

# Estimating the Intrinsic Rate of Natural Increase (IRNI) for tsetse (*Glossina* spp) population

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## Abstract

Climate change may have started altering tsetse (vectors of trypanosomiasis) population's distribution in Africa. Environments that were initially unsuitable for them, may now be getting warm enough to support the flies. It is therefore important to understand the possibility of both tsetse population extinction, in areas that are now getting too hot for them, as well as, the chances of them surviving in cooler regions that are now getting warmer. The intrinsic rate of natural increase  $r$  is a useful metric in determining the suitability of a set of environmental condition for insect population establishment. The relatively simple life history of the tsetse allows us to solve the Euler-Lotka equation to obtain a closed form expression for  $r$ . We use daily average temperatures for the Zambezi valley of Zimbabwe (1960 - 2018) to calculate long time average values of  $r$ . And we created three climate change scenarios for the next 50 years, using daily average temperature data for 2018 as a baseline. Our results show that the growth rate is positive and relatively stable during the cooler seasons, for most of the years of the study period. However, since 2010, tsetse population has been experiencing negative growths more frequently during the hot dry season (October – December). We found that if daily average temperature continues to increase at the rate of 0.08°C per year in the Zambezi valley, tsetse population will go extinct within the next 50 years.

## Introduction

Tsetse (*Glossina* spp) are vectors of human and animal trypanosomiasis - a neglected tropical disease - endemic in many sub-Saharan African countries. Sustained control efforts have reduced disease burden in the last 10 years [1]. However, a recent study showed that climate warming may alter tsetse distribution in Africa: in one hand leading to local extinction of tsetse population in, for instance, the Zambezi valley of Zimbabwe. On the other hand, leading to emergence of tsetse and trypanosomiasis in regions that were initially too cold for the flies [2]. There is a need for an improved understanding of tsetse population growth as a function of changing temperature.

The intrinsic rate of natural increase  $r$  is an important metric in insect population dynamics as it can be used to determine whether or not a set of environmental condition is suitable for an insect population [3]. Several attempts have been made to estimate the natural rate of increase for tsetse population. Some of the methods/assumptions used in a number of those works were invalid, yielding results which are not reflecting the true growth rate of tsetse populations in the wild [4]. Moreover, we could not find any study in the literature that estimated tsetse population growth rates as a function of field temperatures. A standard means of estimating the natural rate of increase for populations is the Euler-Lotka (E-L) equation [3, 5], given in discrete form as:

$$\sum \lambda^{-x} l_x m_x = 1. \quad (1)$$

where  $l_x$  is the probability at birth, that a female individual is alive at age  $x$  and  $m_x$  the expected number of female offspring produced in a unit time by a female aged  $x$ .

The basic reproduction number  $R_o$  is:

$$R_o = \sum l_x m_x. \quad (2)$$

Tsetse have a relatively simple life history; they produce a single larva at regular intervals (+/- 2 days) [6]. The mortality rate is higher in newly emerged adult flies than in mature adults, and as the fly grows older, the mortality rate increases slightly [7]. The very basic life history of tsetse allows us to obtain a closed form solution of the E-L equation to derive an expression for the intrinsic rate of natural increase for tsetse population. We

estimated the rate of increase per-day as a function of daily average temperature for the Zambezi valley from 1960 to 2018, and we calculated long time averages of the rate of increase. Furthermore, we created three climate warming scenarios (0.04 °C, 0.06 °C and 0.008 °C annual increase), over the next 50 years, using the daily average temperature data for 2018 as a baseline. We calculated the average annual growth rate for each of the warming scenarios to determine if the annual growth rate will reduce to a negative value within the next 50 years.

## Materials and Methods

We sub-divide tsetse life-cycle into three distinct stages, namely, larval/pupal, newly emerged and larvipositing adult stages. Tsetse are a well-studied insect; and so their birth, development, and mortality rates have been measured both in the laboratory and in the field [8, 9, 10, 11, 12]. With this knowledge and their relatively simple life-cycle, we present a framework which allows us to solve Euler-Lotka equation analytically for the intrinsic rate of increase for tsetse population. We proceed by making the following simplifying assumptions.

## Model assumptions

- Once the fly attains the age of first ovulation, it retains constant fecundity rate throughout her life.
- We assume that the life-cycle of the fly is divided into three stages, pupa, newly emerged adults and larvipositing adults.
- $p_o$  is the probability of reaching the larviposition loop from "birth"
- $p_c$  is the probability of reaching the point where offspring are counted, from the point of larviposition.
- $c$  is the time interval between successive "births" (which is assumed to be constant).
- $p_l$  is the probability of surviving a larviposition loop.

## Model

Suppose  $l_x$  be the probability at birth of, a female, being alive at age  $x$ ,  $m_x$  the mean number of female offspring produced in a unit time by a female aged  $x$ .

### Basic reproduction number

The basic reproduction number ( $R_o$ ) can be calculated directly from equation (2):

$$R_o = \sum l_x m_x,$$

$$x = c, 2c, 3c, \dots \implies \frac{x}{c} = y = 1, 2, 3, \dots$$

where

$$l_1 = p_o p_l, l_2 = p_o p_l^2, l_3 = p_o p_l^3, \dots \quad (3)$$

and

$$m_1 = p_c, m_2 = p_c, m_3 = p_c, \dots \quad (4)$$

Therefore, from equations (2), (3), and (4),

$$\begin{aligned} R_o &= \sum l_y m_y = p_o p_l p_c + p_o p_l^2 p_c + p_o p_l^3 p_c + \dots \\ &= p_o p_c p_l (1 + p_l + p_l^2 + p_l^3 + \dots), \\ &= \frac{p_o p_c p_l}{(1 - p_l)}, \end{aligned} \quad (5)$$

where  $0 < p_l < 1$ . Notice that  $R_o$  does not depend on  $c$ , moreover, if  $p_o$  or  $p_c \rightarrow 0$ , then  $R_o \rightarrow 0$ . This implies that whenever any of the parameter approaches 0, the population goes extinct.

Equation (5) corresponds to the net reproduction number for tsetse population, in the general model presented in [13].

## The intrinsic rate of natural increase

We can calculate the intrinsic rate of natural increase  $r$  from the Euler-Lotka equation. Suppose all parameter descriptions remain as above, we can rewrite equation (1) by letting  $\lambda = e^{cr}$ . Equation (1) then becomes:

$$\sum (e^{rc})^{-T} l_T m_T. \quad (6)$$

where  $T$  is the integer number of time steps.

Using equations (3) and (4), we can calculate  $r$  directly from equation (6).

$$\sum (e^{rc})^{-T} l_T m_T = p_o p_l p_c (e^{rc})^{-1} + p_o p_l^2 p_c (e^{rc})^{-2} + p_o p_l^3 p_c (e^{rc})^{-3} + \dots = 1,$$

$$p_o p_c p_l e^{-rc} (1 + p_l e^{-rc} + p_l^2 e^{-2rc} + p_l^3 e^{-3rc} + \dots) = 1,$$

$$\frac{p_o p_c p_l e^{-rc}}{1 - p_l e^{-rc}} = 1. \quad (7)$$

Solving for  $r$  in equation (7), yields,

$$r = \left( \frac{\ln[p_l(p_c p_o + 1)]}{c} \right). \quad (8)$$

If  $p_o$  or  $p_c \rightarrow 0$ , then  $r \rightarrow \frac{\ln[p_l]}{c}$ . Since  $0 < p_l < 1$ , whenever any of the parameters approaches 0,  $r$  becomes negative, which implies population extinction. Moreover,  $r = 0, \implies R_o = 1$ .

## Intrinsic growth rate as a function of temperature

We assume that key parameters are temperature dependent. The relationship between these parameters and temperature are given in detail in [14]. We estimated the rate of increase per-day as a function of daily mean temperature, and we obtained the long-time (annual) average ( $\hat{r}$ ) of  $r$ , using:

$$\hat{r} = \frac{1}{N} \sum_{t=1}^N r_t \quad (9)$$

## Temperature Data

For 60 years running, maximum and minimum temperatures are being recorded daily at Rekomitjie, Zimbabwe. Measurement are taken with a mercury thermometer placed in a Stevenson screen. These readings are used to calculate the daily average temperatures from January 1960 to December 2018. Details about the temperature data are provided elsewhere [2].

## Climate change scenarios

The average daily temperatures have increased by 2°C in the month of November, and by 0.9°C for the rest of the year, in the past 27 years in the Zambezi valley of Zimbabwe [2]. Here we project three climate change scenarios.

- Temperature continues to increase, but the rate of increase is slow, i.e., the daily average temperature will increase by 0.04°C per-year.
- The rate of increase in the daily average temperatures is 0.06°C per-year
- Temperature increases fast with a rate 0.08°C per-year. This information will be used to generate temperature data for the Zambezi valley, for the next 50 years.

Our goal is to determine if the annual growth rate in the Zambezi valley will attain negative value within the next 50 years.

## Results

We used the daily average temperature data and equation (8) to calculate the intrinsic rate of natural increase of tsetse population in the Zambezi Valley of Zimbabwe, from January 1960 to December 2018. We then used equation (9) to obtain long time averages for  $r$ . We created three climate change scenarios over the next 50 years, using 2018's daily average temperature as the baseline. We used these temperature projections to calculate the annual average value of the growth rate from 2019 to 2068.

From 1960 to 1986, the annual average growth rate was between 0.00389 at the maximum and 0.00285 at minimum. There were a number of years that the growth rate was really low (for example 1971 and 1976), but the growth rate was also high for other years, making the average growth rate to be relatively stable over this period (1960 -1986). In 1987, the growth rate hit an all-time low of 0.00287. From 1987 onwards, the average annual growth rate has consistently fall below 0.0038. From 2010 to 2018, the average growth rate has dropped even further, hitting a new all-time to of 0.0023 in 2016 (Fig 1).

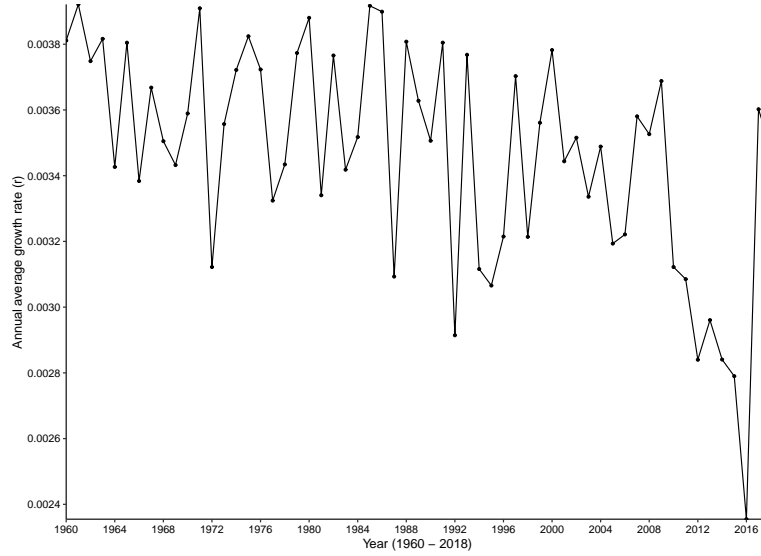


Figure 1: Averaged annual growth rate for tsetse population in the Zambezi valley of Zimbabwe: from 1960 to 2018.

Temperatures vary seasonally, and higher temperatures are usually recorded during the hot-dry season (October – December). We classified each year from 1960-2018 into three classes as follows: first class consists of months from January to April, the second class includes months from May-August and the last class consists of months between September and December, inclusive. For each of these classes we obtained the average growth for each month, separately, throughout the study period. This is to allow us assess the differential values of the average growth rate during the hot dry seasons and the much cooler seasons of the year. The average growth rate did not change much for months between January and April save for 1996 and 2016, where the average growth rate dropped markedly in January and February. In general, the average growth rate was about 0.0045 on the average, from January to April, with more fluctuations recorded from 1992 onwards (Fig 2A).

For months starting from May to August (the cooler time of the year), the average growth rate did not vary much during these months. The growth rate attains it highest value, during this period, the growth rate is about 0.004. The average growth rate is less during June and July compared to May and August, for every year, during the study period (Fig 2B).

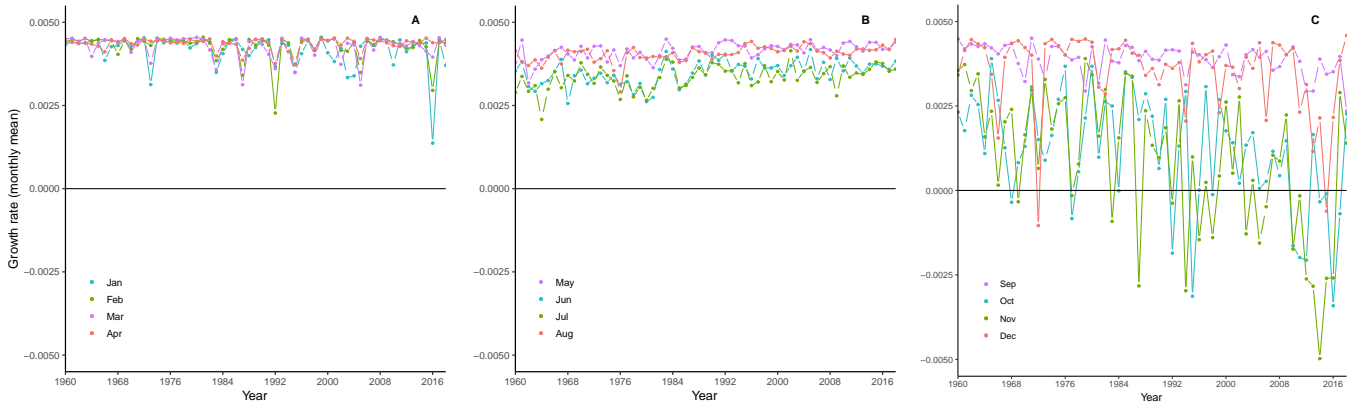


Figure 2: **The average growth rate for different seasons from 1960 to 2018 (A).** Average growth rate for January, February, March and April (B). Average growth rate for May, June, July and August (C). Average growth rate for September, October, November and December. The horizontal lines shows the limit of positive growth; below those lines the population size decreases

There is a major variation in the average growth rate during the last four months of the year. From 1987 to 2018, the average growth rate has been negative for most of the years, during October and November. On a closer inspection, we found only a modest variation in the values of the average growth rate for September, from 1960 to 2010, save for the sharp drop it experienced in 1972. From 2010 to 2018, there have been notable variations in the value of the growth rate during the last four months of the year. During this period, the growth rate usually hits its lowest value during November or October. In 2014, the growth rate dipped below -0.005 - its lowest monthly average ever (Fig 2C).

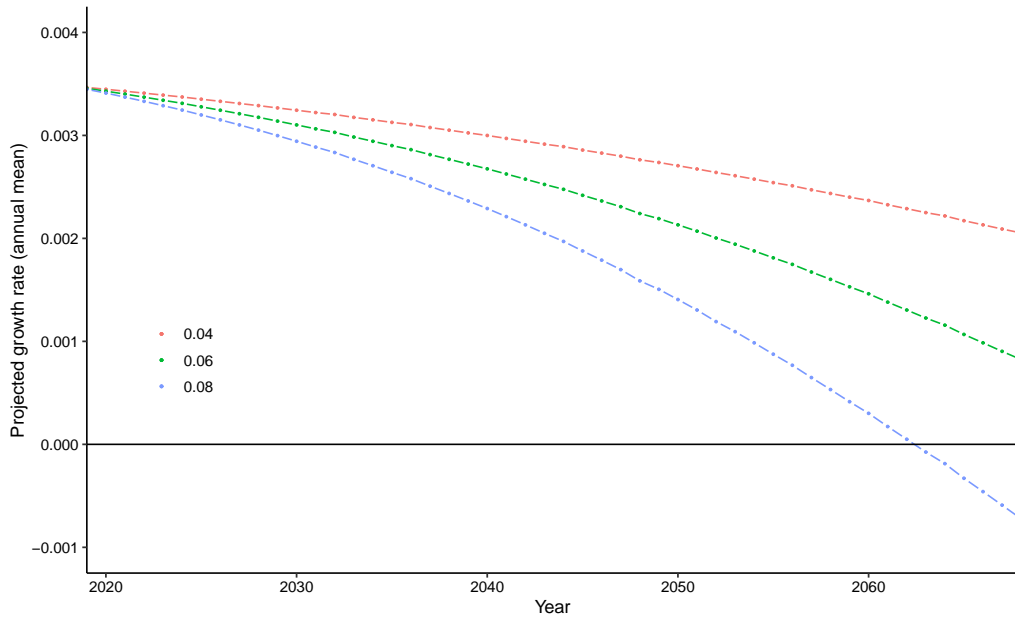


Figure 3: **The annual average growth rate for the three projected climate change scenarios (0.04, 0.06, 0.08 °C per-year), from 2019 to 2068.** The horizontal line, through the vertical axis, shows the point where the average growth rate attains negative values: indicating population extinction.

When the warming rate is slow (at 0.04 °C per-year), the average growth rate continues to decline as temperature increases, but it did not reach a negative value within the next 50 years. For the scenario where the warming rate is 0.06 °C per-year, the  $\hat{r}$  drops below 0.001 but did not reach a negative value. Moreover, when the warming rate is increased to 0.08 °C per-year,  $\hat{r}$  declines steadily until it reaches a negative value in 2063. A negative  $\hat{r}$  value indicates population extinction.

## Discussion

A study showed that increasingly high temperature in the Zambezi valley is responsible for the observed collapse in tsetse population in that region. And the study proposed that if average temperatures continue to increase, there might be local extinction of tsetse population in the Zambezi valley [2]. The current study showed how tsetse growth rate has changed over the past 60 years and predicted the time to extinction for tsetse population in the Zambezi valley given different climate change scenarios. We solved the E-L equation analytically, and we obtained a closed form expression for the intrinsic growth rate  $r$  for tsetse populations. We used the daily average temperature for the Zambezi valley, from January 1960 to December 2018, to calculate the long-time average values of  $r$ . Using the temperature readings for 2018, we projected three climate change scenarios, by generating daily average temperatures for the Zambezi valley over the next 50 years, following three climate warming rates. We used the projected temperatures to calculate the long-time averages of the growth rate.

Our results show that tsetse population growth rate, for the Zambezi valley, has fluctuated year-in-year-out, over the past 60 years. From the 1990s when the average temperatures have increased markedly, the annual average growth rate has continued to reduce. Our results agree with several studies [15, 6], both empirical and theoretical, that have shown that high temperatures are devastating for tsetse populations, and that increasingly high temperatures can drive tsetse populations to extinction [2, 14]. Our results offer insight into how very high temperatures during the hot-dry season is responsible for the decline in tsetse population in the Zambezi valley. During the hot-dry seasons, the very high mortality rates in both pupal and newly emerged adult stages are sufficient to cause negative growth rates, during these months. The proceeding seasons will require highly favourable conditions for the population to rebound before the next hot dry season. As global warming continues to increase the average temperatures in the Zambezi valley all year round, tsetse population will not be able to recover fully from the disastrous impact of the hot-dry season before the next hot-dry season set in, since the initially favourable seasons are no longer as favourable. This may explain the decline in tsetse population, in the Zambezi valley, over the past 10 - 20 years. It is worthy of note that although the annual average values of  $r$  may be positive, it does not necessarily mean that the population is growing, as our estimate is reflecting only the best case scenarios given the environmental condition, in this case temperature. Our result can be seen as an instantaneous maximum growth rate attainable for tsetse population in the Zambezi valley

We have shown that tsetse populations have very low growth rates. For instance, from the 1960s to 1980s where the environmental temperatures were relatively favourable throughout the year, the annual average growth rate was always below 0.004 per-year. This is consistent with the very low tsetse birth rates [9, 16]. Other studies have also estimated very low population growth rates for tsetse populations [17, 9]. We have assumed that no additional mortality is imposed on the study population either by control efforts [ref] or human activities i.e., bush clearing. If any of these assumption is not true, then tsetse growth rate will be less than what we present here. Our result may therefore be a best case scenario for tsetse population which are experiencing the temperatures recorded in the Zambezi valley during these periods

We acknowledge that the E-L equation was premised on the assumption that the population attains a stable age distribution, and where the environment is not limited by resources or space. Some may then argue that tsetse population cannot attain stable age distribution in the field [17]. We argue that this will does not invalidate our results as a first stab at estimating the tsetse growth rate in the field, and the insight it offers into tsetse population extinction in the Zambezi valley, because of the following reasons. Amarasekare et al [18] provided strong evidence that populations can still attain stationary age distributions as long as the fluctuation in environmental temperature is within a thresh hold that will allow reproduction and development processes to continue. We have shown that for most months of the year, in the Zambezi valley, apart from the hot dry seasons, temperature variations have been minimal. The instability in the age distribution is often introduced during the hot-dry seasons [7] of the very hot years. Our estimate may not be accurate to very high degrees but it does provide a very insightful first step towards a more accurate estimates of tsetse population growth rate under varying temperatures.

The current study did not consider density dependent effects. It is worth stating though that density dependence effect are very important in the study of insect populations, especially for tsetse population which can be seriously affected by density dependent effects [19]. However, the E-L equation has been shown to yield comparable estimates of  $r$  to other methods that incorporated density dependent effects. A study [20] did an extensive comparison of five different methods for estimating  $r$  for a fish population and they reported that the density independent assumption on which E-L equation is derived does not limit it validity of the  $r$  estimates derived from it.

A study [18] compared the average growth rate calculated from the E-L equation to the one obtained from

a stage-structured compartmental model. They reported that the growth rates obtained from the two methods compared well, deviating only when the juvenile developmental period is long (several months) and/or when projections involve long time-scale ( $> 50$  years). When the two estimates differs,  $r$  derived from the E-L equation overestimates the true growth rates, and by implication, it overestimates population persistence. They suggested that the accuracy of  $r$ , from the L-E method, declines if it is used to predict insect population extinction beyond a 50-year period. The current study took these cautions into account. Moreover, tsetse developmental period can vary between 20 - 60 days depending on temperature, and it therefore can be categorized as having a relatively short developmental period. In any case, the shortcoming of our method will be that tsetse populations may more likely to go extinct earlier than in 2063 that was predicted by our results.

## Conclusions

The framework presented here is simple and relatively straightforward. We recognize that some of the shortcomings of our formulation may limit the accuracy of our estimates. However, among other things, since we got a closed form expression for  $r$ , it will serve as a metric to easily compare future findings with. Moreover, it is clear that this crude estimate provides a strong evidence that climate change may drive several tsetse populations to extinction within the next 50 years (with a medium warming rate of  $0.08^{\circ}\text{C}$  per-year), especially in temperate regions with similar temperature profile as the Zambezi valley. If our results are true for other insects with similar reproduction/development processes to tsetse, then several insects, of agricultural and/or economic importance, may be at risk of extinction in the Zambezi valley in particular, and Zimbabwe ( or other part of Africa with similar temperature regimes as the Zimbabwe), in general.

We are currently constructing an individual based model which will allow us to factor in several environmental variables at the same time, to estimate the actual growth rate of tsetse population in the wild. This will be used to compare the current results.

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