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

Elisha Bayode Are

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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, due to low temperatures, 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 and obtain a closed form expression for r. We use daily average temperatures of 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 trypanosmiasis - a neglected tropical disease - endemic in many sub-Saharan African countries. Sustained control efforts have reduced disease burden in the last 10 years [WHO factsheet Oct 2019]. 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 [Lord et al 2018]. 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 [ref on r]. Several attempts have been made to estimate the natural rate of increase for tsetse population [refs]. 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. 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 equation, given in discrete form as:

$$\sum \lambda^{-x} l_x m_x = 1. \tag{1}$$

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:

$$R_o = \sum l_x m_x. \tag{2}$$

Tsetse have a relatively simple life history; they produce a single larva at regular intervals (+/- 2 days) [ref]. 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 [ref, Hargrove 2013, world of tsetse]. The very basic life history of tsetse allows us to obtain a closed form solution of the Euler-Lotka equation: and 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 - 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 lifecycle 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 [Ref]. With this knowledge and their relatively simple lifecycle, 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 simplyfing assumptions.

Model assumptions

- Once the fly attains the age of first ovulation, it retains constant fecundity rate throughout her life.
- We assume that the lifecycle 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 succesive "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):

$$R_0 = \sum l_x m_x,$$

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

where

$$l_1 = p_o p_l, l_2 = p_o p_l^2, l_3 = p_o p_l^3, ... \tag{3}$$

and

$$m_1 = p_c, m_2 = p_c, m_3 = p_c, ... \tag{4}$$

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

$$R_0 = \sum l_y m_y = p_o p_l p_c + p_o p_l^2 p_c + p_o p_l^3 p_c + ...$$

$$= p_o p_c p_l (1 + p_l + p_l^2 + p_l^3 + ...),$$

$$= \frac{p_o p_c p_l}{(1 - p_l)}, \tag{5}$$

where $0 < p_l < 1$. Notice that R_o does not depend on c, moreover, if p_o or $p_c \to 0$, then $R_o \to 0$. 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 (Are et al (2019)).

The intrinsic rate of natural increase

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

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

where T is the integer number of time steps.

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

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

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

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

Solving for r in equation (7) , yields,

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

If p_o or $p_c \to 0$, then $r \to \frac{\ln[p_l]}{c}$. Since $0 < p_l < 1$, whenever any of the parameters approaches 0, r becomes negative, which implies that the population goes extinct.

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 (Are and Hargrove(2019)). We estimated the rate of increase per-day as a function of daily mean tenperature, and we obtained the long-time (annual) average ($\hat{r}$) of r, using:

$$\hat{r} = \frac{1}{N} \sum_{t=1}^{N} r_t \tag{9}$$

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 [ref].

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 [ref Lord et al]. Here we project three climate change scenarios.

- Temperature continues to increase in the a slower rate, i.e., the daily average temperature will increase by 0.04 per-year.
- The rate of increase in the daily average temperatures is 0.06 per-year
- Temperature incerases fast with a rate 0.08 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 will attain negative value within this period.

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 daily average temperature as the baseline. We used these temperature projections to calculate the annaul avarge 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 avarage 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).

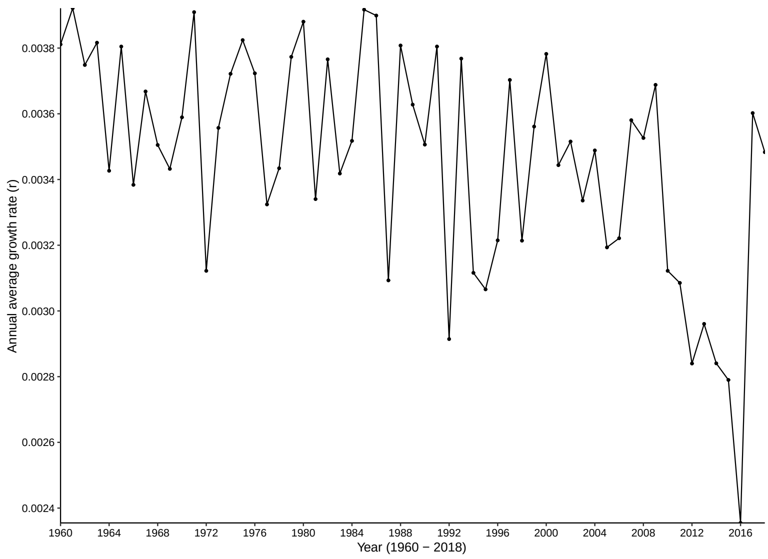

Figure 1: Averaged annual growth rate for tsetse population in the Zambezi valley of Zimbabwe: from 1960 to 2018.

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-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 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, during August and May, on the average, 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).

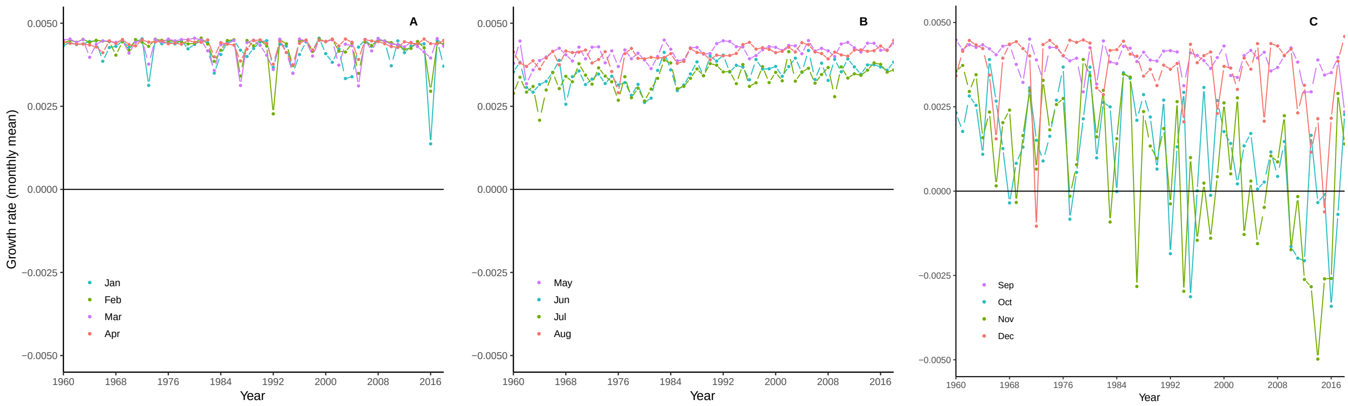

Figure 2: **The avarege growth rate for different seasons from 1960 to 2018** (A). Average growth rate for January, February, March and April (B). Average growth rate for May, June, July and August (C). Average growth rate for September, October, November and December. The horizontal lines shows the 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 for 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 - it lowest monthly average ever (Fig 2C).

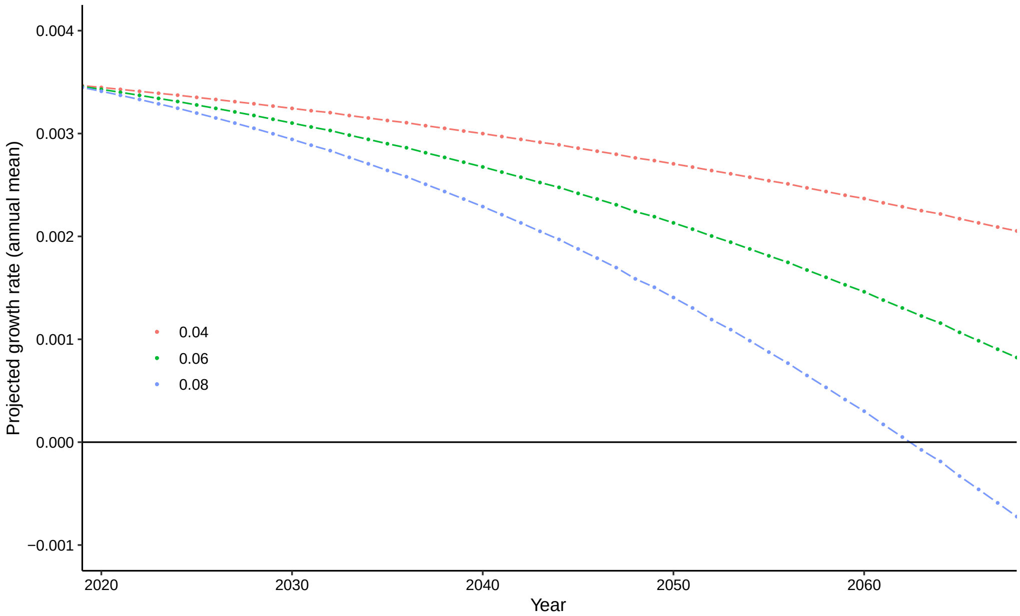

Figure 3: **The annual growth rate, for the three projected climate change scenarios (0.04, 0.06, 0.08 °C per-year), from 2019 to 2068**. The horizontal line, through the vertical axis, shows the point where the avarage growth rate attains negative values: indicating population extinction.

When the warming rate is slow (at 0.04 °C per-year), the average growth rate continues to decline as temparature increase, 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 [ref]. 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 Euler-Lotker 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 temperature 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 varied from year to year over the past 60 years. From the 1990s when the average temperatures have increased markedly, the annual average growth rate has continued to reduce. When we calculated the average growth per month, we found that for

A study compared the average growth rate calculated from the Euler-Lotker equation to the one obtained from a compartmental model. And they reported that the average growth rate estimated from the Euler-Lotker equation somewhat overestimates the true growth rate, and that its accuracy declines if it is used to predict insect population extinction beyond a 50-year period [ref]. The current study took these cautions into account. Moreover, If the forgoing is true, it therefore means that tsetse populations are more likely to go extinct earlier than in 2063 that was predicted by our results.

Conclusion

The Euler-Lotka equation was developed under the assumption of stable population age distribution. This assumption limits the accuracy of our prediction, since Tsetse populations may not be able to attain stable age distribution in the field due to varying temperatures. So, our model may be overestimating the true value of r, since populations fare worse under varying temperatures compared to stable situations.

References

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