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Investigating the Simultaneous effect of Age and Temperature on the Population Dynamics of Female Tsetse Flies

by

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

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December 2011

Declaration

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December 2011

Abstract

Age and temperature are two factors that affect mortality in adult tsetse flies. Both are found to be very important, but the simultaneous effect of these factors on the mortality rate have not been studied. This study seeks to address this, with an application to a population of female tsetse, using a model based on partial differential equations. Adult mortality is age-dependent and is modelled as the sum of two exponentials, with four parameters (coefficients of each exponential): numerical analysis of a population model with this mortality structure predicts exponential growth. Analysis of each of the parameters through parameter variation shows that two of these parameters control the mortality of the nulliparous (ages $0-10$ days) flies only while the other two only take care of flies of mature ages. Measurement of the impact of these parameters on the mortality of tsetse of different ages by the normalized forward sensitivity index method is also carried out. This is followed by fitting the model based on the age-dependent mortality along with a constant tsetse birth rate to data representing the catches of female *Glossina pallidipes* at Rekomitjie Research station, Zimbabwe. Considering a three parameter adult tsetse mortality, parameter analysis shows the effect of one of the parameters to affect the mortality of flies of all ages while a second controls only the mature tsetse flies of reproductive ages. A further analysis resulted in the estimate of these parameters as functions of temperature, thereby leading to the establishment of an age and temperature-dependent adult tsetse mortality. Using data for the daily average temperature records obtained in 1981 on Antelope Island, Lake Kariba, Zimbabwe, daily changes in the pupal duration (adult tsetse birth rate) changes negatively with temperature change. Incorporating this (temperature-dependent) birth rate into the model, together with the established age and temperature-dependent adult mortality, the adult tsetse population dynamics is explored numerically. The latter model is then fitted to population data of female *Glossina morsitans morsitans* obtained from the same Island and for the same period as used for the temperature data. The data suggests peak tsetse population to be in the month of July and lowest in the month of December. The first quarter of the year is predicted to be most favorable for breeding tsetse while the second, showed a period of stable growth rate and a time of tsetse abundance. In addition, the dynamics with both age and temperature showed a non-uniform daily population growth contrary to that with age effect only. This study has enhanced our understanding of tsetse population dynamics for age and temperature-dependent adult mortality with temperature-dependent pupal duration and suggests the period of tsetse abundance on Antelope Island.

Dedication

I dedicate this thesis to my parents Mr. and Mrs. David Ameh, my siblings, my sweet heart, Mr. Vincent Ochigbo and to all my relations (too many to mention). You have all been there for me.

Acknowledgements

Contents

Contents   5

Contents   6

List of Figures

List of Tables

Chapter 1

Introduction

1.1 Tsetse fly, a vector of trypanosomiasis: an overview

We live in a world where insects in one way or another interact with humans and other mammals. Some insects are not only an annoying nuisance but also spread various infectious diseases to humans, livestock or even both. Some of these insects are mosquitoes, sandflies, ticks which transmit malaria, leishmaniasis and Lyme disease respectively. Of particular interest to this study are more than 20 species of heamotophagous (blood sucking) insects of the genus *Glossina* known as tsetse fly.

The vector causes disaster both in human and animals in the spread of the disease known as African trypanosomiasis. This is prevalent in many regions of the African continent and is transmitted when the fly takes a blood meal from humans or animals. Currently, about 36 sub-Saharan Africa countries suffer the consequences of this disease with profound effect on sustainable development in poor African rural settlements. The major income activities in such rural communities are farming and cattle rearing.

Human African trypanosomiasis (HAT), popularly known as "sleeping sickness" due to its nature of development, is the disease affecting humans. The one which affects the animal population is called African animal trypanosomiasis (AAT) or Nagana (Zulu word meaning a low or depressed spirit). It causes a breakdown in human and livestock efficiency thereby leading to a measurable burden on economy and agricultural developments. This is because, infection in a human, brings down the central nervous system thereby compromising the ability of such individuals to produce food or even participate in social activities efficiently. Animals used in merchandise farming to enhance agricultural productivity are targets for these vectors. This is important since animals such as cattle are the major source of milk and also serve as

1

meat for human and some animals' consumption.

In fact, if these vectors are neglected and the disease spreads across the animal population, it not only reduces their productive level but may also lead to a decline of the population through death. This can cause heartbreak to the owners of these livestocks whose livelihoods are heavily dependent on the animals. Moreover, some herdsmen may even lose their jobs as a result of this. More worrying, is the case where the disease is allowed to spread into the human population, which is of great concern for human existence and efficiency. Given all of these concerns and many more not mentioned, we cannot shy away from the importance of these vectors to the society.

1.2 Motivation for this study

The possibility of controlling or eradicating trypanosomiasis requires a good understanding of the dynamics of the vectors responsible for its transmission together with the various factors that affect it. It is established that some of the tsetse biological variables are affected by factors such as age, temperature and seasonality. The effects are observed on their mortality, birth rate and thereby, the population distribution across space and time. The growth rate of any (closed) population is entirely determined by the birth and mortality rates. For tsetse, each of these have been found to be affected by age and temperature separately. It is established that temperature affects the larval and pupal stages of tsetse life cycle and also affects the adult tsetse mortality rate. Several age-related findings in the ecology and life history of these flies have also been established.

Determination of tsetse age, with further investigation on how it affects the flies' survival, is important for studies into the disease transmission. It is noted that older flies are more likely to carry mature trypanosome infections than the younger ones. This is because the older flies would have been exposed more to the disease than the younger flies and so have a higher chance of being infected through infected hosts during feeding. Moreover, it takes some time for the disease in tsetse to develop into the metacyclic (infective) stage. The older flies must have lived long enough, to have the mature stage of the disease. This explains the importance of accurately estimating tsetse age since it creates the possibility of estimating the proportion of flies of various ages that contribute to disease transmission at any time.

Knowledge of the simultaneous effect of age and temperature on tsetse mortality, hence its survival, is currently lacking. These two factors co-exist and contribute to the population dynamics through the flies' mortality rate in their different ways.

In this regard, we are motivated to fill this gap as it will give a deeper understanding of the population dynamics under natural and climatic conditions. It is therefore our aim to explore the simultaneous effect of both age and temperature on the dynamics of the female tsetse population. One of our investigations will be the changes that occur in the adult tsetse mortality with change in temperature and how these are distributed across tsetse of different ages. We will also examine how such changes influence the total population with time. This will be carried out using the assumption of a temperature-dependent tsetse birth and death rates given.

The tool which we will use to carry out these investigations is a partial differential equation (pde) model structured by age and time, with a single dynamic variable for both pupal and adult tsetse population. This will be used under different assumptions on the mortality and birth rate. Such models enable prediction of the future population while considering the effect of two or more different independent variables at the same time. The model will then be analyzed mathematically and also numerically using various simulations to describe the dynamics. Other analyses that will be carried out are: parameter and sensitivity analysis together with estimates of the mean mortality with which we will explore the effect of temperature on age-dependent mortality. Such analyses will provide useful information to public health workers and non-governmental organizations (NGOs) responsible for the vector control in the fight against the spread of disease.

1.3   Structure of the study

Chapter 1 (Introduction) introduces what this study is all about as described in the sections above.

Chapter 2 (Literature review), gives a description of the female tsetse life cycle together with the different aging and sampling techniques applied on the vectors. Chapter 3 (Continuation of literature review) discusses the various methods applied in several studies to estimate tsetse survival and population growth rate.

Chapter 4 (Modelling) provides a formulation of an age structured model using a partial differential equation which accounts for two stages of the tsetse life cycle (pupal and adult stages, with a constant pupal duration). The model is analyzed mathematically and numerically. It assumes a four-parameter age-dependent adult mortality and a constant pupa mortality. This is followed by parameter and sensitivity analysis on the role and impact of the parameters that affect adult mortality. Furthermore, a fit of the model to ovarian age category data

for female flies of *Glossina pallidipes* collected from Rekomitjie Research Station, Zimbabwe and pooled over 6 years is obtained. Sensitivity analysis of the estimated parameters from the fit, is further carried out in this chapter. In addition to this, a three parameter mortality model is presented with parameter variation and the sensitivity analysis on the three parameters further carried out. Two of the mortality parameters, identified to be of biological importance, were used to establish an age and temperature-dependent adult mortality under various assumptions.

Chapter 5 gives the application of some of the results obtained from the previous chapter on the adult tsetse mortality as a function of both age and temperature to the model of Chapter 4. Numerical analysis of the modified model under the assumption of temperature-dependent tsetse birth rate is also carried out. Fit of the model is obtained using monthly population data of female adult *G. m. morsitans* collected on Antelope Island, Lake Kariba, Zimbabwe in 1981.

We then discuss and give our conclusions based on the observations and findings of the three previous chapters in Chapter 6 with recommendation on future research investigations.

Chapter 2

Literature Review 1

2.1 Tsetse life cycle

The life cycle of the female tsetse fly is very unusual amongst insects. Like most insects, male tsetse flies mate almost throughout their life time. Female tsetse flies, conversely, only mate once in their entire life. Male *G. m. morsitans* are observed to meet the females on or near host animal, often when the female is about to take her first blood-meal. The male tsetse settles on her back with a tight grip on her and copulation can continue for anything up to an hour or 2 hours before parting. After separation, the sperm from the male deposited in the female uterus moves from the spermatophore to the spermathecae where it remains and is used for egg fertilization until the death of the fly [80]. Thus, every offspring of that female fly is the product of the sperm from a single male, stored and used for the egg fertilization one at a time.

Generally, there are three major stages (egg, larva and pupa) in an insect's pre-adult life cycle. The development of these stages for most insects, take place outside the female uterus from which the eggs are produced. For insects such as horn flies and stable flies, for example, the place they call home for their eggs is wet dung while some others like mosquitoes deposit their eggs in stagnant water [120]. The females in such insects typically produce large numbers of small eggs, which give rise to larvae that must feed themselves to get the energy and raw materials to reach the pupal stage.

In the tsetse fly, by contrast, the first two stages (egg and three larval instars), take place in the uterus of the mature adult females where the larva is fed and nourished until due for deposition, from a uterine gland, by the milk produced from blood meals taken by the female fly. Little wonder, some authors pointed that they have more in common with mammals than

5

with insects [80, 82] possibly because of the similar responsibility of catering for their young ones.
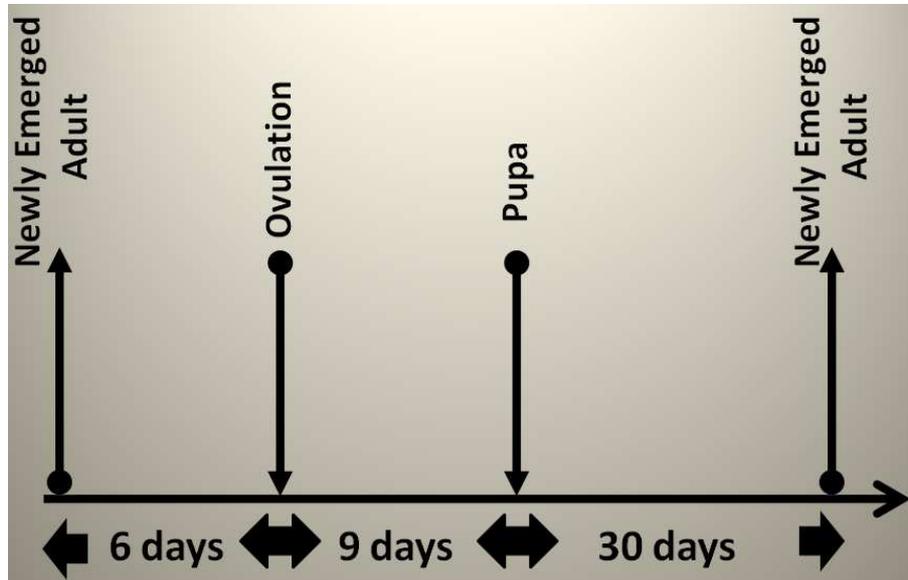
FIG. 2.1. Flow chart of female tsetse life cycle (25^0C)

Each of these stages for the tsetse flies has attracted considerable attention in various studies but most especially, the pupa and adult stages which completely take place outside the uterus thereby interacting with the environmental and climatic conditions. The first ovulation for a newly emerged fly is estimated to take place about six days after emergence. An observation made on pregnant female *G. pallidipes* showed that large amount of fat and protein are transferred to the larva in the uterus, leaving the postpartum female herself with low fat reserves at the end of pregnancy and so, in urgent need of blood meal at such times [40]. The adult female fly immediately after depositing the larva becomes very active in seeking a host to feed on and so is relatively easily found in the field and captured at this stage of pregnancy cycle. The larval stage comprises the first, second and third larva instars. In total, this stage (interlarval period) takes about nine days, although this figure varies with temperature and other climatic factors as observed at Nguruman Kenya [63, 90, 102] and in Zimbabwe [115, 116].

When the larva is fully developed with the completion of the third instar stage, the female fly deposits it in a suitable site chosen to protect the pupa from unfavourable weather conditions. Most times, the larva deposited weighs more than the female that has just deposited it [109]. On deposition on the soil's surface, the larva burrows down to a depth of one or two inches for most species of *Glossina* [1] and immediately develops a puparial case in which development

continues through the pupal phase and to the point where the adult has fully developed and is ready to emerge. During this period of stay in the ground, and until emergence, the pupa uses the fat and protein derived from the milk it consumed and stored while still a larva in the female uterus. The duration of stay in the ground before emergence according to several studies, is highly dependent on temperature [56, 66, 73, 120], varying between $95 - 96$ days at 16^0C to $19 - 20$ days at 30^0C [120]. With an average temperature of 25^0C, it takes a period of about 30 days [80] as demonstrated in FIG. 2.1 before the fly emerges as an adult. And so, this marks the beginning of a new generation as an offspring of the previous matured female fly that gave birth to the newly emerged fly some time back.

2.2 Methods for estimating age in tsetse

2.2.1 Introduction

"For the successful control of any insect pest, an understanding of the many age-related aspects of its ecology and life history may be of considerable value" [68].

Insect vectors are of epidemiological importance both to human and animal populations because, some of these insects (mosquitoes, sand flies, horn flies, tsetse flies) are responsible for the spread of deadly infectious diseases that affect either human or animal population or even both. The transmission rate, prevalence and disease development are found to be age related. Saunders [109] in his studies mentioned the importance of knowing the age structure of a tsetse population in understanding the quantitative epidemiology of trypanosomiasis. Supporting this statement are the outcomes of various experiments on field data whereby the prevalence of matured trypanosome infections of tsetse was noticed to increase with age [51, 67]. On the other hand, the rate of infection declines in older flies of laboratory colony for example, for Trypanosome brucei infection [61] and Trypanosoma congolense infection of *G. morstitans* [125].

In a mark-recapture study carried out on Redcliff Island, Lake Kariba, Zimbabwe [113], the capture probability of male and female *G. morsitans* Westwood was observed to also change with age. One important parameter in any ideal population model is the 'birth rate'. In laboratory populations, this was observed to decrease with age [27]. Another laboratory finding that supports this result was carried out on mated female flies of *G. morsitans* [33]. The outcome was such that a constant rate was observed in the first 60 days of reproductive age or emergence, followed by a sudden decline.

With an age-structured population, the changes occurring in the population over time for flies of different age groups could be measured and would serve as a tool to public health in the identification of the type of technique that would yield effective control of tsetse population. Based on these findings and many others that will be discussed later, it is therefore important to estimate the ages of tsetse flies in the field.

In order to obtain a good understanding of the dynamics of any living population, it is important to develop accurate methods by which the ages of individuals can be determined. In the case of tsetse flies, several methods have been used, although none produces accurate result over all ages, as evidenced by the following review.

2.2.2   Analysis of wing fray

The wing fray technique used to age tsetse flies and other insects was developed in 1946 by Jackson [71] using adult male tsetse flies of known ages that emerged from about $30,000$ pupae of *G. morsitans* Westwood. In the experiment, Jackson examined the progressive wearing of their wings with age. The percentage fray of the trailing margin of the wings was recorded and based on the variations in the level of fray, six wing fray categories were identified.

The first category named 'perfect' consisted of flies without any trace of fray. Such flies could be likened to new born babies free of wrinkles. Most newly emerged teneral flies (flies that are yet to take their first blood meal after emergence) will be classified in this category. These flies having small fat reserve and poorly developed flight musculature, are unable to participate in any serious and long flight activity and thus there tends to be little wear on the wings. Teneral flies have a higher probability of being caught from mobile (human or animal) hosts that happen to move past the vicinity where the young tsetse fly happens to be sitting.

After consuming about $2-3$ blood meals, and have utilized them for flight muscle development and the deposition of fat reserves [19], the flies are then able to fly more actively and the rate of wear on the wings increases.

Flies with only slight fray perhaps obtained accidentally during the capture process were placed in the second category. It was observed during Jackson's [71] experiment that some flies accidentally had their wings damaged in the net of the catchers and this could be misinterpreted as an aging effect.

The third category constituted flies with moderate damage affecting only the proximal part of the margin before the notch. Those flies whose wings had fray both before and beyond the

notch, yet having a large portion undamaged, formed the fourth category. There is no clear distinction between flies in the last two categories mentioned above and may possibly lead to bias in classification of flies according to their correct age category.

With time, the wear and tear on the wings becomes severe, leading eventually to a saw-edge like shape. Flies with such kind of wing fray were placed in category five.

Lastly, some flies are observed to have badly damage and tattered looking wings, with some pieces missing, and these flies form the sixth wing fray category. Naturally, human beings in their old age, have their skin wrinkled due to the length of years spent in life. In the same vein, Jackson calibrated the observed wear against known age with which the wing fray categories were identified. Flies belonging to the last category were observed in the sixth week of emergence during the experiment.

The level of wing fray is presumably not directly due to aging but refers, rather, to a measure of the overall level of flight activity undertaken during a fly's life-and this level must of course increase monotonically with age. Fly activities changes with age [38, 103] as observed in female flies, yet individual fly's involvement in rigorous flight activities such as frequent search for blood meal from preferred host species [89], escape from predators and from being captured, hunt for fresh virgins (amongst male flies), could all bring about high rates of wing fray. The more the flies are exposed to numerous rigorous flight activities, the higher their chance of incurring high damage on the wings.

Female flies are found to be very active in the field in search for blood meal immediately after larva deposition. After the consumption of relatively large proportion of blood meals, become inactive for some time and resumes again on deposition of another larva. This process continues throughout the life of each female tsetse fly. On the other hand, male tsetse are almost always active in the field in relation to both mating and feeding activities, which makes them more vulnerable to having higher damaged wings.

It has been observed that the wings are used not only flying in search of blood meals, but also by the female flies for buzzing (one of the three phases of copulation) [110] and sound production [89].

The wing fray aging method, according to Jackson, is reasonable for estimating the mean sample age as shown on TABLE 2.1. He also pointed out the possibility of flies appearing to be older than they actually are due to temperature effect on the rate of wing fray. Vale et al. [95] later applied this technique to both male and female flies of the same species.
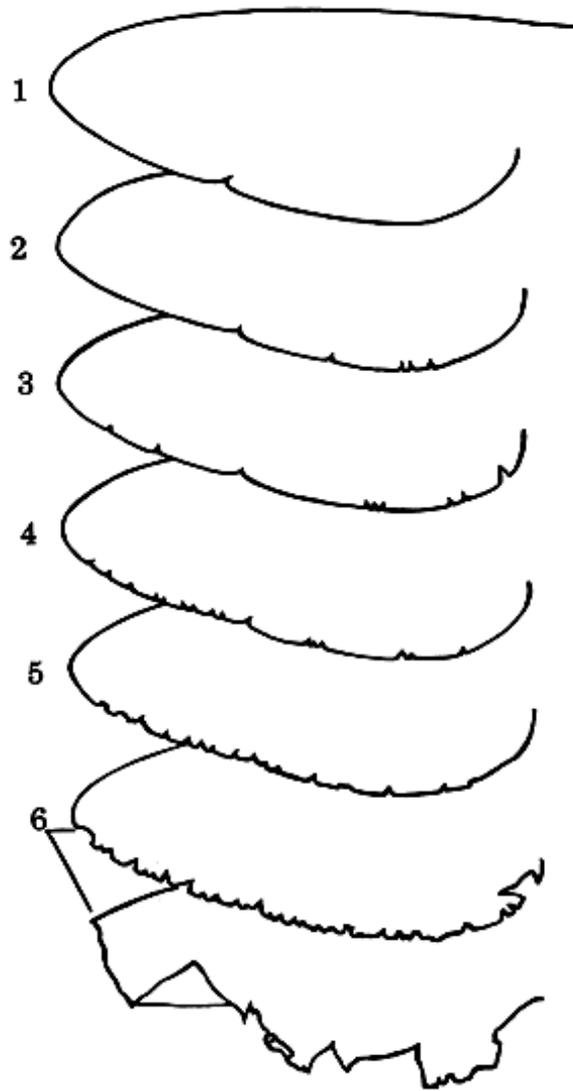
FIG. 2.2. Six wing fray categories developed by Jackson [71]: www.fao.org

The technique is seen as a more convenient way of determining the ages of male tsetse flies and other insects due to the limited availability of alternative practical techniques [89]. Furthermore, the method has proven useful or relevant in separating female tsetse between their second and higher number of ovarian cycles [87]. Taylor demonstrated this by obtaining the ages of flies in the second and third ovarian cycles. According to this author, it serves as a better approach in estimating the number of flies in each age category other than assuming a logarithmic death rate as had been applied [75, 109]. Applying this aging technique too, Snow and Tarimo [12] also obtained the ages of tsetse flies with four or more ovulations. This enabled estimate of the overall mean survival rate of the flies to be obtained.

TABLE. 2.1. Mean age of a sample of 30 male tsetse flies, deduced (within a day) by noting the number assigned to each category [71].

Category	Root mean fray (probable)	Sample: 1	2	3	4
		Age: 17.2	17.3	27.9	29.4
1	1.0	11	9	5	2
2	2.0	10	9	3	6
3	3.0	3	7	12	9
4	4.4	3	4	4	7
5	5.5	1	0	1	2
6	6.9	2	1	5	4
Probable root mean fray		2.4	2.4	3.5	3.7
Deduced age		18	18	27	29

Several other applications based on this technique have been carried out; we shall mention but a few.

One of these is the study that compares the rate of wing fray amongst tsetse emerging from pupae collected in the wild, and those from membrane-fed and goat-fed tsetse [95] with the last two cases applied on laboratory reared tsetse flies. This was carried out on *G. morsitans* with the results showing no difference in the distribution of the rate of wing fray among the three case studies mentioned.

In addition, the effect of an aerial spraying program on the different age distribution of male flies of *G. morsitans* was evaluated using this technique [20]. Although, due to the slow nature in the process of the wearing of wings, the author, Davies discouraged the use of the technique in assessing the development rate between air sprays. This is also due to four distinct results obtained. The first was that there was no sign of breeding occurring between sprays. Secondly, four spray applications covered only one pupal period. Thirdly, female survivors from the spray formed the residual population and lastly, despite the very low rate of insemination between sprays, all female survivors were found to be (inseminated) or pregnant at the time of treatment. Another result obtained based on this method of aging, is the determination of the start point of the female tsetse's pregnancy cycle (Rogers and Randolph 1978b cited in [46]). This was achieved based on the frequency distribution of each wing fray category along with corrected RDW (Residual Dry Weight). Newberry et al. [64] were able to identify the age-specific feeding pattern of tsetse using the wing fray. A very important epidemiological concept, trypanosome infection rate, has also been estimated in flies of different age groups by this technique [51, 76, 93] together with the disease prevalence rate amongst the flies [51].

Irrespective of the shortcomings associated with the technique, it has had a wide range of application not only for tsetse flies, but also for other insects such as blowfly *Lucilia sericata* Meigen (Diptera: Calliphoridae) [22]. In 1960, Cobert [98] used the wing fray to obtain what he called a reliable indication of the parity in the mosquito $Mansonia$ $(Mansonoides)$ $africana$ Theo.

Whereas the wing-fray method has clearly had its uses in the past, it is only an approximate method and tsetse biologists spent many years looking for more accurate ways of estimating age in tsetse flies. We now turn our attention to one such method, which has been widely used in the estimation of the age of female tsetse.

2.2.3   Ovarian dissection

Dissecting the ovaries of female flies is another technique used in determining the physiological age of tsetse flies. The method was first established and applied on female *Anopheles* mosquitoes [85, 99] and is used in determining the ages of most blood sucking insects.

As will become evident below, in tsetse flies the accuracy is somewhat limited to flies with evidence of three or fewer ovulations [108]. Nonetheless, within this range the method gives a more accurate estimate of age than is obtainable from wing-fray alone. Moreover, we will suggest below, ways in which the combined use of ovarian dissection and wing-fray analysis might be used to provide more accurate estimates of age among tsetse that have ovulated more than three times.

Early research revealed that female tsetse flies have two ovaries as is the case with other female insects. Mellanby [35], studied the ovulation cycle of *G. palpalis* (Robineau-Desvoidy), *G. m.* Westwood and *G. swynnertoni* with the assumption that each ovary contains only a single ovariole, see also [1] and [37] as cited in [106]. Later experimental observation on tsetse flies of *G. morsitans*, *G. palpalis*, *G. pallidipes* Austen and *G. brevipalpalis* Newstead, contradicts this assumption [105]. By dissecting the female ovaries, it was discovered that each ovary in the flies contains two polytrophic ovarioles, each in turn containing a single oocyte.

Pioneering experiments on the determination of the physiological age of newly emerged female flies of *G. morsitans* by this method was conducted by Saunders in [104] but the method was made markedly more precise by the work of Challier [2] and we will review the method as presented in the latter work.

The uterus of each dissected fly used in the experiment was examined, investigating whether

it contains an egg or a first, second or third instar larva. The number of follicular relics present, the position of the relics, and the sizes of the four egg oocytes were also investigated. A follicular relic is a trace each ovulation leaves behind with only one relic persisting and corresponds to the most recent ovulation. As also described in Figures 2.3 and 2.4, the age of the fly can be estimated from the size of the uterine content, the relative sizes of the oocytes and from the number of times each ovariole has ovulated.

2.2.4   Ovulation status and tsetse aging limitation

The four ovarioles contained in the ovaries of a female tsetse fly are identified as right inner (RI), left inner (LI), right outer (RO) and left outer (LO) with ovulation taking place sequentially in that order after the female fly has mated and been inseminated. FIG. 2.3 describes the uterine and ovarian cycles of a female tsetse.
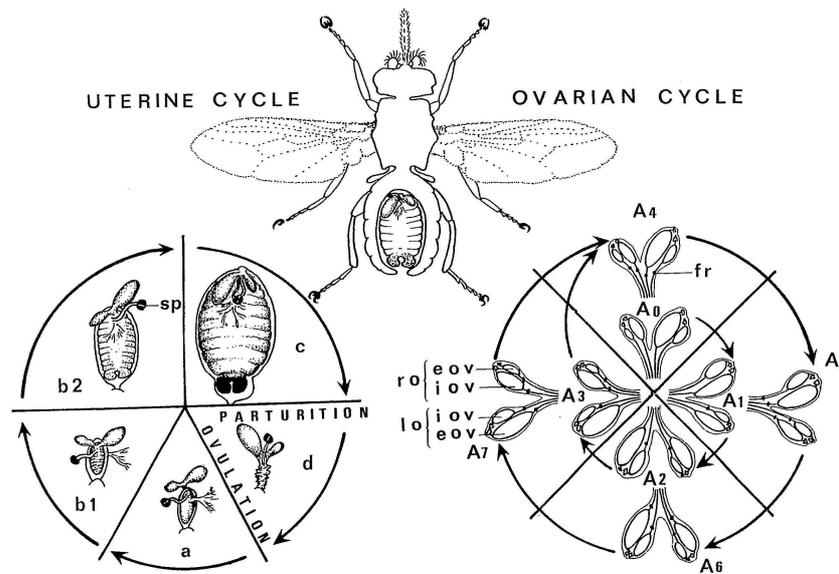
FIG. 2.3. Uterine and ovarian cycles of *Glossina*. Determination of physiological age. Uterine cycle: a: egg; b1, b2, and c: first, second and third instar larva; sp: spermathecae. Ovarian cycle: ro and lo: right and left ovary; i ov and e ov: internal and external ovarioles; fr: follicular relic [58].

In normal flies, the right ovary at emergence is always larger than the left ovary, and each egg follicle differs in size [108]. The presence of an open expanded sac in the follicular tube is an indication that ovulation has taken place in that ovariole. This could also be known by the appearance of a small follicular relic ("corpus luteum") sitting on the posterior end of the follicular tube after the open sac has regressed [108]. The cyclical process of ovulation

continues throughout the entire life of the fly. Moreover, the cycle is very regular in its timing, being dependent largely on temperature. The proportion of the current pregnancy completed is estimated by measuring the sizes of the oocytes and uterine content as earlier stated. Knowledge of the number of ovulations, together with the position of the last ovulation makes it possible then to estimate the age of the female fly.

Ov. Cat.		Est. age in days	Ov. Cat.			Est. age in days
O	Non-ovulated	* 0–8	1	1-ovulated	1a / 1b / 1c	8–12 / 13–16 / 16–19
2	2-ovulated	2a 20–24 / 2b 24–27 / 2c 27–30	3	3-ovulated	3a / 3b / 3c	30–34 / 34–37 / 37–40
4	4,8,12....ovulated	4a 40–44 / 4b 44–47 / 4c 47–50	5	5,9,13..ovulated	5a / 5b / 5c	50–54 / 54–57 / 57–60
6	6,10,14....ovulated	6a 60–64 / 6b 64–67 / 6c 67–70	7	7,11,15..ovulated	7a / 7b / 7c	70–74 / 74–77 / 77–80

Ov. Cat.		Ov. Cat.		Ov. Cat.		Ov. Cat.	
8a	80–84	9a	90–94	10a	100–104	11a	110–114
8b	84–87	9b	94–97	10b	104–107	11b	114–117
8c	87–90	9c	97–100	10c	107–110	11c	117–120
12a	120–124	13a	130–134	14a	140–144	15a	150–154
12b	124–127	13b	134–137	14b	144–147	15b	154–157
12c	127–130	13c	137–140	14c	147–150	15c	157–160

Ov. cat. = ovarian category   a = uterus with egg   b = uterus with 1st or 2nd instar larva   c = uterus with 3rd instar larva empty

* Ovarian category O flies can be subgrouped according to the size of the inner right ovariole (0.4–0.6 mm, 0.6–0.9 mm, 0.9–1.2 mm, 1.2–1.5 mm, see text)

Ovariole without follicular relic   Ovariole with follicular relic

FIG. 2.4. Female tsetse ovulation cycle: www.fao.org

The ages of the flies can be uniquely determined only to the point when each ovarioles have ovulated once, *i.e.* a maximum of four ovulations. Thereafter every ovariole has an associated

relic and it is impossible to separate flies which are in the second ovarian cycle from those in the third or higher cycle.

This brings about the limitation of identifying the ages of flies which have ovulated four or more times using this method. The position of the largest oocyte does position the fly within the ovulation cycle. According to Saunders, if it is found on the right inner position, then the fly will have ovulated 4, 8, 12 (4, 6, 8, 10 ...). On the other hand, if the largest egg follicle is found on the left ovary, then the fly belong to the fifth or higher "odd" ovulation cycle (5, 7, 9, 11 ...) (see FIG. 2.4 and TABLES 2.2 and 2.3) but there is no way of knowing from the ovarian dissection alone.

In female Anopheles mosquitoes, the appearance of serial follicular relics helps in determining the ages of mosquitoes that have ovulated more than four times. Close examination of the ovulation process in female tsetse has shown, however, that serial follicular relics do not, in general, occur. Despite the rare occurrence of such appearance, it was observed in the ovarioles of a female fly of G. *pallidipes* which aided the estimation of the fly's age as 110 days old [108].

In Figure (2.4), flies of ages $0 - 8$ days, considered as nulliparous were classified under ovarian category 0. Subsequent age categories were grouped after an interval of $10 - 11$ days consecutively. The interlarval period estimated in [3] and [80] which forms the interval between each ovarian category is $9 - 10$ days after the first six days of nulliparous stage corresponding to ovarian category 0.

In [109], flies with evidence of 4 or more ovulations whose ages cannot be uniquely determined were grouped into a single category thereby resulting in a huge proportion of the flies being classified in ovarian category 4.

An extension of the ovarian categories developed by Saunders was done in [2]. Rather than grouping all flies with evidence of four or more ovulations into one category as was done by Saunders, Challier established four categories in which such flies were placed according to the similarity in the arrangement of the four egg follicles in a definite order of size. These later formed categories are tagged as composite ovarian categories. It given as $4 + 4n$, $5 + 4n$, $6 + 4n$ and $7 + 4n$ with $n = 0, 1, 2, ...$ Thus the composite ovarian categories usually written as $(4 - 7)$ were obtained and shown in TABLE 2.4. This result, has been of great importance in this field. In summary, tsetse flies are now grouped under eight ovarian categories.

TABLE. 2.2. Ovarian categories with unique ages

Cycle	Category		Description	Age
No evidence of ovulation (nulliparous); largest egg follicle (A) in right ovary	0	0a	Follicle A less than 0.6 mm fly teneral	1-4 days
		0b	Follicle A more than 0.6 mm	4-8 days
First Cycle Evidence of 1 ovulation in right ovary, largest follicle (C); in left	1	1a	Ovariole A contains an open sac; uterus contains an egg	8-12 days
		1b	Ovariole A shows follicular relic; uterus contains an small larva	13-16 days
		1c	Ovariole A contains follicular A_2 fully descended and follicular relic; uterus contains a 3rd instar larva	16-19 days
Second Cycle Evidence of 2 ovulations, 1 in right ovary, 1 left ovary; largest follicle (B) in right ovary	2	2a	Ovariole C contains an open sac; uterus contains an egg	20-24 days
		2b	Ovariole C shows follicular relic; uterus contains a small larva	24-27 days
		2c	Ovariole C contains follicular C_2 fully descended and follicular relic; uterus contains a 3rd instar larva	27-30 days
Third Cycle Evidence of 3 ovulations, 2 in the right ovary, 1 in the left ovary; largest follicle (D)	3	3a	Ovariole B contains an open sac; uterus contains an egg	30-34 days
		3b	Ovariole B shows follicular relic; uterus contains a small larva	34-37 days
		3c	Ovariole B contains follicular B_2 fully descended and follicular relic; uterus contains a 3rd instar larva	37-40 days

TABLE. 2.3. Composite ovarian category without unique ages

Cycle	Category		Description	Age
Fourth Cycle* Even Numbers (6, 8, 10, etc) Evidence of 4 (or more) ovulations, 2 in right ovary, 2 in left ovary; largest follicle (A_2, B_2, A_3, etc) in right ovary	4	4a	Ovariole D contains an open sac; uterus contains an egg	40-44 days
		4b	Ovariole D shows follicular relic; uterus contains a small larva	44-47 days
		4c	Ovariole D contains follicular D_2 fully descended and follicular relic; uterus contains a 3rd instar larva	47-50 days
Fifth Cycle† odd Numbers (7, 9, 11, etc) Evidence of 4 (or more) ovulations, 2 in right ovary, 2 in left ovary; largest follicle (C_2, D_2, C_3, etc) in right ovary	5	5a	Ovariole A_2 contains an open sac; uterus contains an egg	50-54 days
		5b	Ovariole A_2 shows follicular relic; uterus contains a small larva	54-57 days
		5c	Ovariole A_2 contains follicular A_2 fully descended and follicular relic; uterus contains a 3rd instar larva	57-60 days

2.2.5   Aging by pteridine accumulation method

In previous sections we have seen that the wing-fray method could, in principle and with appropriate calibration, be used to get the approximate ages of tsetse flies of both genders across their whole life span. By contrast, the ovarian dissection technique can be used to get much more accurate age estimates-but only for female flies, and then only among flies that have ovulated fewer than four times. What we would really like is some physiological measure that changes regularly and dependably throughout the whole life of the fly. We now consider such an alternative system.

The rate of accumulation of pteridine in the head capsule of insects is another method by which their ages have been determined. This method has been applied to insects such as the old and new-world screw-worm fly *Chrysomya bezziana* [68] and *Cochiliomyia hominivorax* [13] and the stable fly *Stomoxys calcitrans* [44, 100].

Lehane and Hargrove [122] suggested, likewise, that the ages of *Glossina* spp could be determined using this method. This was first used by Lehane and Mail [101] on laboratory tsetse flies of known age. Using field tsetse flies, Lehane and Hargrove [122] observed that the accumulation of the pteridine content in the tsetse is linear with fly age. Experiments on laboratory flies showed that the rate of accumulation is independent of the number of blood meals ingested by the fly but differs with sex with a significantly higher rate of accumulation for the males than was observed in the females [62, 101].

A comparison of the fluorescence levels in laboratory flies of one day old with those accumulated in field flies of the same stock colony was done. Field flies had higher rates of the accumulation than laboratory flies.

Hargrove (unpublished), also made an observation of poor correlations of the pteridine contents of flies of unknown age in the field with wing-fray and ovarian age. In his opinion, the technique should not be used as the primary method of determining the ages of the flies but may serve for a secondary purpose in conjunction with other methods.

2.3   Comparison of the wing fray and ovarian dissection methods

A total of 80 female tsetse flies of *G. pallidipes* were used in a comparison between the wing fray and ovarian dissection methods for estimating age in tsetse [108]. For compatibility in

comparison of the two techniques, Saunders, instead of using the mean sample age as originally applied, treated each flies as an individual and obtained their age using both techniques. A linear relationship was established between the six wing fray categories and the ovarian categories, $0a$ to $5c$ considered as numbers $1 - 17$ by the author. This marked the first published relationship between these techniques. A similar correlation was later observed amongst female flies of *G. f. fuscipes* [45] and further supported in [3] with *G. palpalis gambiensis*. Increase in wing fray with time, using the ovarian age as the time scale was also found based on the same species as the latter [103]. An investigation based on data obtained by Van Wettere et al. [15] and Baldry et al. [79] of *G. tachinoides* Westwood also reveals a similar relationship. Other research observations based on such comparison can also be found in [42, 89] amongst others.

The simultaneous use of these techniques to identify the ages of flies even with four or more ovulations is very important in studying the various contributions of flies of even older ages to the population.

2.4 Wing fray in relation to seasonality, sex, species, and habitat

Factors such as seasons of the year, sex of fly, species and fly's location are noticed to influence the rates at which the wings of tsetse become frayed. There is disagreement between various studies in the variation of wing fray with season. Early work by Jackson [5] suggested that there was no such variation in the rate of wing fray with different seasons. The first observation showing differences with season in the rate of the wing fray for female flies of *G. p. gambiensis* was established by Challier [3]. Judging by the degree of the fray, these flies were observed to be more active in the dry season than the wet. With more activities, there is high chance of these tsetse flies incurring damages on their wings.

In terms of the differential rate of wing fray with sex, Jackson [71] pointed out in his studies that female tsetse flies wear out their wings less rapidly than do the males. Later studies supporting Jackson's observation were carried out by Saunders [108] and Ryan et al. [103].

Furthermore, the rate of fray with *G. palpalis* Robineau-Desvoidy is not the same with that of *G. morsitans* [71].

Variation in the rate of wing fray with flies of different habitats was first observed by Ryan et al. [103]. One of the reasons for such an occurrence, according to the authors, is due

to the differences in the strength of the wings between species of flies or within species of different locations. Taylor [87] found no significant change in the age structure with season but, in a previous study [86], noted positive indications of seasonal variation in population stress. He further made an observation that the lifespan of both male and female tsetse being most favorable during the hot wet season with the mean age being lowest in the cold season. He further made an observation that the lifespan of both male and female tsetse being most favourable during the hot wet season with the mean age being lowest in the cold season.

2.5 Sampling methods and age composition

Several sampling methods have been developed and applied successfully over the years in the capture of tsetse flies. Nevertheless, unequal probabilities of the capture of flies of different ages have been observed between sampling methods from several studies. While some methods are biased towards the capture of the nulliparous flies, others over-sample old flies. This is of concern as it will affect the estimation of the flies' survival rate and hence estimates of the distribution and abundance of the flies. As a consequence, interpretation of the outcome that is based on such data could be misleading. Spradbery and Vogt [30] noted the importance of knowing the nature of the age-dependent trapping bias. This would allow for the correction of the data collected thereby bringing about greater accuracy in the estimation of the population age structure. We shall therefore review some studies that compare the catches of flies of different age compositions using various sampling methods.

Applying the catches by Morris trap, bait ox and hand methods, Saunders [108] compared the ovarian age composition of the flies caught. Starting with a preliminary experiment, female flies of *G. pallidipes* were caught by the trap and hand methods. The hand catch according to the author, was not the standard fly-round but was only done close to the trap. It appeared that the nulliparous and teneral flies were best caught by the hand method while the trap method produced bigger proportions of old flies. These were flies of ages forty days and above (completed four or more ovulations).

Extending this experiment with the inclusion of the bait ox catch method, the main experiment was carried out. Two case scenarios with all three methods were considered.
The first case scenario involved having a bait animal confined in the area with the Morris trap. The outcome of the catch based on this case followed a similar trend with that of the preliminary case. While the hand catch caught large proportions of nulliparous flies, the other two methods produced a reverse result, with the highest percentage of old flies caught. With

the second case scenario, the bait animal was moved over to the hand catch area through dense thicket separating the two catch sites. Similar observations were made on the percentage of flies of different age compositions base on the three methods. There was less difference between the young and the old flies caught by the bait ox method as was the case with the outcome of the trap method.

Subsequently, the same experiments were repeated on the female flies of *G. palpalis* using the same study sites. While there was an obvious distinction between the percent catch of nulliparous and old parous *G. pallidipes* in the previous experiment using all three methods, such obvious distinction was only observed with *G. palpalis fuscipes* from the hand catch method. About 70% more nulliparous flies than old ones were captured. The site in which the bait animal was confined matters in terms of the age groups caught by the hand method for *G. palpalis fuscipes*. Higher number of old flies were caught in the first scenario while the second case scenario constituted more of the nulliparous flies. Trapping method on the other hand resulted in the reverse no matter the case scenario although, no much difference in the percent catch.

Generally, the highest percentage of teneral flies of *G. pallidipes* and *G. palpalis fuscipes* in the same study by Saunders [108], was caught by the hand method during the second case scenario. On the other hand, the trap and the bait ox methods caught the least teneral flies of *G. pallidipes* and *G. palpalis fuscipes* respectively. Such observation on high catch of teneral tsetse by hand catch was also noted by Allsopp [88]. Research findings show that flies are sensitive to human odours which repels them from feeding on humans [7, 8]. This is especially noted amongst non tenerals which have fed before but, with unfed flies (teneral), the urgency for blood meal overrides the repellent effect.

Artificial refuges provide another method by which tsetse flies may be sampled. As observed by Hargrove [124], catches of these flies by the method increase significantly with atmospheric temperature $> 32^0$C. This is not surprising because Buxton [1], in one of the earliest laboratory study on tsetse flies showed how detrimental exposure to high temperature is on tsetse survival.

Supporting this is a recent finding based on field tsetse flies showing an increase in the mortality with increasing temperature [120]. As the name of the technique imply, with such unfavourable conditions the flies tend to seek for refuge in cooler environments.

With respect to age, Hargrove [124] mentioned that refuge techniques are less biased than bait animals. This is because, flies of all ages fed or unfed, are affected by temperature and so seek for such refuges for survival which allows the method, to an extent, to provide good

representation of flies of all ages.

The outcome of another experiment by Hargrove [39] also revealed the importance of choosing the right sampling method in any field work. It was observed that the abortion rates of flies of *G. m. morsitans* and *G. pallidipes* varies with sampling methods. Flies caught on the electric nets were found to have more occurrence of abortion than those caught by the trapping method and this may probably be directly caused by the electrocuting nets.

2.6 Summary

In this chapter we noted the following points:

- Female tsetse flies generally mate only once in their entire life, producing only one offspring (fully-developed third instar larva) at a time.

- It takes about 15 days, depending on temperature, for a newly emerged female fly to deposit her first larva.

- Pupal duration varies with temperature

- Assessing the posterior margin of the wing for the level and position of fray summarizes the method of aging of both male and female tsetse flies by the wing fray technique.

- The ovarian dissection method for determining age in female tsetse flies involves assessing the:

  – presence of follicular relics,

  – position of follicular relics,

  – size of the largest oocyte,

  – uterine content (egg, first, second or third instar larvae) and its size.

  – arrangement of the four egg follicles reading from the left to the right according to the successive ovulation sequence to age flies with evidence of more than 4 ovulations.

- The absence of serial follicular relics in female tsetse ovaries currently restricts accurate aging of tsetse flies to only four ovarian categories.

- Rate of pteridine fluorescence content accumulated in the head capsule of insects serves as another method by which tsetse ages are determined.

- A linear relationship exists between the wing fray and ovarian dissection technique

- There are unequal probabilities in the capture of tsetse flies of different ages by various sampling techniques.

Chapter 3

Literature Review 2

3.1   Tsetse survival and population growth rate

An important parameter that needs to be considered and properly estimated in the study of population dynamics is the survival rate. In any given population there exist several forces, be they endogenous or exogenous, acting on the population and thus determining its distribution and abundance. This parameter according to Challier and Turner [4] serves as a measure of the impact of all those forces acting on the population. Based on its importance, both in epidemiological and demographic study, several methods have been used for the estimation of survival or, its converse, mortality.

One of the earliest methods, developed by Saunders [109] for calculating the daily survival rate of flies of *G. palpalis palpalis*, is the use of survivorship curve. Although the survival curve is not the same as the age-structure of a population [49], the age-structure serves as a guide towards obtaining the survival rate under the assumption of a stationary population. Excluding the teneral adult flies from the calculation, Saunders assumed a logarithmic mortality rate amongst the non teneral flies. The numbers of flies belonging to ovarian category eight and above was thereby determined using an iterative approach. Constructing a straight line through the logarithm of the estimated number of flies in each ovarian category, the survivorship curve for the population was therefore obtained based on the formula

$$y = -0.086 I_x + 2.1468. \tag{3.1}$$

I_x is the probability of a female surviving to any given age from birth at day 0.

Refining this method, Challier and Turner [4] further developed two more methods namely:

the arithmetic and geometric mean methods for the estimation of tsetse survival rate. These methods were based on the log of the probable age composition of flies in each successive ovarian cycles used in [109]. With the antilog taken, the desired result was obtained and compared with the result calculated using the survivor curve method developed by Saunders. The outcome of all three methods yielded similar results. In addition to this, the arithmetic mean method was observed to be far simpler than the others.

Gouteux [81], applied the geometric mean progression formula concurrently with fitting of a constant mortality for flies of the composite age class in the mortality estimation by the least square method. This was followed by the use of a negative exponential function to obtain the fit for the data with flies of all ages. With slight modification due to an error identified in the model, Rogers et al. [23, 102] obtained fit of the model to the same data used by Gouteux.

Several other authors, [6, 53, 75] have also estimated this parameter based on the assumption of a constant mortality amongst the adult flies. Such assumption was made due to the problem associated with the composite ovarian categories. Taylor [87] obtained estimates of the mean survival rate for the female tsetse population from life table data using the Euler-Lotka equation [43]. The use of life table data on the Euler-Lotka equation have also been carried out in various other studies [53, 88, 97] to estimate tsetse mean survival rate.

Another method applied for this estimate is the use of the mark-recapture method. In the 1930s and 40s Jackson [70] applied this method to estimate the survival rate of tsetse flies.

Hargrove [113], in his mark-recapture study, also demonstrated how the mortality of both the adult male and female tsetse of *G. m. morsitans* decreases from a high level immediately after emergence and later increases again with age following the U-shaped pattern of human mortality. Such estimation was obtained by releasing uniquely marked flies on their day of emergence on Redcliff Island, Lake Kariba, Zimbabwe and then followed by subsequent catch and release while keeping daily record of each unique fly caught. This method is a form of cohort study where individuals are followed and constantly kept track of until no more flies survive or can be caught. The outcome of his study [113] for the female mortality was compared with experimental results obtained for female laboratory flies [28, 83] of the same species and similar results was obtained in the field and in the laboratory. Fitting a model of double exponential function to the data [120], the daily survival rate was obtained. The daily mortality rate was then obtained from the derivative of the daily survival model. This finding marked the first established age-dependent survival and mortality rate for field tsetse flies contrary to the usual constant age mortality assumption made in most studies. According to Okiwelu [75], age-specific survival is important for the planning and assessment of tsetse

control measures. This statement was verified for the mosquito vectors of malaria whereby the assumption of constant adult mosquito mortality affected the predicted effectiveness of anti-vectorial interventions [17]. A recently completed study provides a model for age-dependent changes in mortality for tsetse flies [21].

According to Williams et al. [97], the age-specific mortalities for a population at equilibrium with a stable age distribution may be estimated directly from the number of individuals in each age class. Using the Euler-Lotka equation, the authors studied the loss rates of tsetse $G.$ $pallidipes$ Austen. Assuming a constant pupal mortality of 1%/day, and an age-dependent mortality among flies of age category 1 [24], a 2.8%/day mortality was obtained. This must be if the growth rate is zero. It follows that an increase in the mortality of flies belonging to age category 1 of at least 10% was sufficient for a 99% reduction of the population within nine months. The authors clearly stated that the mortality of flies in the field is probably not independent of age. In addition, a decline in the population at a rate of 3.2%/day was observed by killing flies of age class 2 just immediately after their first larva deposition. This brought about a reduction by one-half of the population in 22 days and 99% under 5 months. On the other hand, it would take 87 days for same rate of reduction and 1.5 years to achieve a 99% reduction when flies of age class 5 are killed instead.

The problem associated with the use of most of the methods discussed above as noted by Van Sickle [49] is that the population is assumed to be stationary which is not the case for tsetse populations. Also, it is impossible to separate the adult survival rate from the population growth rate [59].

The method of maximum likelihood applied to ovarian dissection data, is another approach applied in the estimation of tsetse survival rate. This method, in the estimation of tsetse survival rate was first used by Hargrove [114]. Some other later studies that further used this method are [58] and [59] where survival rate was expressed as a function of the flies' mortality and growth rate. Applying the same method with the assumption of stable age distribution, the average survival rate of tsetse was calculated in [60]. The outcome of Hargrove's study was such that the survival rate changes with age in an increasing manner. On the other hand, a decrease was observed for the variability with age.

Another approach developed by Rogers [47, 48] and Dransfield & Brightwell [90] in investigating tsetse population dynamics involves the use of Moran curves [84], an auto regression technique. The method was used in [47] to determine the monthly changes in density-independent mortality acting on tsetse fly populations under natural condition. Applying data of $G.$ $pallidipes$ to this technique, an inverse relationship between the density-independent mor-

tality and the monthly mean saturation deficit was obtained [48]. Usually, such an approach attributes the measure of dryness and not heat generating factors as being the most important factor in tsetse survival. The mark-release-recapture method is found to support temperature as the most important factor instead. As pointed out by Hargrove [119] these results may seem contradictory, but this is not necessarily the case. The reason is that, while Moran curve estimates the mortality over all development stages, mark-release-recapture and ovarian age technique only provides estimates for adult tsetse flies.

In the quest to further investigate this, Hargrove [119] applied both methods to the same data sets considering two different species of tsetse. Mean temperature was found to account for 70 and 50% respectively, of the variance in the estimated mortality rate for both mature male and female of $G.\ m.\ morsitans$. This observation was obtained when flies were not subject to trapping. Saturation deficit on the other hand accounted for only 36 and 33% variance amongst mature male and female tsetse respectively. For $G.\ pallidipes$, maximum temperature and saturation deficit accounted for 36 and 42% of the variance, respectively.

The population growth rate of female $G.\ m.\ morsitans$ on Antelope Island, Lake Kariba, Zimbabwe was predicted using the mean mortality obtained as a function of temperature derived from a linear fit to data collected by the mark-release-recapture method [120]. Estimates of the growth rate were obtained using the formula in [97], with maximum predicted growth rate of 20 fold per year for mean temperature within the range $25 - 27^0$C. Such prediction corresponded to a 23 fold mean rate of increase per year observed for tsetse of same species for an average temperature of 25.2^0C.

Simulation model first applied by Rogers [47] in studying the dynamics of tsetse population, provide another approach for the estimation of a population rate of increase and depending on the mortality assumption. The model was developed so as to define the conditions under which the method of analysis applied, yields a measure of the extent of density-independent mortality.

Modifying the above method, Rogers [48] developed a minimal complex simulation model with an additional assumption of seasonally varying density-independent mortality. This assumption applies only to the adult flies. The aim was to investigate the minimum amount of biological detail needed to describe average population equilibrium levels in the field and their corresponding seasonal changes. The model was fitted to data on $G.\ morsitans$ obtained from the Yankari Game Reserve in Nigeria. The best fit was only achieved when the density-independent mortality of the tenerals was made 3 times more than that of the other adult flies (post-tenerals). Extinction was found possible with an increase above that value.

For flies of *G. palpalis* sampled from the same location, the best fit was only achieved after including density dependence in the puparial and adult population. Negative feed back processes in ecology are sometimes called density-dependent. This regulates any population number allowing for a stable population growth. The effect of changing mortalities on estimates of the age-specific mortality of the fly population was also established using a simulation model [97].

Hargrove & Williams [10] also applied the simulation technique in modelling time series estimates of the population of *G. m. morsitans* on Antelope Island. Estimate of the parameter values that give rise to any model's best fit were obtained by linking the simulation procedure similar to Rogers' [47] to a nonlinear optimization routine. A good correspondence was thereby obtained between the predicted and observed values. With the inclusion of maximum temperature in their model, it was observed that no other meteorological data was needed for a good fit to be obtained as no further significant improvement was observed.

Another approach of great importance in this field is the use of matrix models [32]. The first author to have investigated this method using Leslie model [34] on female tsetse flies was Hargrove [112]. However, an implicit use of such model in calculating various demographic parameters was earlier undertaken in [123]. Using the appropriate matrix, Hargrove estimated the population growth rate from the dominant eigenvalue of the matrix. Relating the log of the estimated growth rate with pre-adult and adult survival probability, inter-larval period and pupal duration using a linear model, the limits to tsetse population growth rate was obtained. A 10-fold change in the population growth rate was observed due to a 1% change in the adult mortality rate. In addition, a change in the mortality rate as compared to that of the birth rate was found to have large effect on the population growth rate. With a sustained 4% daily mortality of female tsetse population even under favourable climatic or environmental conditions, the population would go extinct. This would be achieved with an additional mortality of at least 2% per day to the natural mortality rate (probably within $2-3\%$) when averaged over a whole year. This study by Hargrove [112], according to Rogers [48] was timely as it followed a period during which several studies had claimed that tsetse populations only increase at very modest rates.

Further modification and application of the Leslie matrix was done by Jarry et al. [58] to address the cyclic nature of the female tsetse birth process. Particularly, the relationship between some demographic parameters and the sensitivity of the growth rate to small change in the parameters was addressed. Based on an ideal zero mortality rate, the growth rate was observed on the same site to be between 1.18 and 1.22 depending on the pupal duration. Such

growth rates were noted to correspond to the production of about 457 to 1566 females per female per year. These are slightly lower values as compared to those obtained in [112]. Results from both studies confirm the importance of adult survival in determining tsetse population growth rates. The growth rate was observed to be sensitive to change in the survival rate of young nulliparous females [58]. Earlier estimation showed a production of $308 - 552$ female tsetse per female adult per year [55] and another had a production of $400 - 500$ females per female per year [27] each for $G.\ austeni$ and $G.\ morsitans$ respectively. These figures represent the total production from a single female together with those from her offspring.

A more recent application of the matrix method in describing the dynamics of tsetse population was demonstrated in [78]. The model was particularly developed for female tsetse population and structured by the number of larvae deposited. The effect of temperature both on the pupal duration and the inter-larval period and thereby on the flies' population growth rate was explored. The result showed a life expectancy of 33.3 days for daily adult survival rate of 0.970 with an intrinsic growth rate of zero. It was further observed that the growth rate was insensitive to variance of the inter-larval period. The abiotic effect of temperature on the population growth rate was also observed.

3.2   Summary

- Generally, in the epidemiology of vector-borne diseases, mortality rate, hence the survival rate of any population stands out to be of great importance. The various methods that have been used in several studies to estimate this parameter are the use of

  - Survivorship curve

  - Mark-recapture technique

  - Arithmetic mean method for daily survival estimate

  - Geometric mean method for daily survival estimate

  - Assumption of constant adult flies' mortality

  - Life table data on Euler-Lotka equation

  - Maximum Likelihood method applied to ovarian dissection data

  - Moran curve technique

  - Geometric progression with the least squares method.

- Tsetse population growth rate, another important parameter in any population dynamics has been estimated using

- – Matrix method

- – Euler-Lotka Equation

- – Mark-release-recapture method

- – Simulation method

Chapter 4

Age Structured Mathematical Model

4.1   Introduction

Population dynamic models serve as tools that allow us to predict the population growth in time and space and, for pest species, can provide insight into the development of cost-effective control strategies. The use of mathematical models in describing and predicting the dynamics of structured population existed way back in the 1200's. The famous age-structured population model, marking the first of its kind was developed by Fibonacci, in the year, 1228.

Applying the sequence of Fibonacci numbers to model the growth of rabbit population, it was assumed that the fertility window opens at age 2 months [57]. According to Iannelli [57], this shows that within the context of population problems, age structured models occur in a natural way.

An application of this concept, using a simple model in the early $18th$ century was carried out by Malthus [92] on human population with an exponential growth rate predicted to occur with time.

It is very important to develop mathematical models that capture the changes in a population of individuals with different ages and at various times of the year. Such population dynamics may give understanding of the fertility, survival capacity and behaviour of individuals of different age classes. This makes age an important and natural parameter to be considered in structuring any population.

In past time, mosquitoes, as an example, were biologically assumed to die only from exogenous factors such as predation, disease, swatting and climatic factors and that, by implication, mortality was independent of age as noted in [17]. However, recent investigation [14] on field

31

data for various species has shown that they not only die of exogenous factors but also due to endogenous causes and that mortality does change with age.

With tsetse flies, the population models usually considered in the past also followed similar assumption of the event occurring at a constant rate with age until recently, in 1990 when this assumption was challenged by Hargrove [120]. In his study, it was demonstrated how both the male and female tsetse of *G. m morsitans* die with age following the pattern of human mortality (U-shaped). The details of this finding have been mentioned in Chapter 3. Furthermore, the growth rate of any population depends on both the birth and the death rates which will therefore be influenced by the change in the mortality with age. In addition, with this variation in the mortality with age, estimate of the proportion of flies of different ages that constitutes a population at any time will be aided. This is informative in predicting future population numbers.

In addition, the finding serves as guide to the future development of trypanosomiasis and other vector-borne disease transmission models that examine anti-vectorial interventions [17]. Hence, understanding age-dependent survival and age-structured population dynamics of tsetse flies is crucial for better knowledge of the right intervention that would bring about a reduction of the vector population to a size sufficient to lower the disease transmission rate or even stop transmission entirely.

Therefore, our aim in this chapter, is to develop a pde model for the adult tsetse population structured with age and time and then use data for female *G. pallidipes* obtained from Rekomitjie Research Station Zambezi Valley, Zimbabwe to explore its population dynamics at equilibrium and to predict future expectation of the population. To describe a more realistic population dynamics, we will base our model on the assumption of an age-dependent adult tsetse mortality using the formula obtained in [120].

A single model consisting of a partial differential equation representing the dynamics of both the pupa and adult population will be developed. This will be followed by the analytical and numerical solutions of the system with comparison of both results and its consistency with established results. Furthermore, the role of each parameter in the mortality rate will be investigated by simple parameter variation and applying the forward normalized sensitivity index method [11]. This will give us insight into the role of each of the parameters in the model and their impact on the mortality rate of flies of different ages.

(a) Pupae (raywilsonbirdphotography.co.uk)   (b) Tsetse-fly (fohn.net)

FIG. 4.1. Figure 4.1aa is the photo of pupae developed from female tsetse-fly

4.2 Model description and assumptions

Based on the life cycle described in Chapter 2, not all stages have direct exposure to climatic and environmental factors or are even affected by age. Moreover, the effect of age on the stages apart from the adult stage is still unclear. As a result, we will mainly focus on the pupa(e) and adult(s) population (FIGS. 4.1a and 4.1b respectively) since these are the only two stages that take place completely outside the uterus of the female fly. These two populations, coupled together by birth (newborn of pupa from reproductive adult) and the progression from pupal to adult stage, will be used to describe the dynamics of the general female population. Although, we are aware from research findings that the pupal duration varies with temperature, we will in this chapter assume a constant pupal duration a_c, with the emergence taking place when $a = a_c$. Furthermore, we limit our study to the female population specifically because females constitute the productive part of any population with the capability of giving birth to young ones.

The model diagram represented in FIG. 4.2 shows the interactions that take place between the two populations of interest together with the parameters that control the dynamics.

4.2.1 Model assumptions

We assume that any pupa reaching the age a_c, emerges as an adult. The implication of this is that, no pupae exist beyond the age a_c and that the dynamics thereafter are controlled by the adult mortality. The newly emerged flies will then take 15 days (sum of nulliparous and interlarval period) from emergence to give birth to their first pupa. As such, births of pupae from that adult fly only begin at the age of $a_c + 15$ days and subsequent birth from each individual adult fly takes place with 9 days steps (interlarval period) as obtained in [24]. We
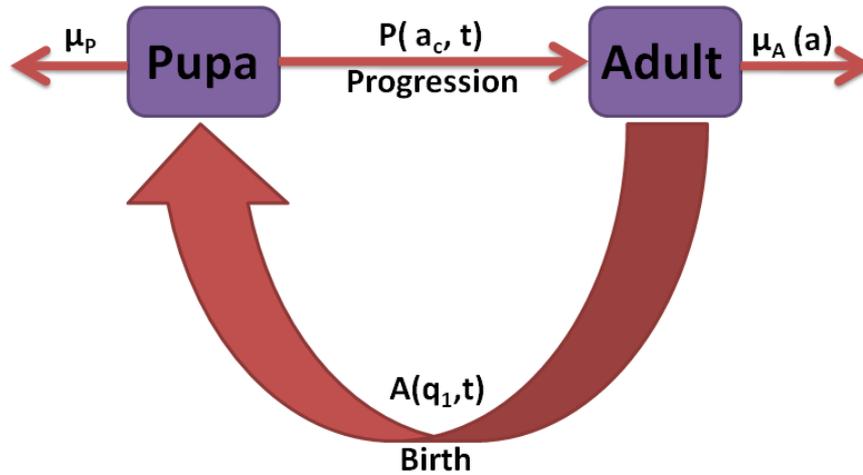
FIG. 4.2. Diagrammatic representation of the pupa and adult tsetse interaction in the population. P and A represent the pupae and adult populations respectively. a_c is the age at which each pupa is considered to emerge as an adult. $q_1 = a_c + 15 + 9k, k = 0, 1, 2, ...$ is the age at which adults give birth to new pupae. μ_P and μ_A are the mortality rates of the pupa and adults populations.

also assumed that the pupal population die at a constant mortality rate of 1% per day [24] while the adult population are assumed to die at an age dependent rate. The summary of the above illustrations are enumerated below:

- Only pupae of age between 0 and a_c exist.

- "Pupae" of age a_c are considered as adults.

- The pupae population die at a constant rate equal to 1%.

- Age-dependent mortality is considered for adult flies.

- Adults give birth to new pupae when they have the ages $a_c + 15 + 9k, \ k = 0, 1, ...$

4.2.2   Model formulation

We develop an age structured model describing the changes that occur at any time t in the pupa and adult population with any age a. The model consists of a single partial differential equation (pde), with age and time as independent variables, that describes both population dynamics. Our choice of the pde is appropriate in describing any dynamic process involving more than one independent variable.

Let $X(a,t)$ denote the density of the total female population (pupa and adult) of age a at time t. The equation of the model for the two populations is therefore given as

$$\left(\frac{\partial}{\partial a} + \frac{\partial}{\partial t}\right) X(a,t) = -\mu(a) X(a,t). \tag{4.1}$$

With the assumption discussed in the previous section, we have that tsetse flies of ages in $[0, a_c[$ are considered as pupae. As a consequence, we assume that the mortality rate is given by

$$\mu(a) = \begin{cases} 0.01 & \text{if } a < a_c, \\ k_1 k_2 e^{-(a-a_c)k_2} + k_3 k_4 e^{(a-a_c)k_4} & \text{if } a \geqslant a_c \ [120], \end{cases} \tag{4.2}$$

representing constant pupal and an age-dependent adult tsetse mortality respectively, both assumed to be non negative. The population for all ages at time, $t = 0$ is given by
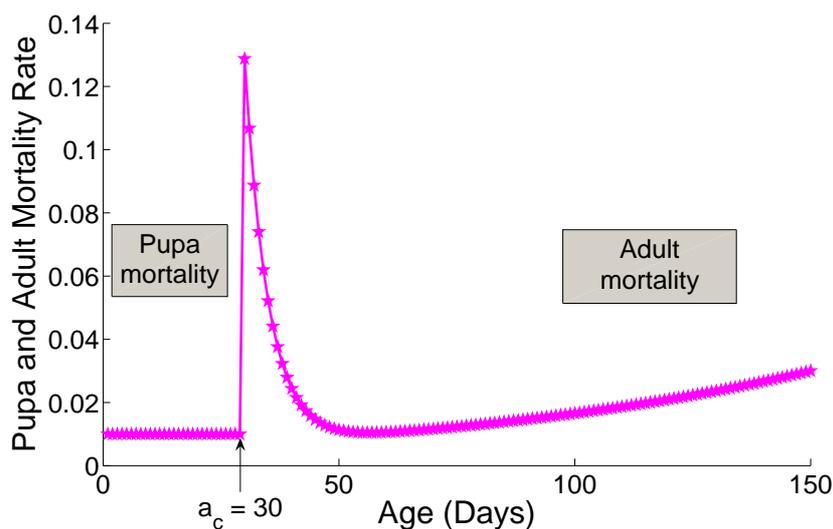
FIG. 4.3. Change in mortality from constant (pupa) rate to age-dependent (adult)

$$X(a, 0) = X_0(a), \tag{4.3}$$

where $X_0(a)$ represents the initial age distribution of the tsetse population. The new births in a single time unit from adult flies of reproductive age as specified in the previous section is given by

$$X(0, t) = \sum_{k=0}^{\infty} X(a_c + 15 + 9k, t). \tag{4.4}$$

We mention here that for the purpose of mathematical analysis, we assume that flies live "for ever" and continue to give birth to new pupae which implies massive tsetse population at all times with continuous outbreaks of trypanosomiasis. The reality is that the mortality for large

ages is so high that no flies will reach those ages and so, all other analysis with regards to the flies' age will be carried out base on the assumption that no adult tsetse live beyond 100 days.

TABLE. 4.1. Parameter Description

Parameter and variable symbol	Description
X	Population density
T	Temperature
μ	Mortality rate
a_c	Transition age from pupa to adult stage

4.3   Mathematical analysis

The aim of this section is to analyze system (4.1)-(4.4) mathematically and numerically. The mathematical analysis starts by using the method of characteristic lines [16, 26, 29, 111] to determine the system's solutions, then we study the asymptotic behaviour of the analytical solution of the model. The numerical analysis consists of studying the effects of the models parameters on its dynamics. Furthermore, a sensitivity analysis is carried out to study the importance of each of the model's parameters.

4.3.1   Method of characteristics

We start by the method of characteristic lines. For this we consider solutions of the form

$$Y(s) = X(a(s), t(s)). \tag{4.5}$$

We determine a curve $(a(s), t(s))$ along which equation (4.1) reduces to an ordinary differential equation (ode). Applying the chain rule method on equation (4.5), we obtain

$$Y'(s) = \frac{\partial}{\partial a} X(a(s), t(s))a'(s) + \frac{\partial}{\partial t} X(a(s), t(s))t'(s).$$

If we arbitrarily choose

$$\begin{cases} a'(s) = 1 \\ t'(s) = 1 \end{cases} \tag{4.6}$$

we obtain

$$Y'(s) = \left(\frac{\partial}{\partial a} + \frac{\partial}{\partial t} \right) X(a(s), t(s)) = -\mu(a(s))X(a(s), t(s)).$$

Then $Y(s)$ satisfies the following ode

$$Y^{'}(s) = -\mu(a(s))Y(s).$$

Moreover, we have

$$\begin{cases} a(s) = s + a_0 \\ t(s) = s + t_0. \end{cases}$$

Thus

$$Y(s) = Y(0)\exp\left(-\int_0^s \mu(\alpha + a_0)d\alpha\right)$$

implying that

$$X(s + a_0, s + t_0) = X(a_0, t_0)\exp\left(-\int_0^s \mu(\alpha + a_0)d\alpha\right).$$

To calculate $X(a,t)$, we consider two cases: $t \leqslant a$ and $t > a$.

For $t \leqslant a$, we choose $t_0 = 0$ and $a_0 = a - t$, we obtain

$$X(a,t) = X(a - t, 0)\exp\left(-\int_0^t \mu(\alpha + a - t)d\alpha\right). \tag{4.7}$$

For $t > a$, we choose $a_0 = 0$ and $t_0 = t - a$, implying

$$X(a,t) = X(0, t - a)\exp\left(-\int_0^a \mu(\alpha)d\alpha\right). \tag{4.8}$$

Combining equations (4.7) and (4.8) and considering equation (4.3) (population at time, $t = 0$), we arrive at the general solution

$$X(a,t) = \begin{cases} X_0(a - t)\Pi(a - t, a) & \text{if } t \leq a, \\ X(0, t - a)\Pi(0, a) & \text{if } t > a \end{cases} \tag{4.9}$$

where

$$\Pi(a,b) = \exp\left(-\int_a^b \mu(\alpha)d\alpha\right)$$

is the probability that a fly survives from age a to age b.

A simple interpretation of the population density can be made in terms of the survival rate as clearly obtained in equation (4.9). For any given age a, the population density is, for each $t \leq a$, shown to be the product of the tsetse initial age distribution and the probability of survival between $a - t$ and a. As time increases (for $t > a$), the population density is given by the new births multiplied by their individual survival. The later equation is an important result to be considered in predicting the population dynamics over a long period of time since any population growth rate is dependent on the birth and death rate (hence survival).

Based on equation (4.9), the tsetse population density, $X(a,t)$ is known provided that we determine the birth rate $X(0,t)$ as a function of time t. To obtain a single equation for this, we represent equation (4.4) by

$$X(0,t) = \int_0^{+\infty} \beta(a)X(a,t)da,$$

where $\beta(a)$ is the age specific fertility given by the sum of the Dirac functions $\delta_{a_c+15+9k}$ at ages $a_c + 15 + 9k, k = 0,1,...,$ that is

$$\beta(a) = \sum_{k=0}^{\infty} \delta_{a_c+15+9k}(a).$$

Substituting the above equation in (4.9) we obtain

$$B(t) = \int_0^t \beta(a)B(t-a)\Pi(a,0)da + \int_t^{+\infty} \beta(a)X_0(a-t)\Pi(a,a-t)da$$

where $B(t) := X(0,t)$.
Setting

$$H(t) = \int_t^{+\infty} \beta(a)X_0(a-t)\Pi(a,a-t)da$$

and

$$K(b) = \beta(b)\Pi(b,0), \ \ b \geqslant 0,$$

we obtain the following Volterra integral equation

$$B(t) = H(t) + \int_0^t K(t-a)B(a)da \tag{4.10}$$

with H and K involving only known data. Equation (4.10) is known as the renewal equation. Further analysis of this equation can be found in [52].

We will now proceed to discuss the asymptotic behaviour of the above solution.

4.3.2 Asymptotic behavior

Equilibrium solution

Equilibrium solutions of equations (4.1) are given by its solutions that are independent of time; that is

$$\frac{d}{da}N^*(a) = -\mu(a)N^*(a), \ \ a \geqslant 0. \tag{4.11}$$

Thus

$$N^*(a) = N^*(0) \exp\left(-\int_0^a \mu(\alpha)d\alpha\right),\ a \geqslant 0. \tag{4.12}$$

Applying equations (4.11) and (4.12) and provided $N^*(0) \neq 0$, we deduce the expression

$$1 = \int_0^{+\infty} \beta(a) \exp\left(-\int_0^a \mu(\alpha)d\alpha\right) da. \tag{4.13}$$

Notice the right hand side of equation (4.13) depends only on the model's parameters. It is called the net population reproduction number defined as the expected number of newborns that an adult female tsetse fly produces over its lifetime. If this number is equal to one, then a non trivial equilibrium solution of equations (4.1)-(4.4) exists. If not, then the zero solution is the only equilibrium solution of equations (4.1)-(4.4).
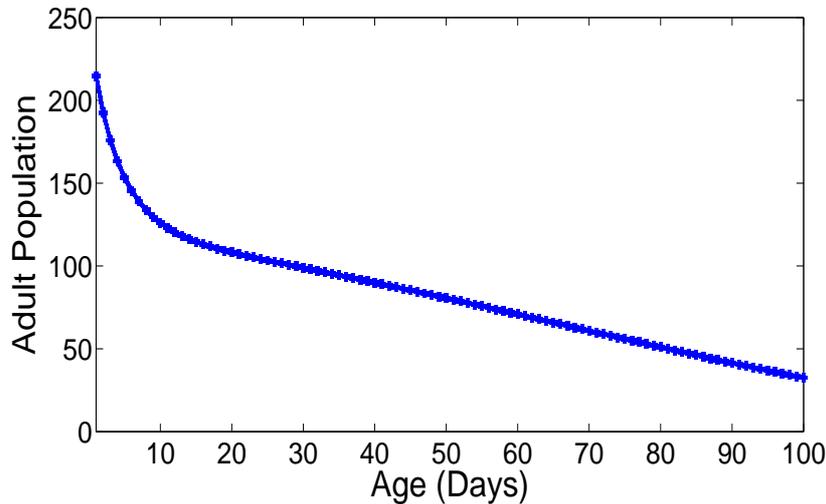
FIG. 4.4. Equilibrium solution

At equilibrium, the solution follows a continuous decline at a fast rate for the newly emerged flies (age $0 - 10$) and slower rate of decline especially for the adult flies in the middle age (young parous) class.

Stable age distribution or persistent solutions

Special solution considered in the Sharpe-Lotka-Mckendrick model [29] is of the form

$$X(a,t) = H(a)G(t),\ a,t \geqslant 0. \tag{4.14}$$

This form of solution is called the stable or persistent solution [29] and it is of practical importance while investigating the solution's existence and the long term dynamics of the

population. As $t \to \infty$, if the solution of equations (4.1)-(4.4) approaches the form of equation (4.14), then the proportion of the population within any age bracket say $[a_0, a_1]$ remains constant and satisfies

$$\frac{\int_{a_0}^{a_1} X(a,t)da}{\int_0^\infty X(a,t)da} \underset{t \to \infty}{\to} \frac{\int_{a_0}^{a_1} H(a)da}{\int_0^\infty H(a)da}.$$

The above expression shows that the age distribution of the population stabilizes at a constant proportion. Given that μ and β are time independent, we substitute equation (4.14) into equation (4.1) and with further simplification, we obtain

$$\frac{\frac{d}{dt}G(t)}{G(t)} = -\frac{\left(\frac{d}{da}H(a) + \mu(a)H(a)\right)}{H(a)}.$$

This implies that $\dfrac{\frac{d}{dt}G(t)}{G(t)}$ and $-\dfrac{\left(\frac{d}{da}H(a) + \mu(a)H(a)\right)}{H(a)}$ are both equal to a constant λ which is independent of time and age.

$$\frac{\frac{d}{dt}G(t)}{G(t)} = \lambda$$
$$-\frac{\left(\frac{d}{da}H(a) + \mu(a)H(a)\right)}{H(a)} = \lambda$$

We obtain the stable age solution given by

$$G(t) = e^{\lambda t}G(0)$$
$$H(a) = H(0)\exp\left(-\lambda a - \int_0^a \mu(\alpha)d\alpha\right).$$

Thus

$$X(a,t) = G(0)H(0)e^{\left(\lambda(t-a) - \int_0^a \mu(\alpha)d\alpha\right)}. \tag{4.15}$$

The parameter λ can be defined from the condition at $a = 0$,

$$1 = \int_0^{+\infty} \beta(a)e^{\left(-\lambda a - \int_0^a \mu(\alpha)d\alpha\right)}da. \tag{4.16}$$

We notice a relation between the birth rate β, the mortality rate μ and the parameter λ for the existence of a stable age distribution [26]. Such an equation is known as the characteristic equation and was discovered in 1922 by Lotka. One can also call the right side of the equation as the net population reproduction rate.

We have the following result:

Lemma 1 *[16] If for some interval $[a_1, a_2]$, there exists $\beta_0 > 0$ such that $\beta(a) \geqslant \beta_0$ for each a in $[a_1, a_2]$. Then there exists a unique $\hat{\lambda}_1 \in R$ such that equation (4.16) holds.*

Proof 4.3.1 *The left hand side of equation (4.16) is a strictly decreasing function in λ. Moreover, if $\beta(a)e^{\left(-\lambda a - \int_0^a \mu(\alpha)d\alpha\right)}$ is bounded and not identically zero, then*

$$\lim_{\lambda \to -\infty} \int_0^{+\infty} \beta(a) \exp\left(-\lambda a - \int_0^a \mu(\alpha)d\alpha\right) da = +\infty$$

and

$$\lim_{\lambda \to +\infty} \int_0^{+\infty} \beta(a)e^{\left(-\lambda a - \int_0^a \mu(\alpha)d\alpha\right)} da = 0.$$

This implies that there exists a unique $\hat{\lambda}_1$ solution of equation (4.15).

The solution, $X(a, t)$ in equation (4.15) is being specified given that we know $G(0)H(0)$ and $\hat{\lambda}_1$ from equation (4.16). Moreover, its asymptotic behaviour is strictly determined by the sign of λ.

Theorem 4.3.2 *If $\hat{\lambda}_1 < 0$, then $X(a, t) \to 0$ as $t \to \infty$. If $\hat{\lambda}_1 > 0$, then $X(a, t) \to \infty$ as $t \to \infty$. For each solution $X(a, t)$, the function $X(a, t)G_0^{-1}e^{-\hat{\lambda}_1 t}$ converges to $H(a)$ as $t \to \infty$ for each a [16].*

The above result, also known as the renewal theorem [16, 94] and proven in [94], shows that the population age distribution approximates a profile determined by $H(a)$ as time evolves. Depending on the sign of λ, the profile could either decay or grow exponentially with time.

4.4   Numerical solution

In this section, we transform the pde represented in equations (4.1)-(4.4) to a finite discrete scheme. It is worth mentioning that since the model does not account for the effect of temperature changes, we assume that the pupa duration, a_c, is constant. As in [80], we choose the value 30 days that corresponds to a temperature of $25^0 C$ which is the average temperature of the period under study. The numerical simulations are represented in FIG. 4.6. Under natural mortality condition (due to age only), for some parameter values, the long time behaviour of the adult female tsetse population predicts an exponential population growth. If these results hold in real life situation, then there is cause for alarm as it gives signal of high rate of trypanosomiasis transmission in the population and with high chance of an outbreak
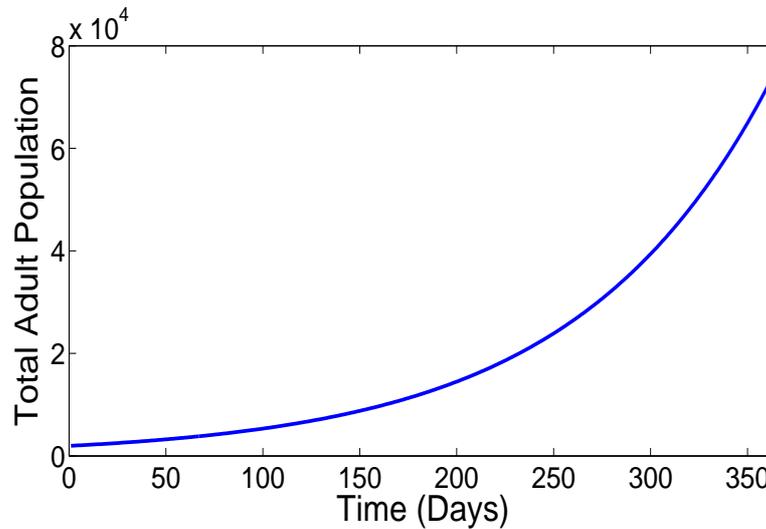
FIG. 4.5. Long term population profile for a stable age distribution

occurring for some species. In addition, it would be very difficult and expensive for the public health and other health workers to carry out any intervention aimed at eradicating the disease through controlling the vector population. However, it should be understood that this exponential growth is typical only when populations are very low. As the population increases, density-dependent effects (increases in adult and/or puparial death rates and/or increases in emigration) serve to stabilise the population in the normal way.

Tsetse flies are slow breeding insects and populations are also subject to annual fluctuations in numbers due to climatic changes and sometimes also to the availability of food (blood meal for tsetse). We will account for one of these factors in subsequent chapters. It is possible to select specific values for the parameters $(k_1 - k_4)$ for adult mortality such that the tsetse population stays relatively constant in time (FIG. 4.7). However, it would be unrealistic to think that the parameters would stay fixed at these levels for any period of time so that the relatively constant population is not in any way "stable". Notice that, for the quasi-constant population shown in FIG. 4.7, k_1, k_3 and k_4, must each take a value double that observed in the field experiment; and for k_2 the value is about 6 times the field value [120].

The plot in FIG. 4.7 gives a clear picture of the changes that occur in the population through time. Assuming equal tsetse population number for each age at the initial time, the population will either increase or decrease for a certain period of time before it "stabilizes" around an oscillating solution. Here, starting with a population of about "2080" tsetse flies irrespective of their ages, we observe an initial decline that is maintained for a period of 45 days after which the solution starts oscillating at constant periods. Based on our model's assumptions,

(a) Adult tsetse population with Age

(b) Adult tsetse population with time
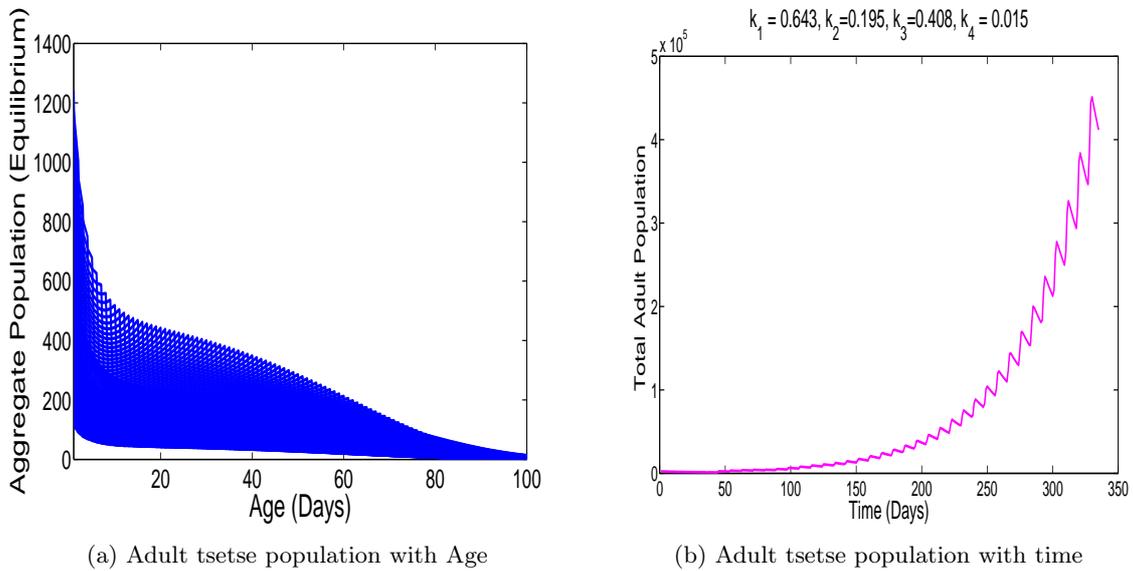
FIG. 4.6. Adult tsetse age distribution at the equilibrium and profile of the total adult tsetse population as a function of time.
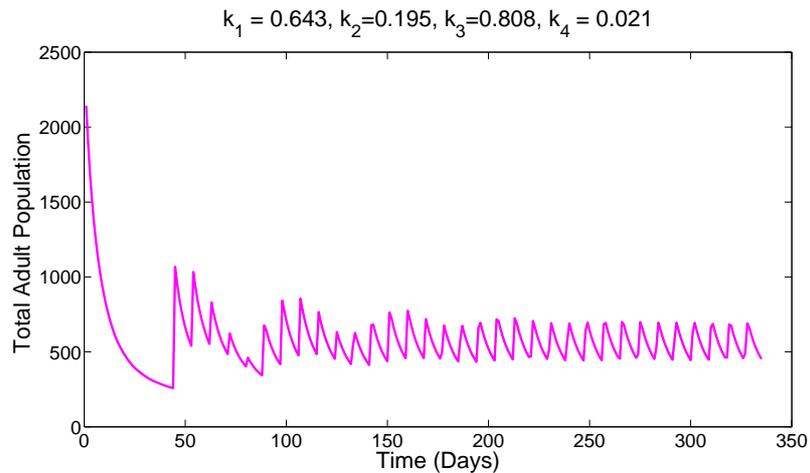
FIG. 4.7. Long term profile with the possibility of stability in the population for some parameter values

these pupae of age 30 days old only reproduce their first pupa offspring after 15 days of adulthood (emergence as adult from pupa at age 30 days). The pupae from such female adult tsetse flies considered as females then take a period of 30 days under constant temperature of 25^0C to emerge as adult flies. Hence, in total, the first generation of the previous adult tsetse only spring forth at that time (after 45 days) which explains the obvious increase in the population at that time and is repeated after same time frame. This can be regarded as the population doubling time as it accounts for the time when a newly emerged daughter

of a female reproduces itself. The sustained oscillations observed after the first increase, occurs after every 9 days. These oscillations are not dependent on the initial population but are direct results from the birth rate. The interval of 9days between any two consecutive oscillations represent the time between two consecutive birth of pupae from a single adult fly of reproductive age. A 60 days interval between the highest peaks for two consecutive cycles is also observed. One can say that the result of the pde model captures the biological behaviour of tsetse population as it has to do with its life cycle controlled by the birth and death rate. These two parameters without doubt, are very important and crucial in the study of population dynamics.

The changes that occur in the population at equilibrium, as in FIG. 4.6a together with that obtained from the analytical solution (FIG. 4.4) are found to correlate with that obtained by the pioneer author of an age-dependent survival rate for field tsetse flies [120]. As these flies age, the population profile follows a continuous decline. A higher rate of the decline takes place at the early age (nulliparous stage) and then followed by a slow rate of decline afterwards. The rate of decline with the much older flies (old parous) is faster than those of the middle age (young parous) and this can be understood from the shape that the daily age mortality takes. With the results of FIGS. 4.6a and 4.6b, it is possible to estimate the proportion of flies of different ages that are present in the population at any given time and their contribution to the population size. The estimate of the proportion of nulliparous (ovarian category 0), young parous (ovarian category $1-3$) and the old parous tsetse flies (ovarian category $4-7$) that constituted such population are 21%, 40%, and 39% respectively.

In the next section we investigate the role of the parameters $k_1 - k_4$ in affecting the mortality of flies of different ages.

4.5 Parameter analysis

Investigating the way the parameters k_1, k_2, k_3 and k_4 affect flies of different ages is necessary to understand the biological interpretation and implications on the mortality of female tsetse flies of different ages. We proceed by varying each of the mortality parameters, one at a time while keeping the others constant. By so doing, we obtain the result in FIG. 4.8.

From FIG. 4.8a we observe that the mortality rate decreases with increasing age for all values of k_1. Moreover, as k_1 increases the mortality rate increases for all ages in $[0, 10]$, while no change in mortality is observed for older ages. While the mortality of the tenerals (of age 0) is increasing with increase in parameter k_2 as in FIG. 4.8b, a decrease is further observed for flies

(a) Varying k_1, with k_2, k_3 and k_4 held constant

(b) Varying k_2, with k_1, k_3 and k_4 held constant

(c) Varying k_3, with k_1, k_2 and k_4 held constant

(d) Varying k_4, with k_1, k_2 and k_3 held constant
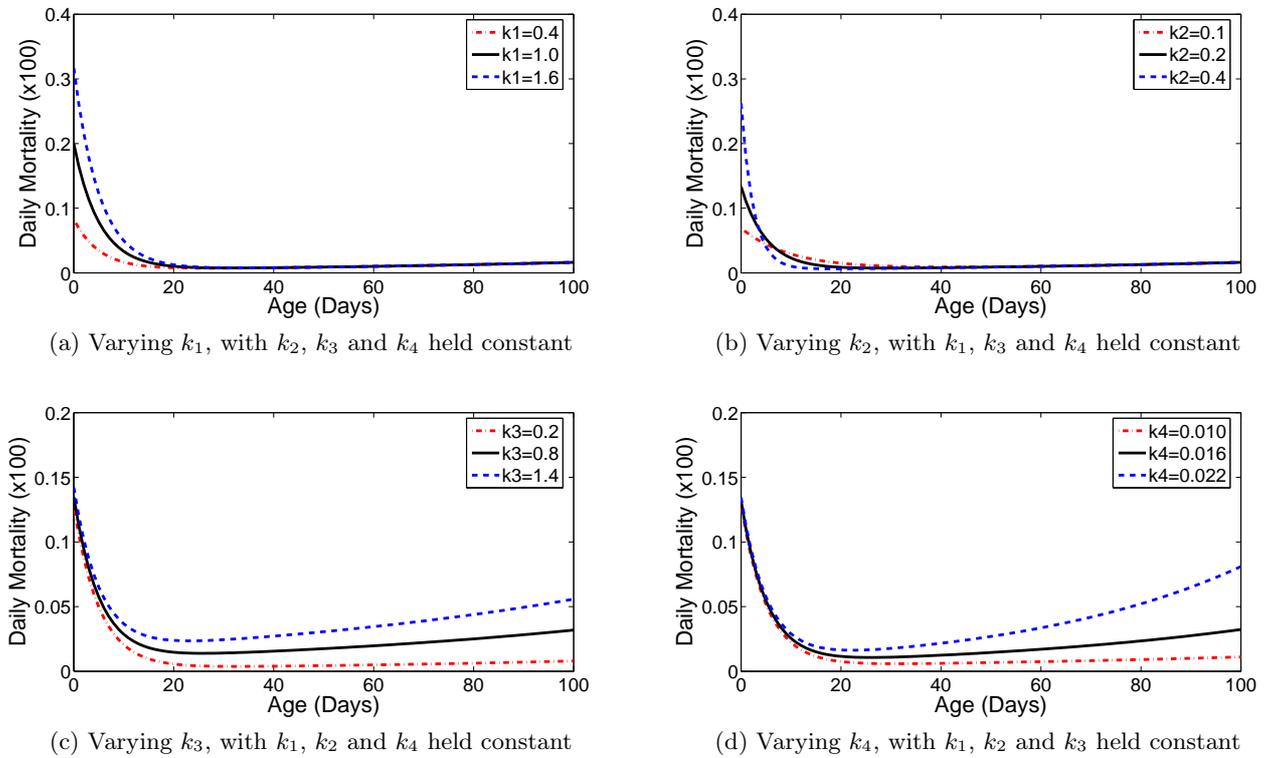
FIG. 4.8. Age-dependent mortality varying each parameters one at a time.

within the age $1-10$ days and contrary to the observation made on k_1. That is to say that, as k_2 is increased, the adult mortality drops more rapidly to the low mortality levels typical of young mature adults. A high value of k_2 would thus be typical of a "healthy" environment for the tsetse flies where they were able to find the first $1-3$ blood meals with relative ease and safety. As with k_1, the effect of k_2 is only seen for about the first 10 days of adult life. The roles of k_3 and k_4 as represented in FIGS. 4.8c and 4.8d are quite different from those of the previous parameters discussed. Changes in these later parameters affect those flies that have had several blood meals (young and old parous) and are of reproductive age. Increasing the values of these parameters, increases the mortality of these flies. This behaviour goes a long way biologically, as it is likened to the effect of temperature on the mortality of both male and female adult $G.\ morsitans$ obtained in [120]. Additional demonstration of the effect of k_3 and k_4 on the adult tsetse mortality is shown using surface and contour plots. Having observed similar behaviour between k_3 and k_4 on the adult tsetse mortality, FIG. 4.9 gives a view on the speed at which each of these parameters drives the mortality. We see that increasing either k_3 or k_4, increases the mortality rate. Nevertheless, while the increase that takes place in the mortality with increasing k_3 is slow, that with k_4 is found to be fast and of a higher side.

FIG. 4.9. Adult tsetse mortality as a function of k_3 and k_4. Increase in each of these parameters, lead to the increase in the adult tsetse mortality. The value on each contour line, as also indicated on the color-bar, represents the mortality rate depending on the color of the line. We notice a higher mortality rate with k_4 than it is with k_3.

The higher mortality for small ages can be explained by the low level of fat contained in newly emerged flies as well as the size 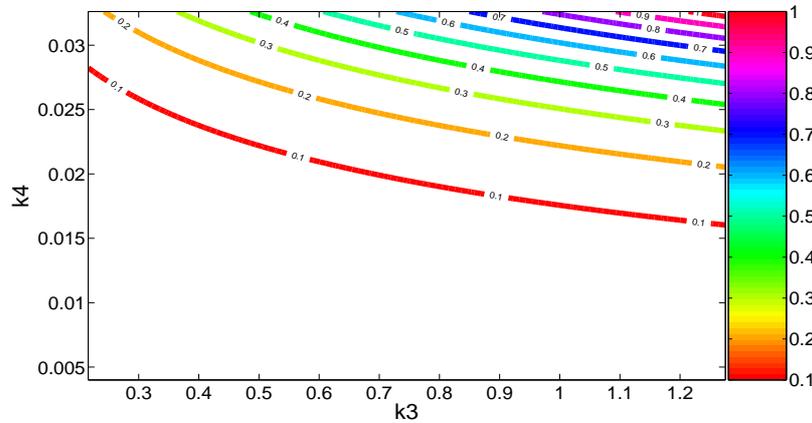and level of musculature development which themselves depend largely on the conditions faced by the pupa from which they emerge. Teneral flies emerging with low fat levels and poorly developed flight musculature are under a high risk of mortality due to starvation. This observation was made on field data of flies of *G. morsitans* and *G. swynnertoni* Austen [72, 120] respectively. These flies, unfed and faced with the possibility of emerging under very high temperature conditions which increase their metabolic rate, thereby burning up the little fat they have faster than necessary, are at the risk of high mortality as depicted in the FIG. 4.8a. The risk arises from the urgent need for the first blood meal to start laying down fat reserves and initiating flight musculature development. The initial high mortality rate shows how crucial these first blood meals are for their survival. After taking the first blood meal, it is expected that they have a better chance of surviving than it was initially. This is not far from what we observe from the figure showing a decline in the mortality rate (increased survival rate) as the age increases during the first 10 days of adult life which is reasonable and realistic. And so with more blood meals for those first few days of their emergence, these flies get their muscles developed and strengthened for other activities. Supporting this observation is the findings of Bursell [19] showing that newly emerged flies need about $2 - 3$ blood meals within the first 10 days of emergence. Increase in temperature, increases the flies' mean mortality rate and so is the effect of increasing k_3 or k_4 to the mortality of the young and old parous flies.

The observations made on the impacts of k_1, k_2, k_3 and k_4 are very important in understand-

ing the impact of some external factors, such as temperature, on mortality. Although, it is important to compare the impacts that each of these parameter have on mortality, no proper measurement/comparison of such impacts have been carried out to this point. In the next section we perform such comparison by calculating the sensitivity index.

4.6 Sensitivity analysis

The sensitivity of any state variable to changes in its parameters is an important investigation as it gives an idea on the parameter's impact on that variable. In our case, carrying out this analysis on the mortality of adult tsetse flies of different ages is crucial as it would further inform us of the parameter to which the mortality is most sensitive. As a result, we will apply the method of normalized forward sensitivity index [11] to obtain each parameter's impact on the mortality of adult tsetse flies of all ages. This is the ratio of the relative change in the variable as a proportion of the relative change in the parameter. Below, is an analytical expression that defines the sensitivity index with specific use of the case of adult tsetse mortality as the state variable.

Definition 4.6.1 *The normalized forward sensitivity index of a variable X that depends in a continuously differentiable way on a parameter p is given by*

$$\Phi_p^X = \frac{\partial X}{\partial p}\frac{p}{X}.$$

Given the explicit expression for $\mu(a)$ for $a > a_c$ as represented in equation (4.2), the analytical expressions for the sensitivity index, $\Phi_{k_i}^{\mu(a)}$, with respect to the parameter k_i are given below:

$$\Phi_{k_1}^{\mu(a)} = \frac{k_1 k_2 e^{(-ak_2)}}{\mu(a)},$$
$$\Phi_{k_2}^{\mu(a)} = \frac{k_1 k_2 (1 - k_2 a) e^{(-ak_2)}}{\mu(a)},$$
$$\Phi_{k_3}^{\mu(a)} = \frac{k_3 k_4 e^{(ak_4)}}{\mu(a)},$$
$$\Phi_{k_4}^{\mu(a)} = \frac{k_3 k_4 (1 + k_4 a) e^{(ak_4)}}{\mu(a)}.$$

where $a - a_c$ is replaced by a for the simplicity of the notations.

Notice that $\Phi_{k_1}^{\mu(a)} + \Phi_{k_3}^{\mu(a)} = 1$. FIG. 4.10 provides a clear view of the distribution of each parameter's impact through the different ages. For ages between 0 and 15, k_1 and k_2 take the highest ranks. With these latter parameters, the impact is observed to be declining slowly with age for k_1 and rapidly for k_2, notwithstanding, an increase is later obtained for k_2 but with

the value staying negative through those ages. This is then followed by a constant increase with age (above 15 days). The same constant change for this age group is observed with k_3 but with an increase also for the lower ages. On the other hand, the reverse is the case for k_4. Starting with low impact on flies of initial ages, a continuous increase is observed through tsetse flies of all ages which places it on the highest rank.
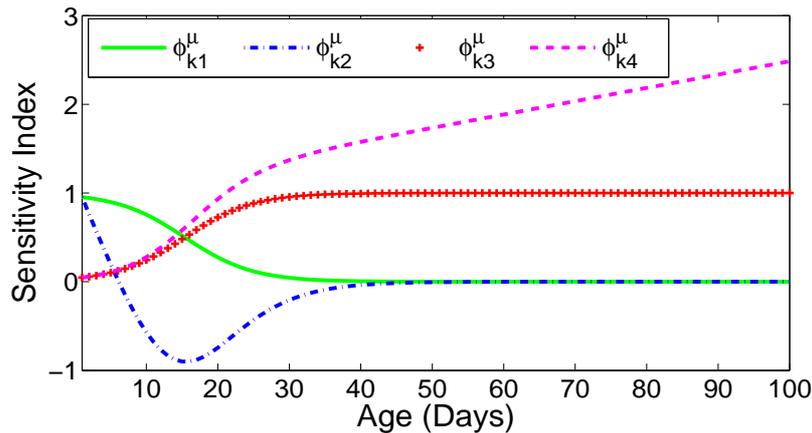
FIG. 4.10. Parameter impact on the adult tsetse mortality using $k_1 = 0.643$, $k_2 = 0.195$, $k_3 = 0.408$ and $k_3 = 0.015$ as baseline.

These observations, based on estimate of the sensitivity index of the mortality with respect to each parameter, more or less confirm those made from the parameter variation and suggests that mortality in parous flies is insensitive to changes in k_1 and k_2, whereas younger flies are sensitive to changes in these parameters. The reverse is true with k_3 and k_4 with sensitivity highest in the older age groups.

In summary, these results show that any little change in parameter k_4, may lead to a tremendous amount of changes on the flies' mortality for all ages thereby affecting the dynamics of the population. With k_2, a huge increase in its value would be required to be able to have great impact on the mortality of the general age distribution. Biologically, k_3 and k_4 affect the adult flies mortality in a similar way to the effect of temperature on the mean mortality of some *Glossina*.

In the next section we fit our model to ovarian age data based on the four mortality parameters of equation (4.2) and further explore the role and impact of the estimated parameters that would be obtained from the model fit.

4.7   Model fit and parameter estimation

"There is no sense in producing theories if they are not to be tested in the field" Gilbert
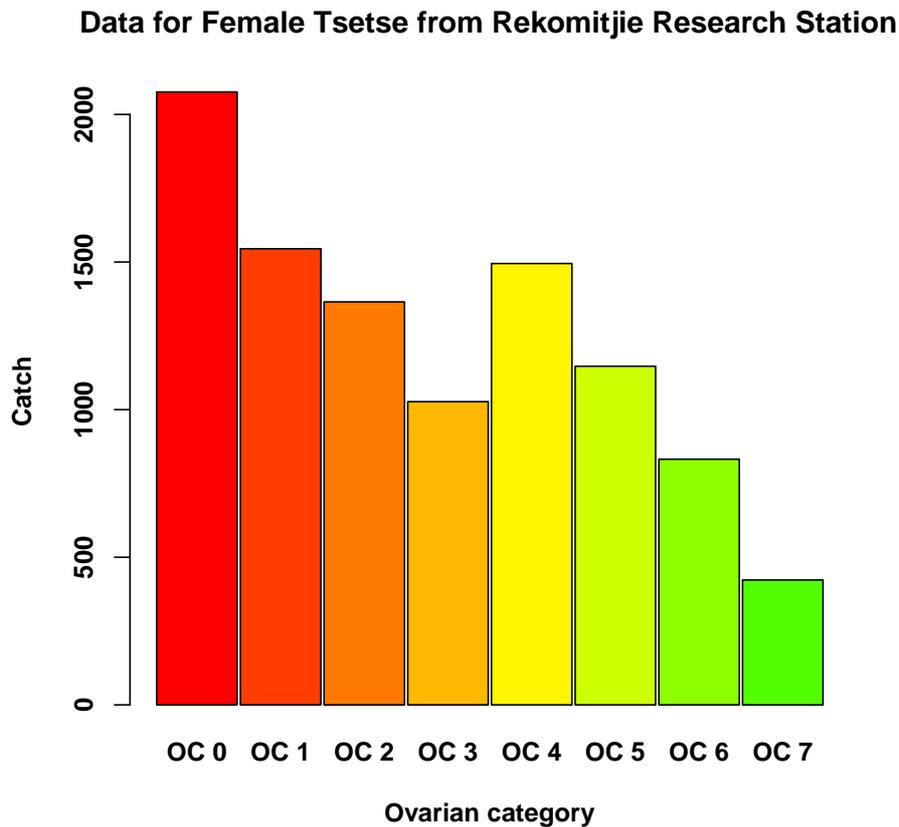
FIG. 4.11. Ovarian Category Data of female *G. pallidipes* obtained from Rekomitjie Research Station, Zimbabwe from $1989 - 1994$.

Model validation and fitting to real data are essential in the field of epidemiology, demography and ecology. It is important to test and validate such models using field data which are representations of real life situations. The importance of this procedure is that it gives guidance on what, if any, adjustments need to be made to the initial model assumptions. With this, prediction can be made of future expectations and any conclusion drawn would be of great value to public health.

Age distribution data for female adult tsetse of *G. pallidipes* obtained from Rekomitjie Research Station, Zambezi Valley Zimbabwe as described in Chapter 2 and represented in FIG. 4.11 are used to validate the model of equations (4.1)-(4.4).

In any given equilibrium population, one would expect a decline in the population number with age as obtained in both the analytical and numerical solutions with age (FIGS. 4.4 and 4.6a). But, as could be noticed from plot of FIG. 4.11 representing the catch of flies, such expectation is truncated after a particular ovarian category. This is observed to take place at ovarian category 4 with the spike in the number of tsetse flies caught. The reason for this spike at that point is that, the fourth ovarian category is the beginning of composite categories as it contains flies of ovarian categories 4, 8, 12 due to our inability to uniquely identify the ages of flies which have ovulated more than $3-4$ times as earlier discussed in Chapter 2. All subsequent categories pose the same problem.

Applying the least square curve fitting optimization tools (method 1) to our model (pde) and the generalized reduced gradient (GRG2) optimization tools (method 2) on the discrete age-dependent version [120] of our model, we fit these models to these data. These tools tend to estimate the optimal parameter values which minimize the residual sum of squares error that give rise to the fit.

(a) Model fit obtained from method 1

(b) Model fit obtained from method 2
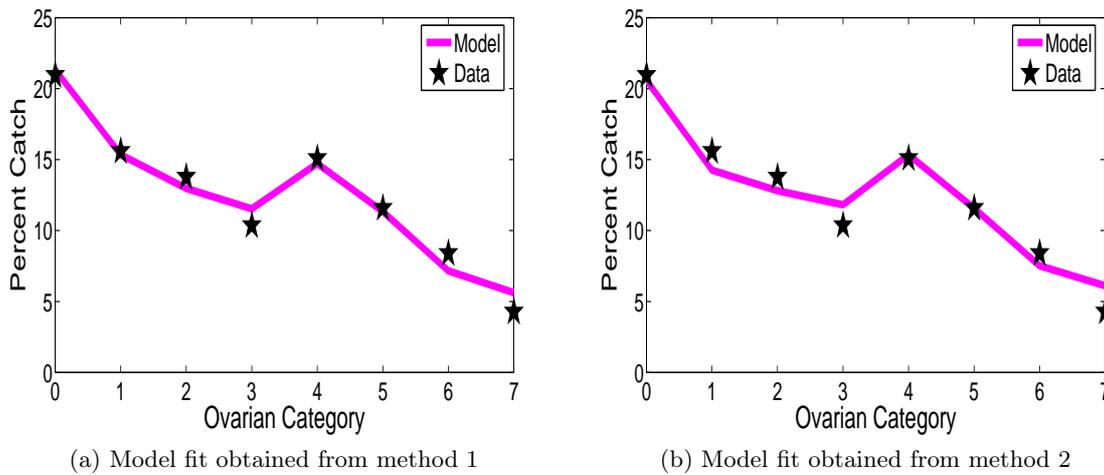
FIG. 4.12. Fit of female tsetse population model (equations (4.1)-(4.4)) to data structured by ovarian age category using two different methods that minimizes the residual error for which the parameters are optimized.

The model's fits and the estimated parameters obtained based on the two methods mentioned above are represented in FIG. 4.12 and on Table 4.2 respectively.

As represented in FIG. 4.12, the model's fit is over and underestimated for only few ovarian categories with reasonably good fits obtained using both methods but with much better fit obtained using method 1 (FIG. 4.12a).

TABLE. 4.2. Optimized parameter values for the continuous model (method 1) and that from the discrete version (method 2) together with the estimated parameter values obtained using method 2 for data of *G. morsitans* on Redcliff Island [120]

Parameters	[120]	Method 1	Method 2
k_1	0.643	1.1183	1.1266
k_2	0.195	0.1828	0.2366
k_3	0.408	0.0991	0.0884
k_4	0.012	0.0346	0.0385
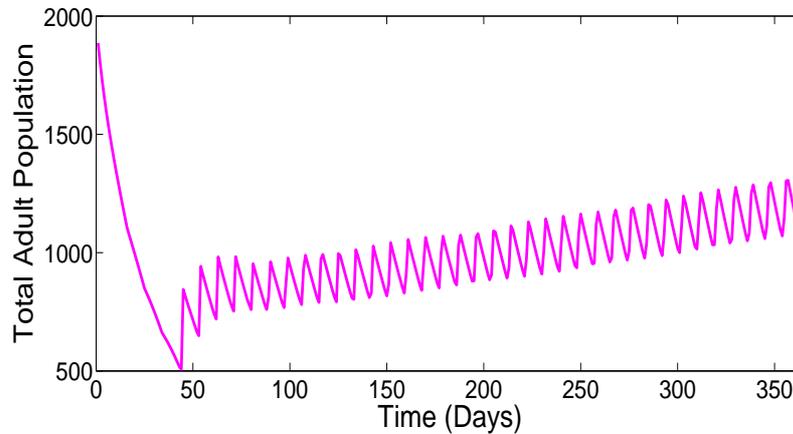
FIG. 4.13. Solution with time using parameters obtained from method 1.

Using the estimated parameters of method 1, an exponential growth rate is predicted for the adult population as shown in FIG. 4.13 but not as high and fast as the one with the initial parameters [120] used (FIG. 4.6b). Notwithstanding, the observed oscillations in the population growth take the same time steps in both results. Population growth generally depends on both the individual birth and mortality rate. Hence any factor affecting any of these is thus affecting the general population dynamics indirectly which should be well understood before implementing any control measure on the population. For this chapter, the population growth rate is found to be controlled indirectly by the changes in the mortality parameters.

In this section, we used a four parameter (k_1, k_2, k_3 and k_4) model for the adult tsetse mortality [120] in our analyses. In a study published recently [21], we fitted the model to survival data using the non-linear fitting routine, 'nl', in Stata 11. Then, by using an F statistic testing for significance, we showed that k_1 is not significantly different from k_3 reducing hence the number of parameters in the model to three only.

In the next sections, we will consider the model with three parameters only from [21].

4.8   Adult tsetse mortality with three parameters

Whereas early analysis of mortality in adult tsetse was based on the four parameter model summarised by Equation (4.2), later analysis [21] showed that a simpler three parameter model, where $k_1 = k_3$, provided a fit to the data that was not statistically worse.

With $k_1 = k_3$, the expression for the female adult tsetse mortality can be rewritten more simply as

$$\mu(a) \quad = \quad K_1 \left(K_2 e^{-aK_2} + K_3 e^{aK_3} \right), \tag{4.17}$$

where $K_1 = k_1$, $K_2 = k_2$ and $K_3 = k_4$.

In this section, we carry out similar sensitivity analysis of the adult mortality with each parameter using the new formula and then compare the outcome with the previous results of the four parameter mortality formula.

(a) Varying K_1, with K_2 and K_3 held constant   (b) Varying K_2, with K_1 and K_3 held constant
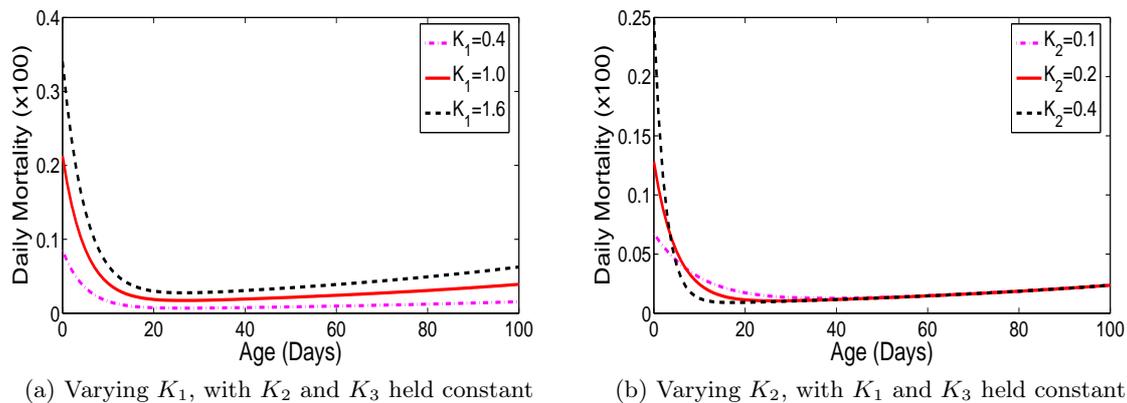
FIG. 4.14. Role of K_1 and K_2 on the mortality of tsetse flies through all ages.

Firstly, applying the same procedure of parameter analysis on equation (4.17), we observe that changes in parameter K_1 affect the mortality of flies of all ages. This is because in equation (4.17) the mortality rate is the product of K_1 with the sum of both the decreasing and increasing exponentials. Maximum effect of this parameter change is noticed with teneral flies and specifically in flies of age 0. Changing K_2 affects the mortality of younger flies only while K_3 strictly affects the mortality of older ones.
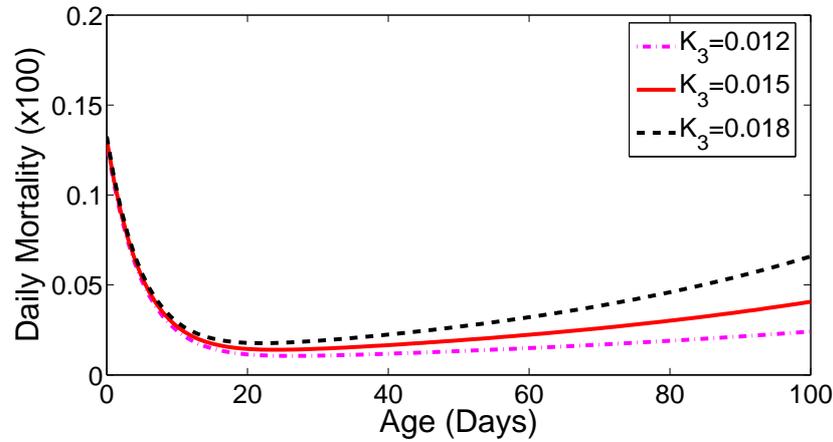
FIG. 4.15. Adult mortality varying parameter K_3.

$$\Phi_{K_1}^{\mu(a)} = 1$$
$$\Phi_{K_2}^{\mu(a)} = \frac{K_2(1 - K_2a)e^{-aK_2}}{K_2e^{-aK_2} + K_3e^{aK_3}}$$
$$\Phi_{K_3}^{\mu(a)} = \frac{K_3(1 + K_3a)e^{aK_3}}{K_2e^{-aK_2} + K_3e^{aK_3}}.$$

Using the baseline parameters obtained in [21], we plot in FIG. 4.16 the sensitivity indices $\Phi_{K_i}^{\mu(a)}$ $i = 1, 2, 3$ with respect to K_1, K_2 and K_3 as a function of age a.
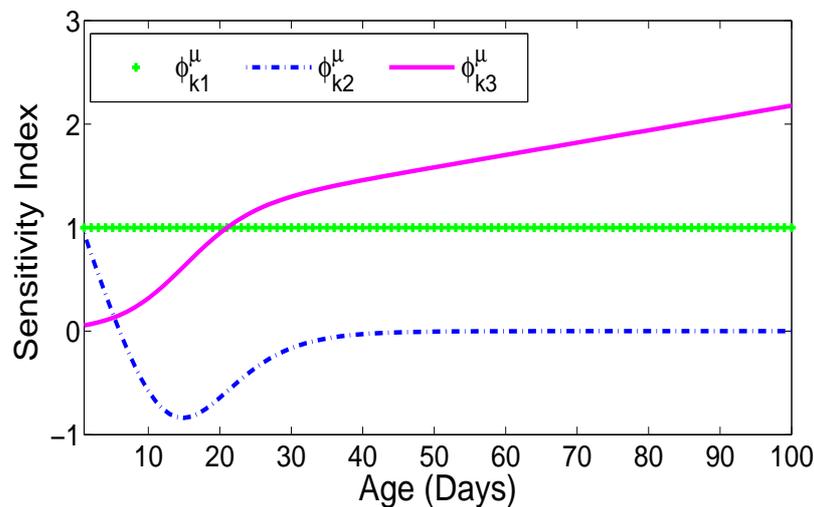
FIG. 4.16. Sensitivity index of adult mortality with $K_1 = 0.605$, $K_2 = 0.201$ and $K_3 = 0.0119$ as baseline parameters.

The graphs indicate that the mortality rate is more sensitive to K_3 than to K_1 and K_2. They also indicate that $\Phi_{K_1}^{\mu(a)} = 1$ meaning that, for all ages, an increase of 1% in K_1 results in

the same increase of 1% in the mortality. For the sensitivity index with respect to K_3 we notice a constant increase with age, the index rises almost linearly from 1.3% at age 0 (which corresponds to the age $0 + a_c = 30$ days) to 4.5% at age 100 $(100 + a_c)$. The sensitivity index of K_2 is negative for small values of a, indicating a small negative impact on the mortality rate for young adults. For older flies, this index increases to reach zero meaning that K_2 has almost no impact on mortality. The sensitivity analysis tells us that if an external factor such as temperature, for example, affects the mortality of older ages more than that of younger ages then it will change the value of K_3 more than the other parameters. Conversely, if this factor affects all ages equally then K_1 will be most affected.

4.9 Analysis of the mean mortality with stable age distribution

Estimating the mean mortality of adult tsetse flies is necessary as it presents the rate at which the flies population pooled over all ages die over time and also gives the possibility of estimating the mean age of the population. One important reason why this estimate is relevant to this study is that it creates the possibility of answering one of the questions for which this study aims at addressing. It has to do with the interaction between age and temperature in the mortality of the adult flies. We will explore this by considering the estimate of the mean mortality as functions of K_1, K_3 to establish a relation between the mean mortality with temperature.

We are interested, in this section, only in the mean mortality at the equilibrium. Its expression is given by:

$$\bar{\mu} = \frac{\int_0^{+\infty} \mu(a)N(a)da}{\int_0^{+\infty} N(a)da}, \tag{4.18}$$

where $N(a)$ is the numbers of tsetse of age a at the equilibrium given by

$$N(a) = N(0)e^{\left(K_1\left(e^{-aK_2} - e^{aK_3}\right)\right)} \text{ [21]}.$$

with $N(0)$ is the number of flies of age zero.

The integral $\int_0^{+\infty} \mu(a)N(a)da$ represents the total mortality over all ages and the denominator $\int_0^{+\infty} N(a)da$ is the total female adult population.

Analytically, it is difficult to solve equation (4.18) due to the double exponential and thus, we seek an approximate solution of the equation numerically. Varying each of parameters

K_1, K_2, and K_3 one at a time, we observe in FIG. 4.17a that, for all values of K_3, the mean mortality is a linear function of K_1 passing through the origin, while FIG. 4.17b gives a quadratic relation of the mean mortality (also passing through the origin) with K_3 holding for each K_1. Moreover, for the parameter values from Table 4.2, the sensitivity index of the mean mortality with respect to K_1 (resp. K_2, K_3) is equal to 0.668 (resp. 0.008, 1.391). This indicates that the mean mortality is twice as sensitive to changes in K_3 than in K_1. Moreover, we observe that K_2 has almost no effect on the mean mortality this gives some reasons why we can ignore the effect of K_2 on our approximation of the mean mortality without significantly affecting it. In addition, the data for which the effect of temperature (equation (4.22)) on the adult fly's mean mortality was generated does not take into consideration the nulliparous flies where the mortality is most strongly affected by K_2. This was due to the sampling method applied which does not have representation of nulliparous flies and this gives additional reason why it is more appropriate to compare the outcome of the mortality from that experiment with that which we will obtain using K_1 or K_3 or even both. In practice, most studies of such kind on tsetse flies are usually carried out with the omission of the nulliparous flies so as to avoid misinterpretation in the final output. We are particularly interested in the parameter for which there is increase in the mortality of flies of all age which may be of great advantage in bringing down the total tsetse population thereby reducing the transmission rate of the disease caused by the flies.

With all these observations, we are yet to obtain an explicit expression for the mean mortality as functions of K_1, K_3 or both with which we can work out its relation with temperature. Therefore, we will obtain plots of the mean mortality with each of K_1 and K_3 and apply a regression fit to get the explicit expression needed.

Lemma 2 *The mean mortality at equilibrium is equal to zero when either K_1 or K_3 is equal to zero.*

Proof 4.9.1 *Recall that*

$$\bar{\mu} = \frac{\int_0^{+\infty} \mu(a)N(a)da}{\int_0^{+\infty} N(a)da}$$

with

$$\mu(a) = K_1 \left(K_2 e^{-aK_2} + K_3 e^{aK_3} \right)$$

and

$$N(a) = N(0)e^{(K_1(e^{-aK_2} - e^{aK_3}))}.$$

Clearly, if $K_1 = 0$, then $\bar{\mu} = 0$. If $K_1 \neq 0$, we rewrite the mean mortality as follows

$$\bar{\mu} = \frac{\displaystyle\lim_{a \to +\infty} \int_0^a \mu(a)N(a)da}{\displaystyle\lim_{a \to +\infty} \int_0^a N(a)da}$$

$$= \frac{N(0) - \displaystyle\lim_{a \to +\infty} N(a)}{\displaystyle\lim_{a \to +\infty} \int_0^a N(a)da}.$$

If $K_3 = 0$, then $\lim_{a \to \infty} N(a) = N(0)$. This implies that the numerator of $\bar{\mu}$ is equal to 0. Moreover, $\lim_{a \to +\infty} \int_0^a N(a)da > 0$, then $\bar{\mu} = 0$.

Based on the fundamental proof showing that the mean mortality equals zero when K_1 or K_3 are equal to zero values. In order to obtain an explicit expression of the mean mortality with each of these parameters, we therefore force the mean mortality as represented in FIG. 4.17 to pass through the origin.

(a) Mean mortality with K_1 (b) Mean mortality with K_1
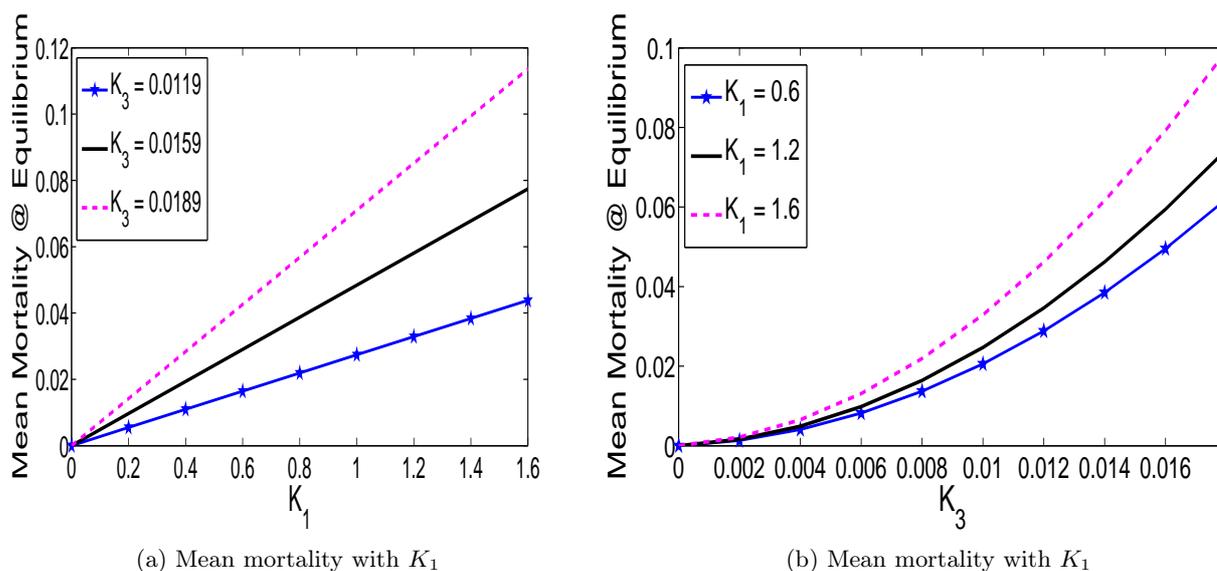
FIG. 4.17. FIG. 4.17a shows a linear relationship of the mean mortality with K_1 passing through the origin, increasing linearly with K_3 while FIG. 4.17b gives a non-linear relation of the mean mortality also passing through the origin with K_3 holding for each K_1.

FIG. 4.17 shows the relation between the mean mortality (denoted by $\bar{\mu}(K_1, K_3)$) and each of parameters K_1 and K_3. We observe that for each fixed value of K_3, the mean mortality, $\bar{\mu}$, is a linear function of K_1. This with the fact that $\bar{\mu} = 0$ when $K_1 = 0$ imply that

$$\bar{\mu}(K_1, K_3) = \alpha_1(K_3)K_1. \tag{4.19}$$

Moreover, for each fixed value of K_1 $\bar{\mu}$ is quadratic function of K_3. This with the fact that $\bar{\mu}$ equals 0 when $K_3 = 0$ imply that

$$\bar{\mu}(K_1, K_3) = \alpha_3(K_1)K_3^2 + \beta_3(K_1)K_3. \tag{4.20}$$

Thus

$$\alpha_1(K_3) = \frac{\alpha_3(K_1)}{K_1}K_3^2 + \frac{\beta_3(K_1)}{K_1}K_3.$$

Furthermore, we have $\dfrac{\beta_3(K_1)}{K_1} = \alpha_1'(0)$ and $\dfrac{\alpha_3(K_1)}{K_1} = \dfrac{\alpha_1''(0)}{2}$. This implies that $\dfrac{\alpha_3(K_1)}{K_1}$ and $\dfrac{\beta_3(K_1)}{K_1}$ are constant. Hence

$$\bar{\mu}(K_1, K_3) = K_1 K_3 \left(AK_3 + B\right)$$

where $A = \dfrac{\alpha_3(K_1)}{K_1}$ and $B = \dfrac{\beta_3(K_1)}{K_1}$ where K_1 can be any constant value preferably 1. We obtain $A = 475.5$ and $B = 0.4167$.

Theorem 4.9.2 *The mean mortality is a bilinear function of K_1 and K_3 given by*

$$\bar{\mu}(K_1, K_3) = K_1 K_3 \left(AK_3 + B\right) \tag{4.21}$$

with $A = 475.5$ and $B = 0.4167$.

4.10 Adult tsetse mortality with age and temperature

For female *G. m. morsitans* on Antelope Island the relationship between mean mortality averaged over all ages and temperature was given by [120]:

$$\bar{\mu}(T) = e^{(0.083T - 0.85)}. \tag{4.22}$$

T stands for temperature and $\bar{\mu}(T)$ denotes the temperature dependent mean mortality of female adult tsetse flies.

Having obtained explicit expressions of the mean mortality with K_1 and K_3 together with their combination as in equation (4.21), we seek to investigate the interaction of both age and temperature on the mortality. We obtain

$$AK_1K_3^2 + BK_1K_3 = e^{(0.083T - 0.85)},$$

where $A = 475.5$ and $B = 0.4167$. And so with the two parameters it contains, we have either

$$K_1(T) = \frac{e^{(0.083T - 0.85)}}{K_3(T)(B + AK_3(T))} \tag{4.23}$$

or

$$K_3(T) = \frac{1}{2A} \left[-B \pm \sqrt{B^2 - \frac{4Ae^{(0.083T - 0.85)}}{K_1(T)}} \right]. \tag{4.24}$$

From equations (4.23) and (4.24), there are several possible ways of obtaining the adult tsetse mortality as functions of both age and temperature. We will discuss but a few of these for each case under various assumptions.

Assumption 1: $K_3(T) = $ **constant**

We obtain FIG. 4.18.
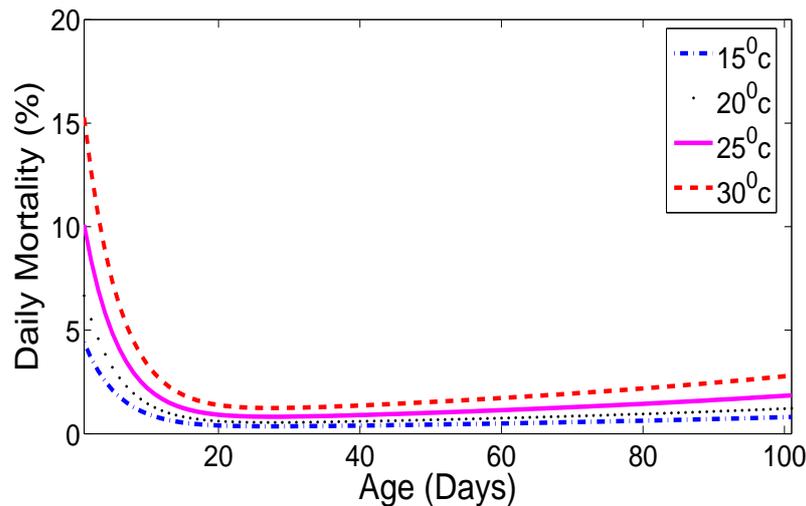
FIG. 4.18. Daily mortality when K_3 is constant.

Increases in temperature increase the mortality of newly emerged flies more than that of the mature tsetse as driven by K_1 as represented in FIG. 4.18. This result is similar to that with K_1 being temperature-dependent and independent of K_3.

Assumption 2: $K_3(T) = aT + b$

The mortality plot based on this is shown in FIG. 4.19. The outcome of Assumption 2 as depicted in FIG. 4.19 is similar to that in FIG. 4.18 but with higher mortality rate for the latter.
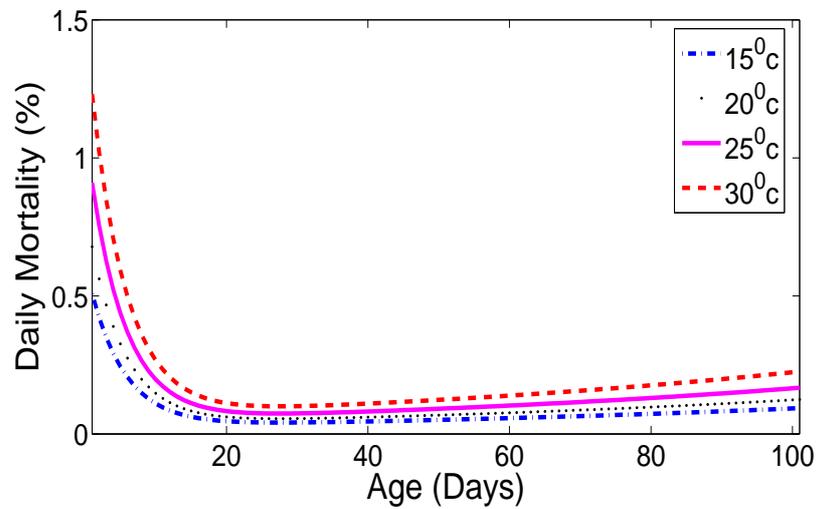
FIG. 4.19. Daily mortality when K_3 is linear with temperature.

Assumption 3: $K_3(T) = 1/(aT + b)$
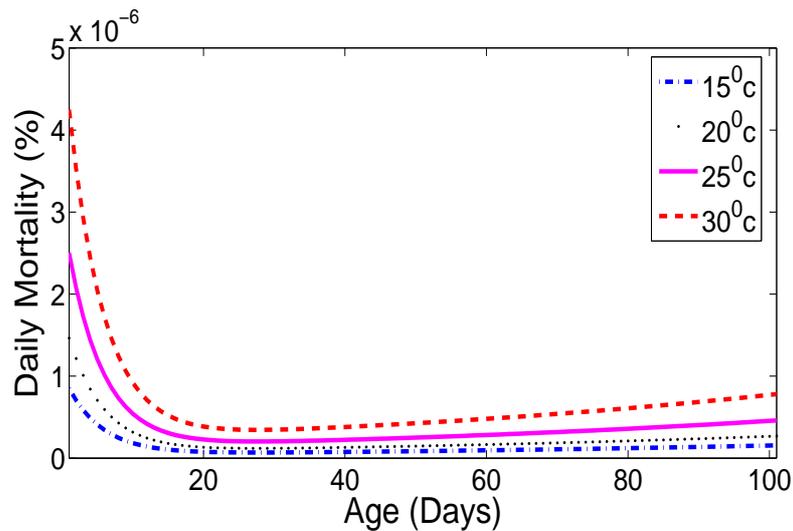
FIG. 4.20. Daily mortality when K_3 is an inverse function of temperature.

FIG. 4.20 is the result of Assumption 3 and we observe very low mortality rate based on this assumption with unrealistic values.

All of the above assumptions, with K_1 being temperature-dependent, clearly indicate that the effect of temperature on the mortality of female adult tsetse flies is distributed over flies of all ages. It is such that as temperature increases, mortality of tsetse flies of all ages increases.

Assumption 4 $K_1(T) =$ constant.

As previously carried out, substituting equation (4.24) into equation (4.17) and based on this assumption, we obtain FIG. 4.21.
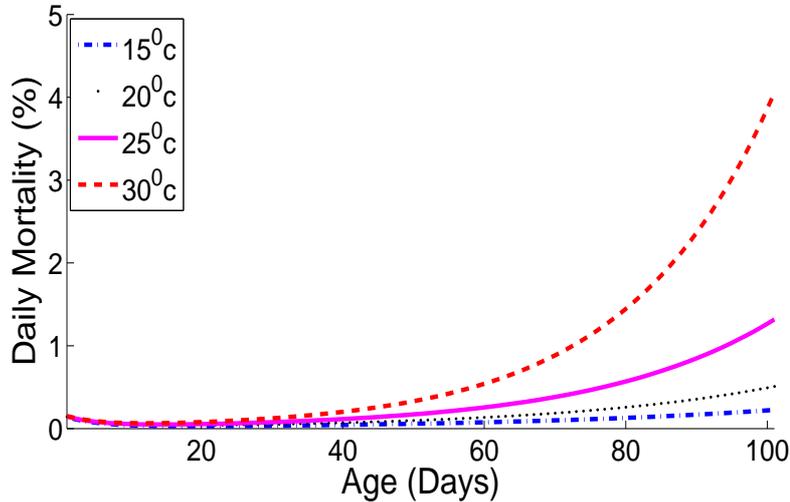
FIG. 4.21. K_3 as a function of temperature where K_1 is constant

In the case where K_1 is assumed to be constant, we observe a different effect of temperature on the mortality of tsetse flies of different ages. While increases in temperature increase the mortality of newly emerged adult tsetse flies with K_1, it increases the mortality of the mature flies with K_3 as given in FIG. 4.21. This will in turn lower the number of the reproductive age groups in the population.

To further explore the simultaneous effect of both age and temperature in the population dynamics through its effect on the tsetse survival, we will develop a mathematical model (system of pde) similar to that applied in this chapter but considering adult mortality as a function of both age and temperature. This will be accompanied with a temperature-dependent pupa duration accounting for adult tsetse birth rate.

4.11 Summary

In this chapter, we studied the dynamics of female tsetse population under the assumption of constant pupal duration with an age-dependent adult mortality using a mathematical model based on a partial differential equation. The model analysis predicts an exponentially growing population within one year for certain mortality parameter values. However, for some other parameter values, the possibility of a stable population is noted. In both cases, constant

oscillations at an interval of 9 days, representing the time interval between two consecutive birth of pupae, are obtained. A continuous decline of the population with age is predicted due to natural endogenous cause (aging) with tsetse in ovarian categories $1-3$ having the highest contribution to the population size.

Analysis of a four parameters (k_1, k_2, k_3, k_4) age-dependent adult mortality formula showed that k_1 and k_2 control the mortality of the immature adult tsetse; k_3 and k_4, on the other hand, affect mature tsetse of reproductive age. Increase in the latter parameters leads to increase in the mortality of tsetse in a similar way as with the effect of temperature on adult tsetse mortality as observed in [120].

Carrying out a sensitivity analysis on all four parameters of the mortality expression, we observed that parameter k_4 has the highest impact on the tsetse mortality while k_2 has the least effect.

A good fit of the age distribution population model to ovarian age category data of female *G. pallidipes* was obtained and showing a good representation of the model with respect to age. Following the analysis of a three-parameter (K_1, K_2, K_3) adult tsetse mortality formula obtained in [21], the role of K_1 distributes over tsetse of all ages. K_2 and K_3 on the other hand play their role across the immature and mature adult tsetse respectively. Whereas K_3 has the greatest impact on adult tsetse mortality, K_2 has the least effect of the parameters.

An observation of a constant change in the estimate of the mean mortality at equilibrium for all time with each parameters enabled the comparison of the age-dependent adult mortality with a temperature-dependent adult mortality both obtained in [120]. Whereas a linear relationship of the mean mortality with K_1 is obtained, a quadratic relationship is the case with K_3. Further analysis resulted in having K_1 and K_3 each as functions of temperature and finally led to several forms of an age and temperature-dependent adult tsetse mortality.

If only K_1 is temperature-dependent then an increase in temperature leads to increase in the mortality of tsetse of all ages; but if K_3 is temperature-dependent, increasing temperature leads to the increase in the mortality only among mature adult tsetse.

Chapter 5

Dynamics with Age and Temperature Effect

5.1 Introduction

Climatic factors are very important to be considered in any insect population study. Temperature as one of these factors is never constant through the year and is known, from laboratory [1] and field [120] studies, to affect adult tsetse mortality. In [120] a linear relationship between temperature and the log of the adult tsetse mean mortality was obtained. The effect is such that an increase in temperature leads to an increase in the flies' mortality. The emergence of pupae as adult flies which accounts for the birth rate have also been established from several studies to vary with temperature. With tsetse death and birth rate both affected by temperature, it is then very important to consider this factor when studying tsetse population dynamics as it allows for a more accurate prediction of the trend the future population may follow. Establishing the relationship between tsetse mortality and temperature is one thing. Having knowledge on the rate at which the tsetse flies of different ages die due to natural endogenous cause is another thing. The question now is, what level of impact would the interaction of the two factors have on the adult tsetse mortality and hence the total population dynamics. This brings us to the main purpose of this study which no previous investigations have addressed.

As a result, in this chapter, we will modify the previous models by incorporating temperature-dependent adult birth rate through the pupal duration using the daily mean temperature record obtained from Antelope Island, Lake Kariba. Changes in the adult tsetse mortality with both age and temperature will also be incorporated.

Finally, the fit of our model to data for the monthly catch of female *G. m. morsitans* will be obtained. We now present the modified model.

5.2 Population model with age and temperature dependent mortality
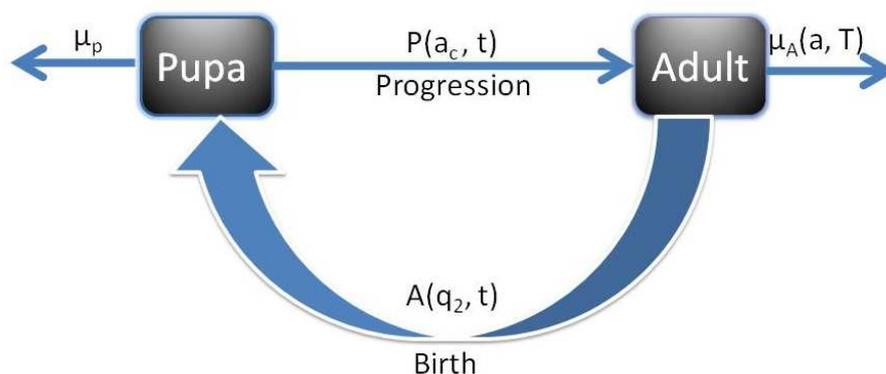
FIG. 5.1. Model diagram with tsetse birth rate changing with temperature through the pupa duration, $a_c = a_c(T(t))$ given as a function of temperature which depends on time (t) with $q_2 = a_c + 15$.

Considering adult tsetse mortality due to age and temperature with temperature-dependent pupa duration, we present our mathematical model for the tsetse population dynamics as in equation (5.1).

$$\left(\frac{\partial}{\partial a} + \frac{\partial}{\partial t}\right) X(a,t) \;=\; -\mu(a,t)X(a,t) \tag{5.1}$$

with initial age distribution (assumed to be a known constant) and pupa birth rate (time dependent) respectively given by

$$X(a,0) \;=\; X_0(a), \tag{5.2}$$

$$X(0,t) \;=\; X(a_c(t) + 15 : 9 : Amax, t), \qquad Amax \text{ is the maximum age.} \tag{5.3}$$

Here the age specific mortality is given by

$$\mu(a,t) \;=\; \begin{cases} 0.01 & \text{if } a < a_c(t), \\ K_1(t)\left(K_2 e^{-(a-a_c(t))K_2} + K_3 e^{(a-a_c(t))K_3}\right) & \text{if } a \geqslant a_c(t). \end{cases} \tag{5.4}$$

where $\mu(a,t)$, $a_c(t)$ and $K_1(t)$ denote $\mu(a,T(t))$, $a_c(T(t))$ and $K_1T(t)$, respectively. The expression for estimating the pupal duration, $a_c(t)$ from which the daily changes in the pupal duration due to daily temperature change as shown in FIG. 5.3a was obtained is given by

$$a_c(t) = \left(1 + e^{(\alpha + \beta T)}\right)/k \quad [120],\tag{5.5}$$

where α, β, and k are estimated coefficients [120]. Equations $(5.1) - (5.3)$ make up the complete model for the population dynamics of tsetse population while considering the effect of temperature on both the birth and adult mortality rates. The analytical solution of the model is not presented here due to its complexity, arising from the adult mortality formula (equation (5.4)), together with the daily changes in the birth rate (equation (5.5)). Nevertheless, the model was solved numerically, as it gives a good approximation of the model behaviour. The results of the numerical solution are presented in section 5.3, with further application to adult tsetse population data as shown in section 5.4.

A regression fit was carried out on data for the daily record of the average temperature of Antelope Island, Lake Kariba Zimbabwe in 1981, as shown in FIG. 5.2. The resulting equation to the fit which describes the daily changes in temperature for that period is given in equation (5.6).
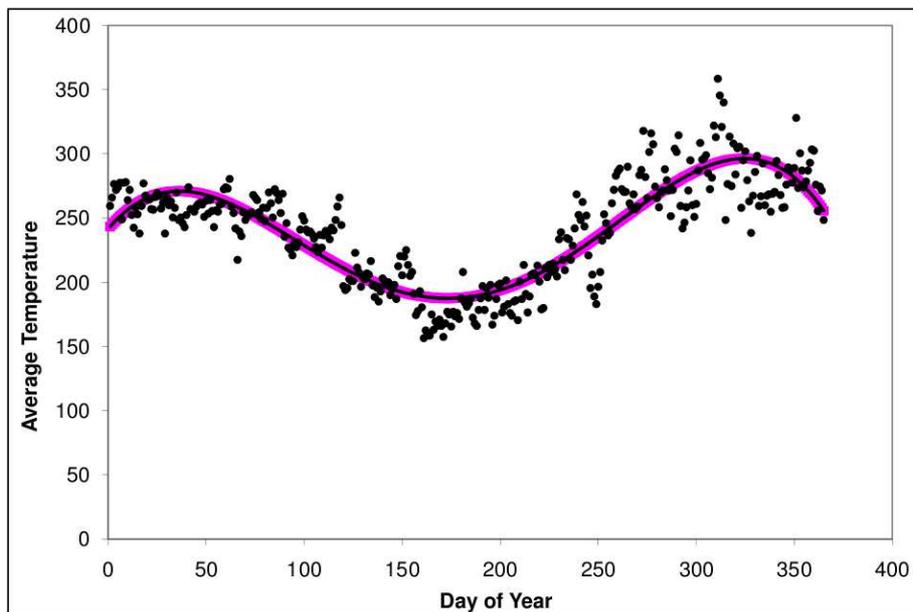
FIG. 5.2. Regression fit (lines) of daily temperature, $(T(t))$ data (dots) on Antelope Island, Lake Kariba in 1981. The equation of the fit is given in equation (5.6).

$$T(t) = -0.0000002216t^4 + 0.0001578133t^3 - 0.0329230653t^2 + 1.8071666526t + 241.60, \quad (5.6)$$

where t (starting from zero) is time in days. FIG. 5.2 is a representation of the daily average temperature record together with the fit from which equation (5.6) is obtained. Based on equation (5.5), the plot for the daily pupal duration, influenced by the daily average temperature of equation (5.6) is represented in FIG. 5.3b. Note that T is the temperature in degrees centigrade $x10$; i.e., a value of 250 equates to 25.0^0C. Note also that the sharp transient decline in temperature between time, 300 to 400 days marks the timing of the onset of the rainy season. Towards the end of the rainy season the temperatures rise again for some weeks before falling with the onset of the cool dry "winter" period.

(a) Daily changes in temperature

(b) Changes in pupal duration with daily temperature
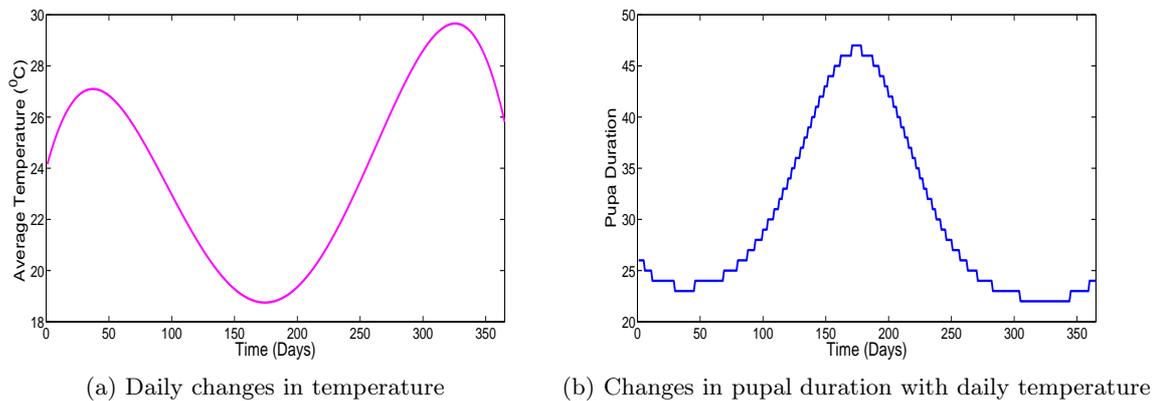
FIG. 5.3. Estimate of the pupal duration (a) according to daily mean temperature (b) record obtained from Antelope Island Lake Kariba.

5.3 Numerical solution with age and temperature-dependent mortality

From the previous chapter, we obtained the adult tsetse mortality in terms of age and temperature under different conditions. We shall now discuss the case where K_1 depends on both K_3 and temperature and that for which K_3 depends on both K_1 and temperature but with focus on the former.

5.3.1   Dynamics with K_3 being constant

In this section, we consider the equation

$$K_1(T) \ = \ \frac{e^{(\delta T - \gamma)}}{K_3(B + AK_3)},$$ (5.7)

with $\delta = 0.083$, $\gamma = 0.85$, $A = 475.5$, $B = 0.4167$. Here we present the case where parameter, K_1 is obtained as a function of temperature, with K_3 being constant. Applying the daily temperature of equation (5.6), we deduce the plot in FIG. 5.4a. Further application of this in the adult mortality of equation (5.4) and then solving the population model of equations (5.1) − (5.3) numerically, yield the dynamics as shown in FIG. 5.4b.

(a) Parameter K_1 as a function of temperature   (b) Daily number of the adult tsetse flies

FIG. 5.4. (a) Daily changes in parameter K_1 due to changes in daily temperature represented in equation (5.6). (b) Adult tsetse population for K_1 changing with temperature, $K_2 = 0.201$ and $K_3 = 0.0119$ [21].

Considering the values of K_2 and K_3 as estimated in [21] and applying the formula for K_1 as in equation (5.7), we observe the dynamics for the adult tsetse population to follow an increasing trend. A slow increase is observed in the first year until after the first quarter of the second year where the dynamics changed from a slow growing population to a high and fast growing population.

5.3.2   Dynamics with K_1 being constant

Here, we consider the case where K_3 depends on temperature under the assumption that K_1 is constant. The expression for K_3 is given as

$$K_3(T) = \frac{1}{2A}\left[-B \pm \sqrt{B^2 - \frac{4Ae^{(0.083T-0.85)}}{K_1}}\right]. \tag{5.8}$$

where the values of A and B, as obtained in the previous chapter, are given as 475.5 and 0.4167, respectively. We have earlier observed the role of K_3 to basically affect tsetse flies of

(a) Parameter K_3 as a function of temperature

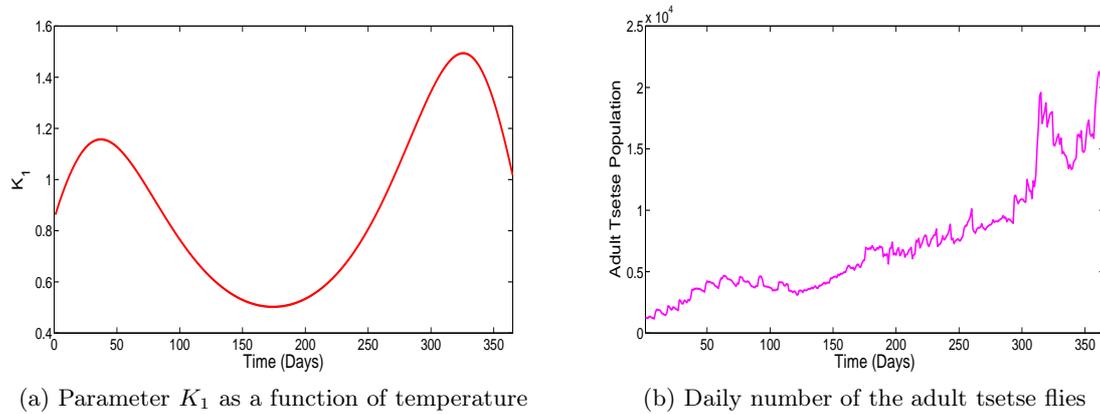(b) Daily number of the adult tsetse population
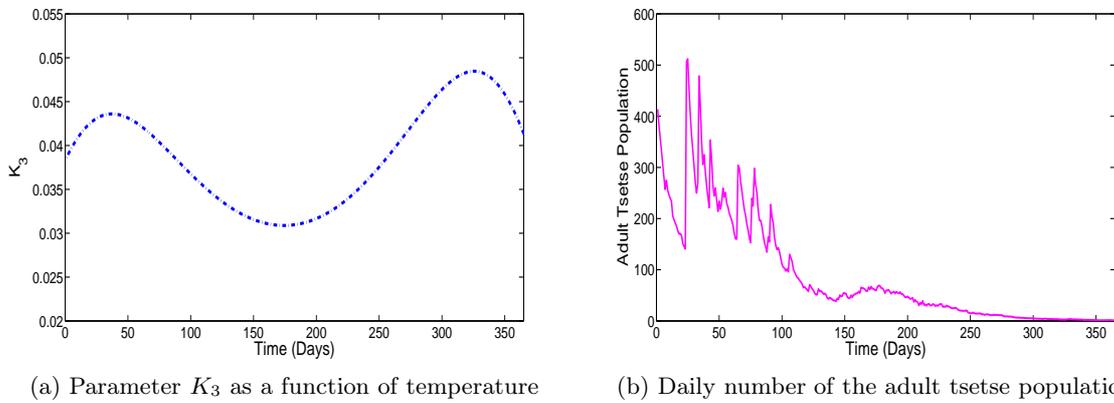
FIG. 5.5. (a) Daily changes in parameter K_3 due to changes in daily temperature as represented in equation (5.6) while (b) is the adult tsetse population that resulted from changes in K_3 with $K_1 = 0.605$ and $K_2 = 0.201$ [21]

all ages except those in the nulliparous stage. The adult tsetse population dynamics deduced by applying the assumption for this parameter as it reflects in equation (5.8), is represented in FIG. 5.5b. We notice that the long term behaviour predicts a quick decay in the population within a year. This outcome is not surprising given that with higher temperatures, very high mortality rate as in FIG. 4.21 is observed for flies of the reproductive age groups.

Having obtained results of the effect of temperature on the total tsetse population (FIGS. 5.4b and 5.5b) through the birth and adult tsetse mortality rates (adopting the mortality parameter values estimated in [21]), we shall now proceed to validate our model using data representing the monthly catch of tsetse of $G\ m.\ morsitans$. Considering the assumption that K_1 depends on temperature, as described in subsection 5.3.1 of the previous chapter, and that the pupal duration varies with temperature, estimates of the parameter values that best represent the data, will be obtained.

5.4 Data description and model fit

The data we will be using in this section is a representation of the monthly population estimates for female *G. m. morsitans* in 1981 on Antelope Island, Lake Kariba, Zimbabwe. In the plot of FIG. 5.6a, which is a representation of the data, the population is at its lowest in the month of December while July records the month with the highest number of female *G. m. morsitans* in that year.

(a) Monthly catch of female *G. m. morsitans*   (b) Model fit to population data of FIG. 5.6a
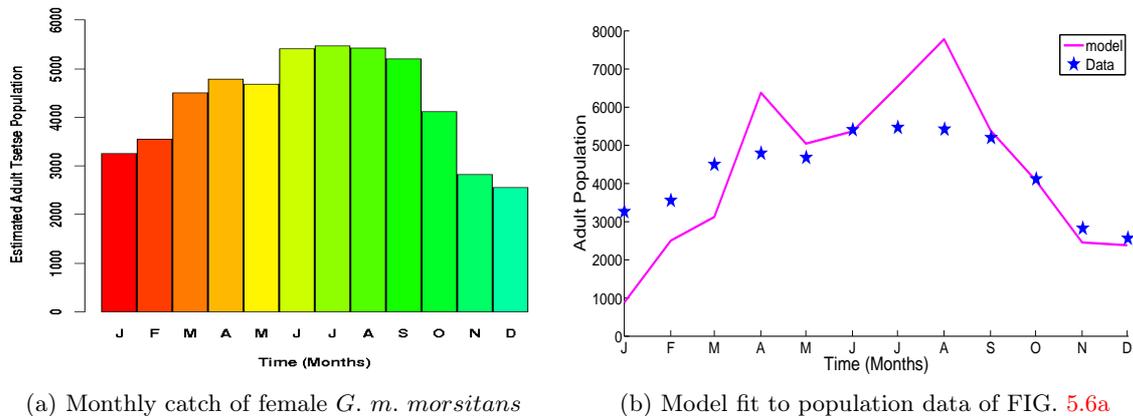
FIG. 5.6. (a) Data representation and (b) fit of the population model of equation (5.1) to the population data of female *G. m. morsitans* obtained on Antelope Island, Lake Kariba, Zimbabwe in 1981. $K_2 = 0.1801$, $K_3 = 0.01213$, $\alpha = 5.6$, $\beta = -0.289$, $k = 0.0473$, $\delta = 0.0999$, $\gamma = 0.8084$, $A = 475.5$, $B = 0.3786$.

Given the monthly population data described above as depicted in FIG. 5.6a, we obtain the fit of our model to it by using the result of the adult mortality with the assumption that K_1 depends on temperature (equation (5.7)). This is shown in FIG. 5.6b where we notice correlation between the model and the data, both having the same shape. The model as also suggested by the data predicts an increasing population in the first quarter of the year and stable population during the second quarter. It is followed by a decline in the population for the last quarter of the year and suggests first and second quarter to be the favourable period for the breeding of these tsetse flies.

Although the model exaggerates the tsetse population for some months while some others are underrepresented, we observe a linear relationship between it and the data. The relationship is shown in the regression fit of FIG. 5.7a with the tsetse population data represented on the $y-$ axis while the mathematical model (equations (5.1)-(5.3)) is on the x-axis. This also suggests that the model is a good representation of the data used. Extending the time for the dynamics to cover two years, we notice the periodicity in the profile the population of *G. m.*

morsitans on Antelope Island follows as captured in FIG. 5.7b.

(a) Data versus mathematical model

(b) Model prediction for the adult tsetse population
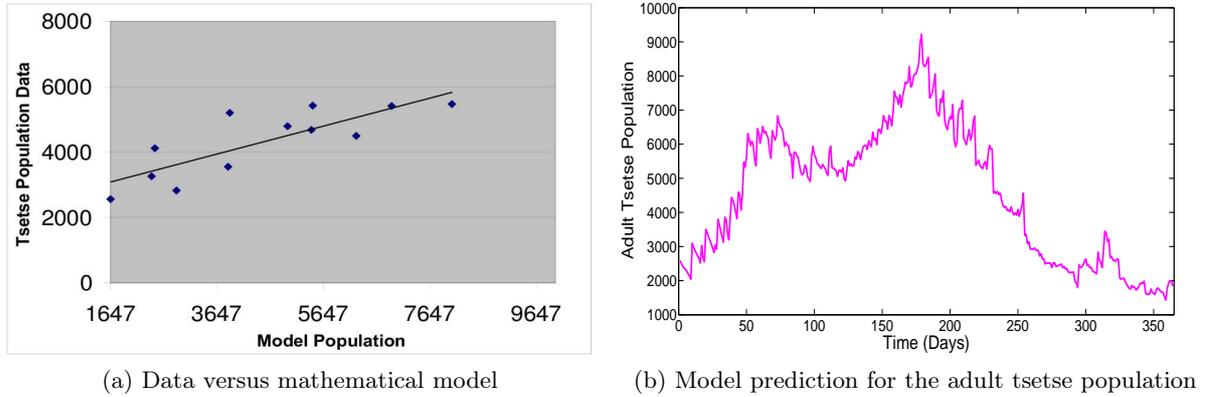
FIG. 5.7. (a) Linear regression fit of data for female $G.$ $m.$ $morsitans'$ population on Antelope Island versus mathematical model for the adult tsetse population with $R^2 = 0.70$. (b) One year model prediction of the population.

5.5   Summary

In this chapter, we investigated the combined effect of age and temperature through their effects on adult tsetse mortality, and a temperature-dependent pupal duration (adult birth rate) on the population dynamics of adult tsetse. Applying a three-parameter (K_1, K_2, K_3) model for adult tsetse mortality, with K_1 being temperature-dependent, the dynamics predict a slow exponential growing population within a year, for the values of K_2 and K_3 as obtained in [21]. Due to the changes in daily temperature, the daily growth rate is unequal, contrary to the observation made while considering the effect of age only in the previous chapter. A fast decay of the population within a period of one year is obtained when K_3 being temperature-dependent is applied in the age-dependent adult tsetse mortality while using the values of K_1 and K_2 as estimated in [21].

We obtained the fit of our model to tsetse population data and observed that the most favourable breeding period for tsetse falls within the first quarter of the year where a continuous population increase is observed. The reverse is the case during the last quarter of the year. In the second quarter, a stable growth is predicted by the model.

Finally, a linear relationship between the mathematical model (equations (5.1)-(5.3)) and the tsetse population data of Antelope Island, Lake Kariba, was observed based on a linear regression fit of the model with the data as shown in FIG 5.7a.

Chapter 6

Discussion and Conclusion

In this thesis, we formulated two models under different assumptions to study the population dynamics of female tsetse flies. The first model, developed in Chapter 4, assumes dynamics that are controlled solely by an endogenous factor, aging effect. Based on this assumption, the age dependent population described in FIG. 4.6a of that chapter, shows a continuous decline in the population with age. Such decline appears to be faster among the nulliparous and old parous, than it is with the young parous tsetse flies. This is important as it presents to us the contribution of tsetse flies of the different ages classified under those three categories and also shows the population profile as tsetse progress from one age to the next. Another result presented in that chapter shows that with time, the population could grow uncontrollably with constant oscillations occurring after every 9 days, which is controlled by the birth rate. Also, estimates of the proportion of tsetse of different age groups in the population, based on the model numerical results, show that the teneral (nulliparous) tsetse are least in number. According to the mortality expression [21, 120] applied in our model, the newly emerged (teneral) tsetse flies have the highest mortality rate. This also corresponds with the observation made by Jackson [72] whereby mortality was found higher among small members of tenerals *G. morsitans* and *G. swynnertoni* Austen. The numerical result in section 4.4, shows that the population composition is constituted mostly of young parous tsetse flies and these are tsetse in their early reproductive age. As expected, any population dominated by such age class is bound to experience exponential increase rate if not controlled by density dependence or any climatic factor that tend to increase their mortality rate. For some authors like Williams et al. [97], this is a group that should serve as the targeted age class for any control measure that is aimed at reducing tsetse population in order to achieve a more effective result within a short time frame. Tsetse in such age class have lived long enough to have possibly acquired the disease due to their exposures in feeding on several hosts with enough time to have had

the disease in its metacyclic stage (period of being infectious). With the large population size of young and old parous as compared to those of nulliparous tsetse flies (section 4.4), there is a chance of high transmission rate through flies in these categories.

In reality, any population is affected by factors such as density dependence, climatic and environmental factors. For the tsetse population, several studies have found the importance of each of these in regulating its population. Temperature in particular, as one of the climatic factors, has been found to be very important to the different tsetse developmental stages. As a result, we formulated a model that assumes the combined effect of age and temperature on the mortality of the adult tsetse with temperature varying birth rate and how these affect the population dynamics. The outcome, given in Chapter 5, shows variation in the daily population growth rate unlike the uniformity observed with the age effect only. This is partly due to the daily changes in adult tsetse mortality, for the different age distribution, with temperature and also controlled by the variation in the birth rate with temperature. Based on the model fit on data for female tsetse, $G.\ m.\ morsitans'$ population, while considering the effect of both age and temperature, tsetse population's most favorable breeding season is predicted to be during the first quarter of the year. This coincidentally happens to fall within the hot-wet season of Zimbabwe from where the data was collected. According to Taylor [87] and Okiwelu [75], the life span of tsetse of $G.\ m.\ morsitans$ Westwood (Diptera: Glossinidae) and $G.\ morsitans$ respectively, is also at its best during such period. We have observed increase in tsetse mortality rate with increasing temperature. During the first quarter of the year, our temperature data shows that, Antelope Island, in Zimbabwe, experiences very high temperature. It is then expected, with such high temperature, based on our results in section 4.10, and supported by the finding in [120], that tsetse population would be faced with the challenge of high mortality rate. Nevertheless, with rainfall at such period, there could be provision for shelter from the heat of the sun through the fresh leaves, grasses and trees. With this, the intensity of the heat on the tsetse may be reduced which may support the breeding of tsetse during that period of the year. In addition, there is rapid rate of pupa emergence as adult tsetse during the hot seasons within a short time frame, this may also possibly contributes to the high growth rate.

Accumulation of tsetse population numbers, during the first quarter of the year may have contributed to tsetse population attaining its peak in the second quarter of the year as suggested by the data and also predicted by our model. However, the second quarter of the year is a period observed to be with very low population increase rate, leading to a stable population. This outcome is not surprising because, such period is a time when Zimbabwe experiences cool and dry weather conditions in which pupae spend longer period in the ground before emerging

(if not dead) as an adult tsetse resulting in low adult tsetse birth rate. An observation made in [88] also supporting such result. Without any doubt, the birth rate is one of the two major factors that controls the growth rate of a population. Taylor [87] estimated the mean age of both male and female tsetse *G. m. morsitans* Westwood (Diptera: Glossinidae) to be lowest during the coolest period of the year which falls within the second quarter in Zimbabwe during which low growth rate is observed.

Any tsetse control carried out during the first quarter (hot-wet season) of the year, according to the result from the model fit to data in Chapter 5, may require much effort and resources, with the risk of not achieving an excellent result. The second quarter (cool-dry) may also require much resources and efforts but not as much as the first quarter would require. The last quarter (hot-dry) of the year suggests to be more promising towards achieving an excellent result in eradicating trypanosomiasis through tsetse control within a short frame of time with less resources and effort. This is due to the negative growth rate in form of a continuous decline of the population size predicted during this period. Supporting this suggestion, is the result of the investigation made by Phelps and Clarke [31] on male tsetse flies whereby only about 35.2% of the total male tsetse population was eliminated during the cool-dry period while about 75.5% elimination was observed during the hot-dry season. This suggests the best period for carrying out any intervention program aimed at eradicating trypanosomiasis through tsetse control to be during the hot-dry season.

Furthermore, there is a possibility of reduction in the transmission rate of trypanosomiasis during this period due to the reduction in the tsetse population.

In conclusion, the role of seasonality on tsetse population dynamics and trypanosomiasis infection rate has been a thing of debate in this field with only few studies [41, 75] done in this regard. Here, we only explored the effect of temperature as one of the seasonal factors. On this note, we would recommend that, further investigation be carried out, with the application of both temperature and rainfall data in studying such population dynamics, for better understanding of seasonal effect.

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