objective was to use the ODE model to predict the impact of temperature change on tsetse fly distribution. The results of this investigation suggested that even

small increases in temperatures would seriously affect tsetse populations. The greater the increase in temperature, the sooner the tsetse population would have gone extinct.

The tsetse population went extinct by October 1988 when temperature was increased by 0.1 °C, whilst they would have gone extinct in October 1984 if temperature increased by 0.5 °C. If temperature stayed constant our model predicts that the population would have died out by November 1989.

Our study has shown that decreasing temperature by 0.5 °C would have produced good conditions for tsetse population growth to persist. Decreasing the temperature further resulted in higher tsetse population growth. These results suggest that during the experiment on Antelope Island, the temperature was perhaps already too high for *G. pallidpes*. It is possible that the effect of temperature is exaggerated due to our model using ambient temperatures, and due to the exclusion of the other climatological factors (saturation deficit, humidity). Further studies, which take these factors into account, need to be undertaken.

7.2 Limitations

The data for pupal duration is from the laboratory study carried out by Phelps and Burrows (1969*c*). This study was done using *G. m. morsitans* not *G. pallidipes*. Since we know that *G. m. morsitans* and *G. pallidipes* behave differently, we could shorten or lengthen the assumed emergence rate and investigate if that has any significant impact on the population. The adult mortality rates were estimated by mark-recapture studies on Antelope Island between February 1980 and November 1981, which is the same data we used for this study. The observed mortality rates were not necessarily constant between 16 °C and 24 °C (Fig. 3.10), but we assumed they were constant. This assumption might affect our predicted population. Future studies will attempt to investigate the impact of this assumption.

7.3 Future work

7.3.1 Trypanosomiasis

Understanding tsetse population dynamics can be of importance for the implementation of effective tsetse control strategies which will lead to better techniques for trypanosomiasis control and possible elimination of the disease. Global temperatures have been

increasing in the recent decades, and they are expected to keep increasing. It is, therefore, important to understand how vector population dynamics will be altered by the increasing temperatures.

To investigate the effects of temperature on tsetse fly population dynamics and their influence on trypanosomiasis disease distribution we will incorporate our model into existing SIR compartmental models for trypanosomiasis. Figure 7.1 shows one of the models used to model the disease dynamics of trypanosomiasis considering both humans and tsetse populations (Kajunguri *et al.*, 2014).

H and V are the model variables referring to the human and vector populations, respectively. Susceptible individuals get infected at rate σ_H, infected people recover at rate δ_H, people are recruited at rate $\beta_H$and the mortality rate is ν_H. For the vector, tsetse flies are born at rate β_V, with susceptible flies getting infected at rate λ_V and all tsetse dying at rate μ_V. To make the model temperature dependent, β_V and μ_V will be functions of temperature. To model both pupae and adult flies separately we will use our model to define the susceptible vector population and only adult flies will transition to I_V after being infected; pupae cannot be infected.

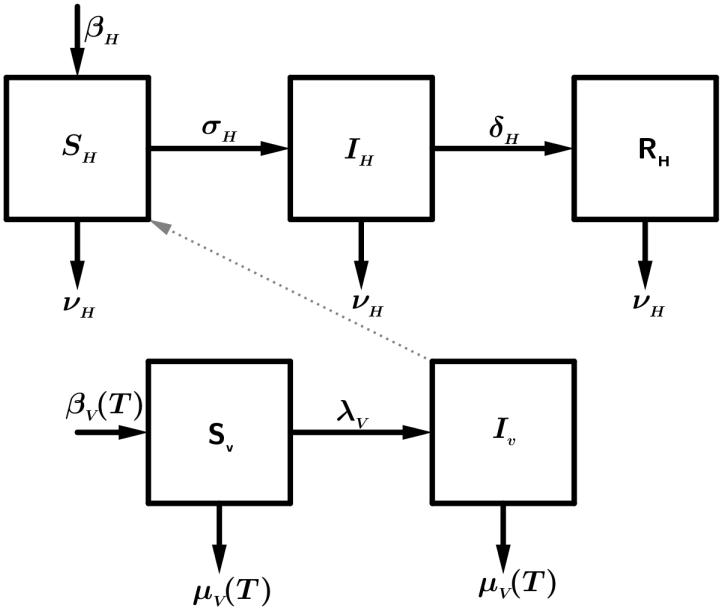


Figure 7.1: Schematic diagram of the compartmental model for trypanosomiasis

7.3.2 Model improvement

Our ODE model assumes exponentially distributed waiting times in all compartments, but we know that this is not the case for the pupal period. Our model assumes that waiting times until adult emergence are exponentially distributed so that pupae start emerging immediately after deposition. In fact the probability of emergence for the first 95% of the pupal period is zero. Adding extra compartments take into account the delay between the time pupa is deposited and the time it emerges, which is influenced by temperature. This can be modelled by thinking of the pupal period as a process with n stages, that is the pupae moves through n stages at the rate λ'. Instead of having $P \to F$, we will have $P_0 \to P_1 \to ... \to P_n \to F$. Instead of $P = e^{-\lambda t}$, P is now represented by the following equation

$$P_n = \sum_{j=0}^{n} Ce^{-\lambda t}.\frac{(\lambda t)^n}{n!} \tag{7.3.1}$$

for $n = 0, 1, 2, 3, ...$ where C is a constant and t is time. Adding each compartment results in further delay (Loder *et al.*, 1998). For example when $C = 1$, $\lambda = 0.35$ and considering different values of n we see how the shape changes, distribution changes as shown in figure 7.2.

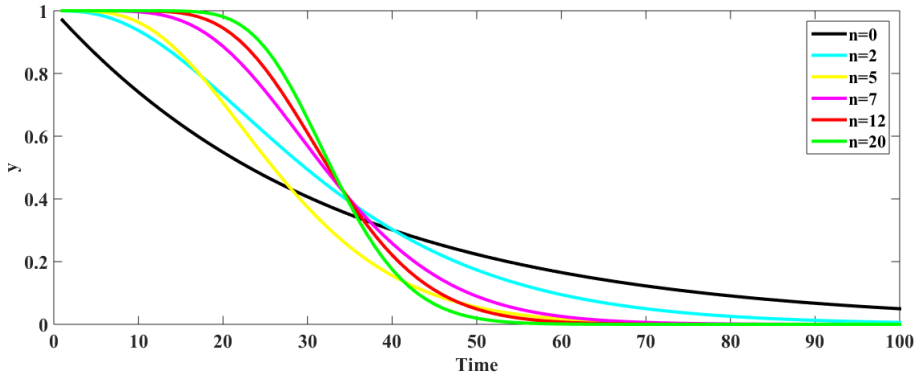


Figure 7.2: Graph showing how the distribution changes with different number of compartments

As an example, we will consider the pupal period to consist of four compartments. We will extend the model further, by adding density-dependent pupal mortality, m. The

use of n compartments does not imply physical connection among the different compartments, it is just a mathematical device that allows for delay that was not taken into account by the initial model (Loder *et al.*, 1998). Figure 7.3 shows the schematic diagram of the n-compartment model.

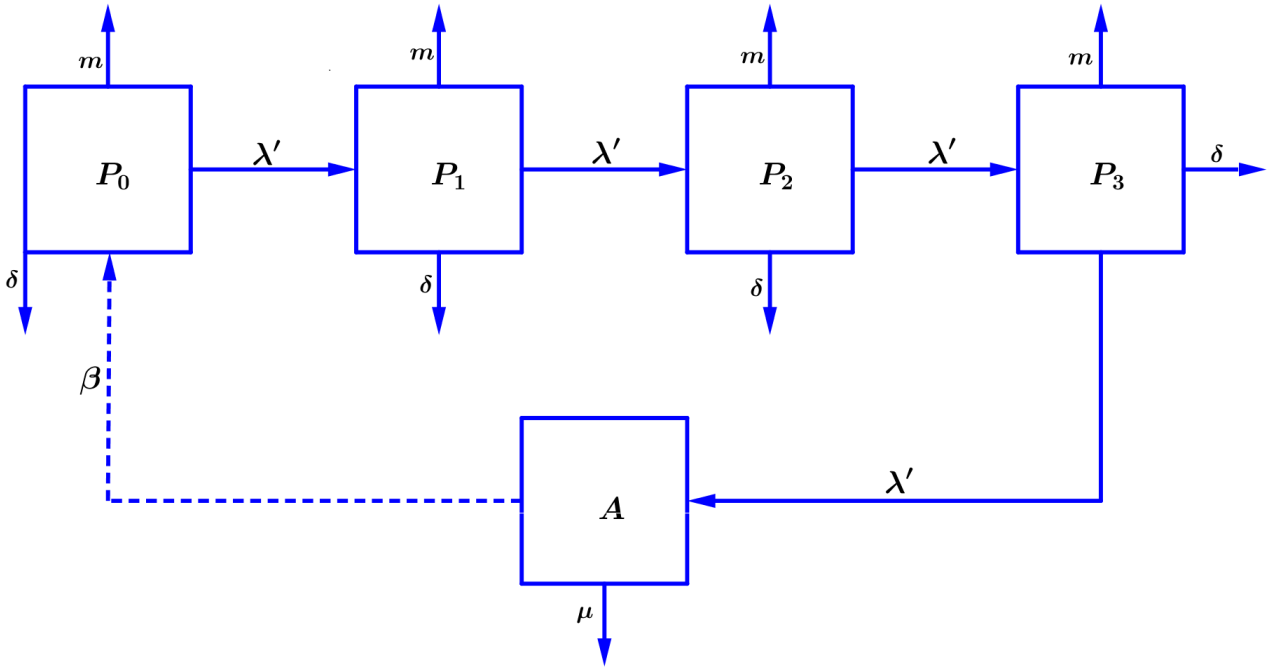


Figure 7.3: Schematic diagram of the 4-compartment model and density-dependent mortality.

The n-compartment model can be further improved by considering two classes for the adult population.

Teneral flies experience higher mortality rates than adult flies (Hargrove, 1975*b*). To incorporate this finding into our model, we divide the A compartment into two compartments A_0 and A_1 which represent teneral (immature) female flies and mature adult female flies respectively.

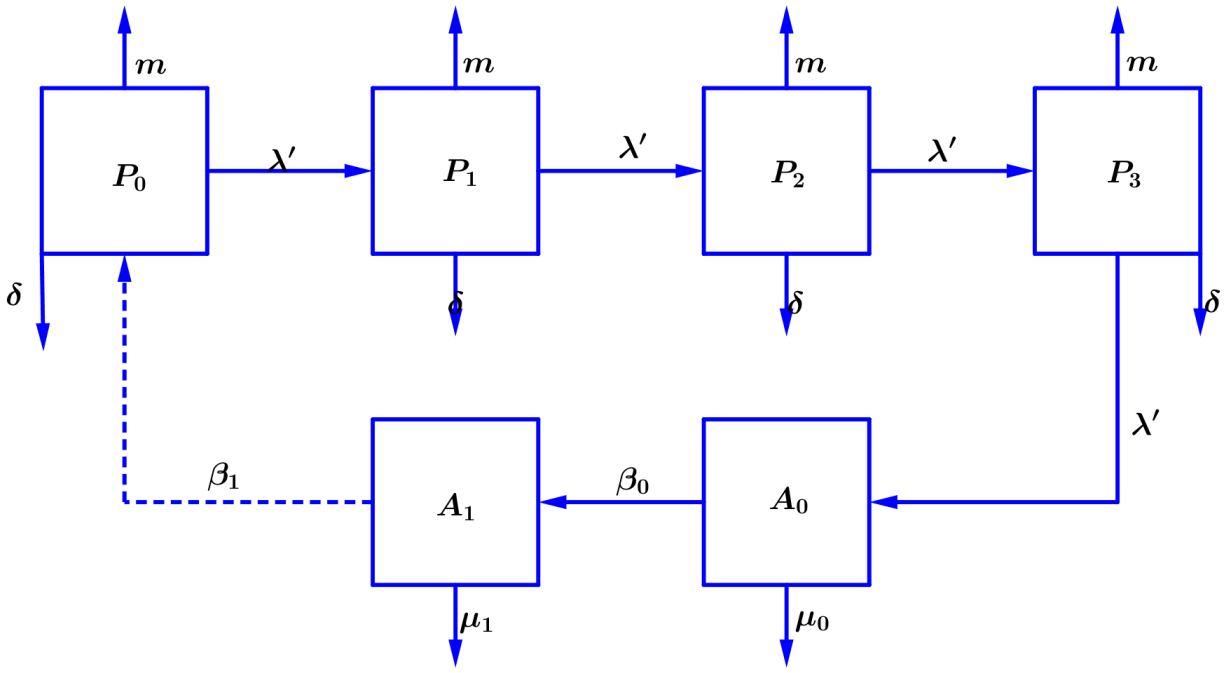


Figure 7.4: Diagram of the extended n-compartment model with density dependent smortality

For future work, we will develop these proposed models further and we will compare their performance to the ODE model used in this project. We want to investigate the necessity of these extra compartments. Further research will help us decide which climate factors other than temperature have a significant impact on tsetse population growth rates.

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