

Insect Demography: ***

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Abstract As insect populations decline, due to climate change and other environmental disruptions, there has been an increased interest in understanding extinction probabilities. Generally, the life cycle of insects occurs in well-defined stages: when counting insects, questions naturally arise about which stage to count and the appropriate point to start counting. Using tsetse flies (vectors of the trypanosomiasis) as a case study, we develop a model that works for different counting points in the life cycle of a fly. We analyse reproductive numbers and extinction probabilities, and show that several previous models used for estimating extinction probabilities for tsetse populations are special cases of the current model. We establish that the reproduction number is the same for different counting points, but that the extinction probability is different for each counting point. We demonstrate, and provide a biological explanation for, a simple relationship between extinction probabilities for the different counting points, based on the probability of recruitment between stages. These results offer insights into insect population dynamics and provide tools that will help with more detailed models of insect populations. Demographic studies of insects should be clear about life stages and counting points.

Keywords Extinction probability · Insect Demography · Tsetse (*Glossina* spp) · Geometric Distribution

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1 Introduction

Insects play key ecological roles, both positive and negative, for the health of plants and animals, including humans, and for the environment in general [?,?]. Many are important vectors of plant and animal diseases, often of public health importance [?,?,?], others are beneficial in, for example, pollination, some serve as source of protein for massive numbers of species of animals including humans [?]. Biologists are accordingly interested in insect population persistence for various reasons. On one hand, conservationists are concerned about the ecological implications of extinction of insect populations, whereas vector biologists may be interested in the control/elimination of insect vectors of disease. [?,?,?]. In whichever way we look at things, the study of insect population dynamics is clearly an important area of research.

There have been claims, in the literature, that various insect populations are exhibiting catastrophic declines in numbers in different parts of the world [?,?,?,?]. Hallmann et al [?] reported an alarming decline of 75% in the biomass of flying insects over a 27 year period, in 63 protected areas of Germany. Similar findings of major decline have been reported across the globe [?,?]. For instance, there was a decline of 50% in the population abundance of European grassland butterflies between 1990 and 2011 [?], and it has been reported that tsetse populations have been declining in the Zambezi valley of Zimbabwe [?]. If the magnitude of the declines is as serious as reported, the earth may soon witness extinction of several insect species.

Since insects are cold blooded, their body temperature is basically determined by the ambient temperature that they are experiencing – making them particularly vulnerable, for example, to the effects of global warming. There is therefore a growing concern about how increases in global temperature, and other environmental disruptions, will impact insect populations. In recent years, questions involving extinction of several insect populations are now being asked more frequently [?]. Accordingly, there is a need to continue to improve the accuracy of our prediction of the probability of extinction events in insects – and indeed other animals and plants.

The life history of insects occurs in well-defined stages and the possibility therefore exists of counting insect population according to the numbers of different stages. One may choose to count the numbers in a particular juvenile stage or, alternatively, at some more mature stages. The question then arises as to whether it makes any difference which developmental stage is counted when one is calculating – for example – the probability that an insect population goes extinct. We investigate this problem, using populations of tsetse (*Glossina* spp.) as an illustrative example. Tsetse are vectors of trypanosomiasis [?,?];

a deadly disease called African sleeping sickness in humans and *nagana* in livestock [?]. The life cycle of the fly involves five distinct stages; namely, egg, larva, pupa, newly emerged adult, and mature adult – the last stage in females being defined as those flies that are larvipositing [?]. We ask whether it matters which stage we count: in particular, how would accounting for different insect life stages affect our calculation of the probability that an insect population will persist under various circumstances?

Several workers have developed varieties of mathematical models to explain different phenomena in insect population dynamics, but are generally not clear about which developmental stage(s) are being counted [?, ?, ?, ?, ?, ?, ?]. As far as we are aware, no published work in the literature has explicitly considered the implication of counting insects at different stages for the estimation of extinction probabilities for insect populations. Hargrove [?] developed and analysed a branching process model to derive expressions for extinction probabilities, times to extinction, reproduction number and variance for closed populations of tsetse. The results reported were consistent with published work in the literature on tsetse vital rates, and showed that quite small increases in mortality rates, could drive any population of tsetse to extinction. Kajunguri et al [?] improved on some of the assumptions in [?], specifically, the assumption about the sex ratio of pupae produced and how this affects extinction probabilities. They also provided mathematical proofs of earlier results. The work has been extended to provide estimates of extinction probabilities, growth rates, reproduction number and times to extinction as a function of the temperature that the flies are experiencing [?].

In the above studies, the modelling framework was built on the assumption that the pioneer population starts with one or more newly emerged adult female tsetse. In the current study, by contrast, we generalise the approach – allowing that the population can start with either larvae/pupae, or newly emerged adults, or mature/larvipositing females and we compare the outcomes for each of these scenarios. We establish a relationship between the extinction probabilities for tsetse populations where the pioneer population consists only of individuals at one of the three life stages defined above. We analyze the extinction probability for tsetse population where there are individuals in the different life stages. We discuss, in detail, the implications of our results to tsetse population persistence, particularly in the context of tsetse control/eradication exercises.

1.1 Brief description of tsetse life cycle

Tsetse typically mate once in their life-time: the sperm transferred by a fertile male, during mating, is sufficient for the female to fertilize all subsequent

eggs throughout her life. A female fly produces, typically every 9-11 days, a single larva, which may weigh as much or even more than she does herself. The larva burrows into the soil and pupates within minutes. The pupal period lasts 30 - 50 days [?], depending on soil temperature. After the pupal period, an immature adult emerges. It takes 7-9 days, depending on temperature, for the newly emerged adults to attain full maturation – a process which involves the development of a mature thoracic musculature and the accumulation of fat reserves. During this period females are typically inseminated by a male tsetse, and virtually all will have ovulated by the age of 10 days [?]. The fully developed adult typically larviposits every 9-11 days afterwards [?]. Unlike other insects, such as mosquitoes, which can produce up to 100 eggs at a time [?], tsetse produce a single offspring at a time, consequently, their birth rate is lower than in almost all other insects.

2 Mathematical Model

Methods that are currently being used to count tsetse in the laboratory as well as in the field, may affect the accuracy of tsetse population persistence estimates. Accurate prediction of insect population persistence is important for several reasons. For instance, tsetse may be reared for experimental purposes both in the laboratory, as well as in the field. Therefore, flies at different levels of development may be used to initiate tsetse populations. For instance, in 1979, Vale et al [ref] introduced two species of tsetse (pupae) to the Antelope island, Lake Kariba, Zimbabwe, for a mark-recapture experiment. In instances as the aforementioned, this modelling framework can be used to estimate the establishment probability, and the reproduction number, for tsetse populations, starting with either pupae, newly emerged or larvipositing adults.

Our model of tsetse demography is based on two flow diagrams (Figures 1 and 2). The first flow diagram illustrates the biological processes associated with tsetse life cycle. The state variables and the parameters are described below.

- L : Newly deposited larvae
- A_e : Emergent adults
- A_o : Adults in the larviposition loop
- p_ℓ : Probability of completing a larviposition loop
- p_d : Probability of depositing a live female larva
- p_e : Probability a deposited female larva emerges as an adult
- p_ν : Probability a newly emerged adult reaches the larviposition loop

The second flow diagram presents the counting system. The C inside the dashed box indicates the point where tsetse are counted, while A_o is as described above. The counting point can vary: one may choose to count tsetse at the juvenile stages, or at the mature stages e.g. larvipositing females. The framework we present here allows us to calculate the extinction probability and

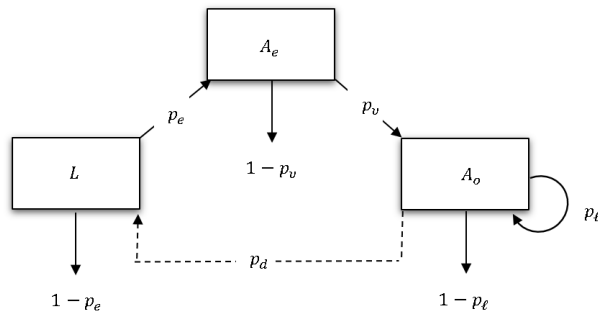


Fig. 1 A Schematic diagram for tsetse lifecycle. The directed arrows pointing to, and away from the boxes, indicate various biological processes in the lifecycle of a female tsetse. These include larviposition, emergence as young adult, and development from young adults to mature adults. The lines pointing downward show losses at various life stages.

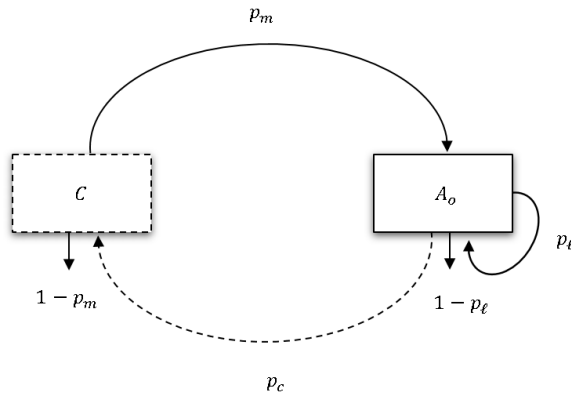


Fig. 2 Schematic diagram for counting tsetse. The dashed box indicates that the stage at which the individuals are counted can vary. The dashed line from A_o to C , shows the process of producing offspring that are counted, while the solid line from C to A_o indicates the process of being counted, and developing to maturity (reaching larviposition loop).

the basic reproduction number for tsetse population, for all possible counting stages.

The list below shows variables and parameters description.

- A_o : Adults entering larviposition loop
- C : The census point
- p_m : Probability from being counted to becoming “mature” (entering the loop)
- p_c : Probability from loop completion to producing something that is counted
- p_r : Probability of recruitment ($p_r = p_m p_c$)

2.0.1 Model formulation

To make our mathematical derivations simple and compact, we use the *odds* associated with the probability that a female completes a larviposition loop and the probability that it produces a female offspring before dying, to derive the offspring distribution function for tsetse populations.

An individual at the census point:

- reaches the loop with probability p_m
- goes around the loop producing offspring that will be counted or else dying,

the probability of producing before dying p_b has odds of:

$$\sigma_b = \frac{p_b}{1 - p_b} = \frac{p_\ell p_c}{1 - p_\ell} = \sigma_\ell p_c$$

.

The total number of censused individuals produced by a censused individual is:

- 0, if it does not reach the loop (probability $1 - p_m$) and
- k , which could also be 0, if it reaches the loop and then fails after k successes, with probability $p_m p_b^k (1 - p_b)$.

The generating function is:

$$G(s) = 1 - p_m + p_m(1 - p_b) \sum_k p_b^k s^k = 1 - p_m + \frac{p_m(1 - p_b)}{1 - p_b s}.$$

We get \mathcal{R} , the reproduction number, by calculating $G'(1)$, where

$$G'(s) = \frac{p_m p_b (1 - p_b)}{(1 - p_b s)^2}.$$

Hence,

$$\mathcal{R} = G'(1) = \frac{p_m p_b}{(1 - p_b)} = p_m \sigma_b = p_m p_c \sigma_\ell = p_r \sigma_\ell$$

[JD: If we do it right, I feel like we shouldn't need or want a separate section for each starting point. I'm particularly against doing \mathcal{R} over and over again: we should be able to make the point that when we move the dashed box around, p_m and p_c can change, but their product should remain the same (for a biological reason) and therefore \mathcal{R} should also remain the same. We should do that above, and then the model has a single \mathcal{R} .] **[EB: I have effected changes as suggested. Please see below]**

Depending on the counting point, p_m and p_c will vary, but their product will remain the same for all counting points. Therefore, $\mathcal{R} = p_d p_e p_\nu \sigma_\ell$. This implies that regardless of the life stage we decide to count the flies, the expected number of offspring produced by an individual in that stage, which will be

counted at the same stage, is the same for all counting points. In other words, all individuals in the different life stages are expected to replace themselves with the same number of individuals of the same life stage as itself when it was counted.

We get the probability y that a tsetse population, starting with a single individual in the count point, goes extinct, by solving $G(y) = y$. We can simplify things by solving $G(1 - z) = 1 - z$, where z is the non-extinction probability, and then factoring out a z . This gives:

$$z = p_m(1 - 1/\mathcal{R}).$$

Therefore, the probability of extinction for tsetse populations at any counting point is:

$$y = 1 - p_m(1 - 1/\mathcal{R}). \quad (1)$$

We can derive extinction probabilities for tsetse populations at the individual counting points by making simple substitutions for the probabilities of recruitment between stages in p_m in equation (1), as appropriate.

In the following section, we obtain extinction probabilities for the three possible counting points in the lifecycle of a female tsetse.

3 Counting tsetse at different life stages

When we change the counting stages by moving the dashed box (Figure 2) closer to the ovulation loop, \mathcal{R} stays the same but p_m gets larger until it reaches 1 when the dashed box gets to the ovulation loop. This allows us to realise different extinction probabilities for the three counting points as follows: we start from a single newly deposited female larva, and ask for the extinction probability for tsetse population starting with a single new deposited larva. We assume that the larva reaches the larvaposition loop (emerges and then matures) with probability $p_m = p_e p_\nu$, completes a larviposing loop with *odds* σ_ℓ , and produces surviving female larvae with probability $p_c = p_d$. When we make appropriate substitutions in y , the extinction probability for a population of tsetse with a newly deposited larva in the initial population is:

$$y_l = \frac{1 - p_\ell(1 - p_d(1 - p_e p_\nu))}{p_\ell p_d}, p_\ell p_d \neq 0.$$

This can be written more compactly in terms of \mathcal{R} as:

$$y_l = 1 - p_e p_\nu(1 - 1/\mathcal{R}) \quad (2)$$

In similar fashion, we can obtain the extinction probability y_e for a tsetse population starting with a single newly emerged adult fly, by substituting $p_m = p_\nu$ in y above. We find:

$$y_e = \frac{1 - p_\ell(1 - p_d p_e(1 - p_\nu))}{p_d p_e p_\ell}, p_d p_e p_\ell \neq 0.$$

This can be rewritten in terms of \mathcal{R} as:

$$y_e = 1 - p_\nu(1 - 1/\mathcal{R}). \quad (3)$$

Furthermore, when larvipositing female are counted, p_m will be equal to 1. The extinction probability y_o for a population of tsetse starting with a single larvipositing female tsetse in the initial population is, therefore:

$$y_o = \frac{1 - p_\ell}{p_d p_e p_\nu p_\ell}.$$

This can be expressed in terms of \mathcal{R} as:

$$y_o = 1/\mathcal{R} \quad (4)$$

It is easily verifiable that whenever $\mathcal{R} > 1$ the following inequality holds:

$$y_o \leq y_e \leq y_l \quad (5)$$

Remarks

- In our analysis so far, we have focused on populations starting with a single individual in the initial population. In real situations, however, we may have N number of individuals in the pioneer population. When the initial population consists of N larvae, or N newly emerged adults or N larvipositing adults, respectively, assuming that for these populations, the reproduction and survival processes are independent, extinction probabilities for each counting stage will be raised to power N . That is, the extinction probability will be y_l^N , y_e^N and y_o^N , respectively, for the three counting points.
- Obviously, if female tsetse populations go extinct, the entire population goes extinct with probability 1. Consequently, the current analysis focuses strictly on female tsetse populations. We account for this in our model by expressing p_d (probability of depositing a live female larva) as: $p_d = \delta\beta$, where δ is the probability that a deposited larva is alive, and β the probability that a deposited larva is female. These two parameters (δ and β) will allow us to capture both male:female sex ratio in the population, and the abortion rates in tsetse population. If we set $\beta = 0.5$ and $\delta = 1$, the current model corresponds to the model presented in [?]. These assumptions imply that a deposited larva has an equal chance of being male or female. And that a deposited larva will be alive with probability 1 when deposited.

4 Extinction probability for populations starting with individuals at different life stages

A real population consists of several individuals in the three different life stages. Therefore, the extinction probability for a population consisting of individuals at different life stages, in the pioneer population, can be estimated from the results we obtained above for counting at the different life stages. If we assume that extinction probabilities for each counting point are independent, then the probability that a tsetse population, which starts with N_1 larvae, N_2 newly emerged adult females and N_3 larvipositing adult females, goes extinct, is;

$$\tilde{y}_c = y_l^{N_1} y_e^{N_2} y_o^{N_3}.$$

4.1 Example 1

We provide an example to show that previous estimates for extinction probabilities for tsetse populations are special cases of the current framework. It can be shown easily that the models presented in [?, ?, ?] correspond to the scenario presented above - counting newly emerged adults. In [?], the following parameters and descriptions were used to derive a probability distribution function for female tsetse population:

- ϵ , the probability that a female is inseminated by a fertile male
- Ω^ν , the probability that a newly emerged adult survives until first larviposition
- λ^τ , the probability that an adult survives until it deposits a pupa (completes a cycle)
- β , the probability that a deposited pupa is female
- ϕ^σ the probability that a deposited pupa emerges

The probability that a female tsetse produces exactly k surviving daughters in her life time is p_k , given as:

$$p_k = \frac{\epsilon \Omega^\nu \lambda^{k\tau} (1 - \lambda^\tau) \beta^k \phi^{k\sigma}}{(1 - \beta \lambda^\tau (\frac{1}{\beta} - \phi^\sigma))^{k+1}}, k > 0 \quad (6)$$

Setting $p_\nu = \epsilon \Omega^\nu$, $p_\ell = \lambda^\tau$, $p_d = \beta$ and $p_e = \phi^\sigma$ in $G(s)$ above, shows that the models used in the works cited above, are special cases of the current model.

5 Numerical Results

We adopt the parameter descriptions presented in example 1, and simulate the model results using R studio (version 1.1.463) [?]. We assume that key parameters are all temperature dependent and their relationship with temperature follows from [?, ?, ?, ?].

Figure 3 shows extinction probabilities for different counting points as a function of different levels of fixed temperatures, which the flies are experiencing. Extinction probabilities for the three counting points are plotted for the same range of temperature (15°C - 33°C) and different initial population sizes. For temperatures within the survival limit for tsetse populations (16°C - 31°C) [?], extinction probabilities are highest for populations of tsetse starting with a single larva. Extinction probabilities are least when we start with, and count, only female adults in the larvipositing loop. Extinction probability is 1 for all counting points outside the range (16°C - 31°C) (Fig 3 A). When the starting population size become larger, say 100, extinction probabilities approach 0 for temperatures in the range 16 - 31°C for all counting points (Fig 3B).

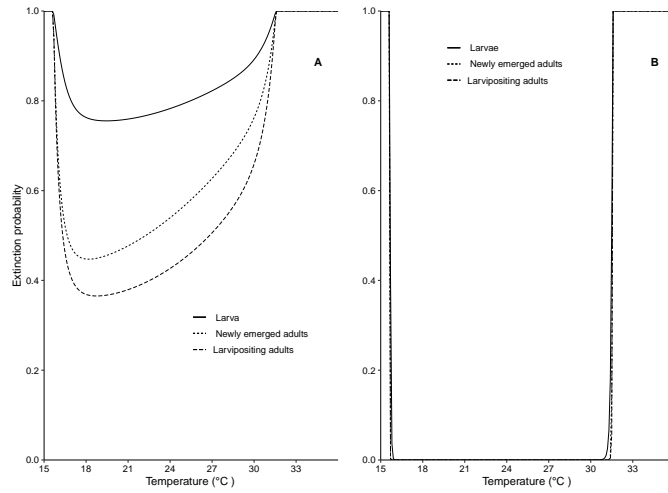


Fig. 3 Extinction probability as a function of temperature (15°C - 33°C) for different counting points. (A) When pioneer populations consist of a single larva, or newly emerged adult, or larval positing adult, respectively. (B) When pioneer population consist of 100, larvae, or newly emerged adult females, or larval positing adult females, respectively.

We assume a fixed temperature of 24°C, and simulate extinction probabilities as a function of the daily mortality rates for female pupae (for the three counting points) starting with different initial population sizes. Extinction probabilities increase, and approach 1, as the daily mortality rates for female pupae increases. This is true for the three counting points. When pupal mortality rate is $\geq 3.1\%$ per day, the extinction probability is 1 for the three counting points (Fig 4B).

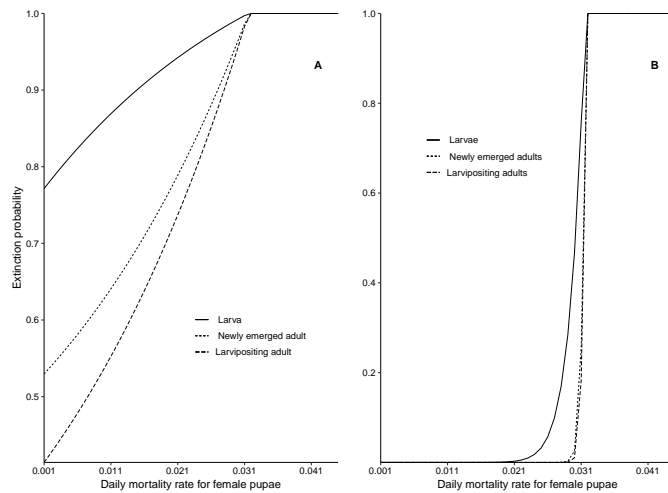


Fig. 4 Extinction probability as a function of daily mortality rates for female pupae, at 24°C, for different count points. (A) Each line represents extinction probabilities for a single larva, or newly emerged adult or larvipositing adult, respectively, in the initial populations (B) When pioneer populations consist of 100 larvae, or newly emerged adults, or larvipositing adults, respectively.

We present extinction probabilities as a function of the daily mortality rates for newly emerged adults. Extinction probabilities increase, for the three counting points, as the daily mortality rate for newly emerged adults increases. When the size of the initial population is increased to 100, for all counting points, extinction probability is 0 for daily mortality rates below 12% per day. Extinction probability rapidly goes to 1, for all counting points, as daily mortality rate for newly emerged adults is $\geq 15.1\%$ per day (Fig 5).

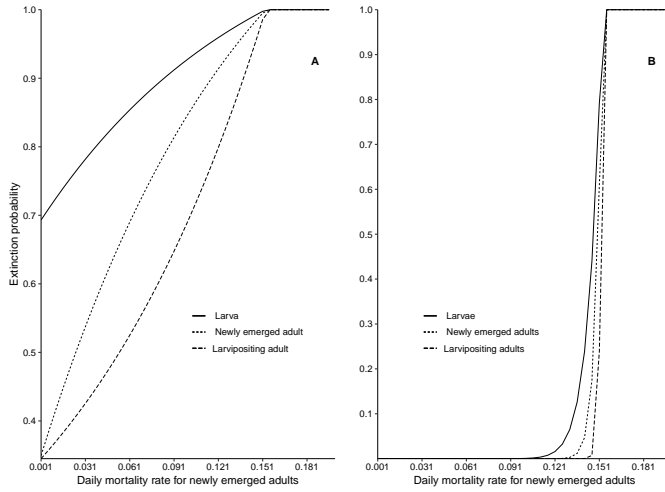


Fig. 5 Extinction probability as a function of daily mortality rates for newly emerged adults at 24°C, for different count points. (A) Each line represent extinction probabilities for a single larva, or newly emerged adult or larvipositing adult, respectively, in the initial populations (B) When pioneer populations consist of 100 larvae, or newly emerged adults, or larval positing adults, respectively.

Extinction probabilities are plotted as a function of daily mortality rate for larvipositing adult females, for different counting points. There is a marked difference in extinction probabilities when the starting populations consist of a single larva, newly emerged adult or larvipositing adult, respectively. However, when the initial population is increased to 100, extinction probabilities go to 1, rapidly, for all counting points, when the daily mortality rate $\geq 3\%$ per day for larvipositing adults (Fig 6).

When we increase the starting population to 500, for all counting points, extinction probabilities stays at 0 for all values of the daily mortality rate for adult females which are less than 3% per day, daily mortality rates for newly emerged adults that are less than 15.1% per-day and daily pupal mortality rates that are less than 3.1% per-day. Moreover, when the daily mortality rate for larvipositing female reaches 3.1% per day, daily mortality rate for newly emerged adults exceeds 15.1% per-day and daily mortality rate for female pupae exceeds 3.1% per-day, extinction probability rapidly goes to 1.

5.1 Extinction probabilities for different levels of abortion rates

Abortion rates, in female tsetse, can be as high as 18%, or even more in laboratory [?]. Abortions have also been observed to increase up to 2% with high temperatures in the field [?]. Here we investigate the impact on extinction probabilities of abortions in larviposoting female tsetse. We allow all other parameters to take constant values at 24°C. We then plot the extinction probability as a function of abortion rate. We define abortion rate as 1 - the probability

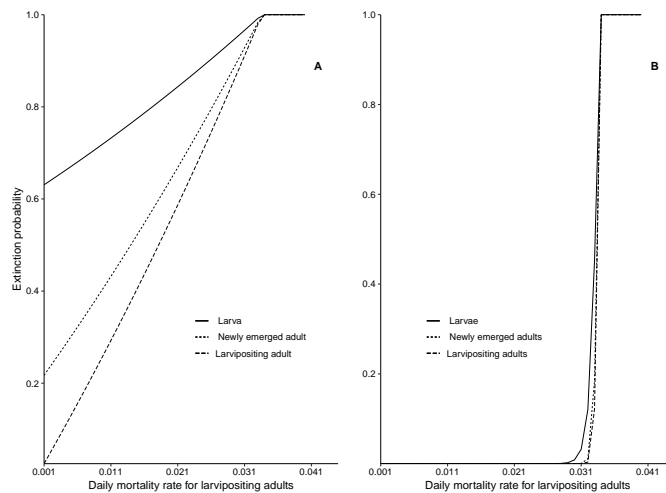


Fig. 6 Extinction probability as a function of temperature and daily mortality rates for larvipositing female adults at 24°C, for different count points. (A) Each line represent extinction probabilities for a single larva, or newly emerged adult or larvipositing adult, respectively, in the initial population (B) When pioneer populations consist of 100 larvae, or newly emerged adults, or larvipositing adults, respectively.

of a live birth. Extinction probability is highest in populations starting with female larvae, followed by populations starting with newly emerged adults. Extinction probability is smallest in populations starting with larvipositing females. Results show that extinction probability is not greatly affected by abortion rates $< 50\%$, when the initial population > 100 . However, as abortion rates approach and surpass 55% , extinction probabilities rapidly go to 1 for all populations (Fig 7).

6 Discussion

The life cycles of holometabolous insects, such as tsetse, can be divided into five distinct stages, egg, larva, pupa, immature adult, mature (larvipositing) adult— each with distinct physiological features, and with differing responses to various environmental factors. In tsetse, for example, the survival probability is high in the egg and larval stages, which are retained in the mother's uterus [?]. Similarly, the pupa – which spends its life underground – often suffers low mortality, except at extremes of temperature [?], although it may also be subject to density-dependent losses due to predation or parasitisation [?,?]. Mature female adults, too, exhibit low mortality [?]: it is only the newly emerged, teneral adult that exhibits high mortality rates and which appear particularly susceptible to high temperatures [?]. In this study, we investigate whether counting different stages influences our estimates of insect population persistence and basic reproduction number. We developed different models for each counting point, and analysed extinction probabilities and the basic re-

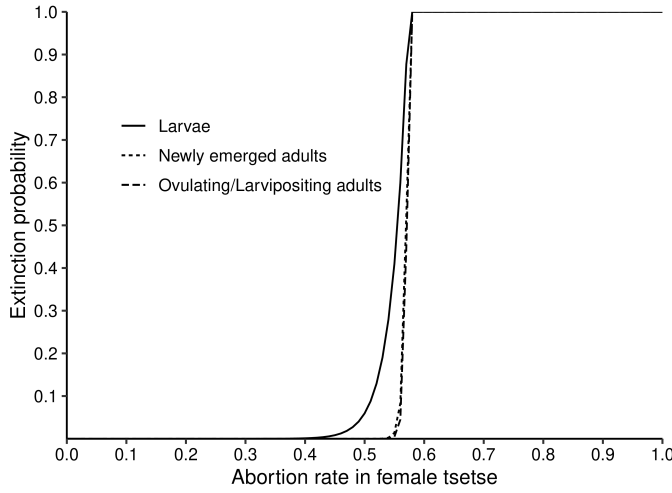


Fig. 7 Extinction probability as a function of abortion rate at 24°C When pioneer populations consist of 100 larvae, or newly emerged adults, or larvipositing adults, respectively.

production number for the different life stages. We compared extinction probabilities for all starting points and derived a relationship between them. We developed a general model, for tsetse populations, that works for all counting points.

We demonstrated that the our estimate of the basic reproduction number was independent of our choice of the stage we counted. It does not matter whether we start with larvae, newly emerged adults or larvipositing adults, the average number of offspring an individual female is expected to produce remains the same. On the other hand, the estimated extinction probability is different for each counting stages. If the initial population consists of a single larva, extinction probability is higher than when the initial population consists of individuals that are either newly emerged or larvipositing adults. As indicated above, each stage of the tsetse life cycle typically experiences different mortalities [?]. The newly emerged adults, for instance, have higher mortality rates than the larvipositing adults [?]. Even though the basic reproduction number does not depend on the stage that we count, a population which starts with larvipositing adults will have a higher chance of escaping extinction than a population which consists of larvae or newly emerged adults in its initial population. Notice, however, that this effect is only well marked when the size of the initial population is low. When the number of larvae, or newly emerged adults in the initial population is large, say > 500 , then it does not matter which stage we chose to count, the probability of extinction remains the same for all stages.

We calculated extinction probabilities as a function of fixed temperatures between 15°C and 35 °C for different counting points. The results agree with pre-

vious findings on temperature survival limits for tsetse population [?, ?, ?]. No tsetse population, regardless of the counting stage, can survive temperatures $< 16^{\circ}\text{C}$ or $> 31^{\circ}\text{C}$, if exposed to these temperatures for a long period. When the initial population consists of a single individual, extinction probability did not drop below 0.3, regardless of the counting stage, even at optimal temperatures. When the initial population consists of a large population (>100 for each counting stage), extinction probability is zero for all temperatures within the limits $16^{\circ}\text{C} - 31^{\circ}\text{C}$, for all counting points (Fig 3). The larger the size of the initial population the greater the chance of survival of tsetse populations. Tsetse populations can escape extinction at temperatures close to the lower and upper survival bounds, provided the initial population size is large (Figs 3-6).

We set the temperature to 24°C , which is the ideal temperature for optimal growth in tsetse population [?, ?], and calculated extinction probabilities at different levels of pupal mortality. For a population consisting of a single larva, extinction probability is high, at 0.78, even at low daily mortality rates for female pupae (0.1% per-day). A population starting with a single larva is likely to go extinct even if the pupa is kept at optimal temperatures. A population starting with a single larvipositing adult has the highest chance of escaping extinction compared to other counting stages. As the daily mortality rates among female pupae increases to 3.1% per day, extinction probability goes to 1 in all cases. Moreover, when the size of the initial population is increased to 100 for each counting stage, the population will not go extinct for daily mortality rates for adult pupae that do not exceed 2.1% per-day. At 25°C , no tsetse population can survive if subject to a pupae daily mortality rate of 3.1%. [?].

We obtained extinction probabilities as a function of daily mortality rates for newly emerged adults, by fixing the temperature at 25°C . This allows us to assess the mortality in newly emerged adults that will be sufficient to drive tsetse populations to extinction, when all other factors are kept at optimal levels. When daily mortality for newly emerged adults is 0.1% per-day, extinction probability, for a population starting with a single larva is 0.7. When the population starts with a single newly emerged adult, or a larvipositing female, the extinction probability is 0.35 when for the same daily mortality rates (0.1% per-day) among newly emerged adults (Fig 5 A and B). Any population starting with a single individual in any of the counting stages, will be go extinct when daily mortality rates in newly emerged adults are as high as 15% per-day. As the sizes of the initial population increase to 100 each, extinction probability stays at zero for daily mortality rates, for newly emerged adults, below 12% per-day. Substantially high levels of mortality are thus required to achieve extinction if mortality is increased only in newly emerged adults.

Control techniques that are presently being used for increasing tsetse mortalities (such as tiny targets etc [?, ?, ?, ?]) are more likely to kill larvipositing adults

than immature adults, since the immature adult phase only lasts for about a week and thereafter all adults are mature - so there are many more of them - and many more can be killed. Moreover, newly emerged adults have poorly developed thoracic musculature and low fat reserves, these two factors may limit their ability to fly the distances for them to be killed at stationary baits. Mobile baits such as insecticide treated cattle on the other hand, tend to be more effective in catching newly emerged adults than stationary targets [?]. Hargrove et al [?] carried out a large scale experiment that used odour baited traps to sample *Glossina m. morsitans* Westwood and *G. pallidipes* Austen in Zimbabwe. For both species, very small numbers of newly emerged flies compared to larvipositing adults were caught. Consequently, a sustained daily mortality rate of about 3.5%, which is the daily mortality rate that will achieve elimination in larvipositing adults, will be sufficient to eliminate a closed population of tsetse (Fig 5 A and B).

We calculated extinction probabilities as a function of daily mortality rates for larvipositing female adults by keeping the temperature at 25 °C. When the pioneer populations consist of single individuals of the three stages, and the daily mortality rate for larvipositing females is increased from 0.1% per-day to 3% per-day, extinction probabilities go to one at different rates, for different counting points. No tsetse population can avoid extinction if the daily mortality rate for larvipositing females exceeds 3.1% per-day[?].

Our results agree with previous findings suggesting that as long as the female's survival probability is high, the impact of relatively high abortion rates would be minimised [?]. Furthermore, we have shown here that when populations are large, abortion rates will have to be >55 % to drive tsetse populations to extinction, as long as the environmental conditions are suitable (24°C) for the larvipositing flies.

7 Conclusion

The general model works for all counting points, for different decomposition of the recruitment rates between the life stages. We showed that extinction probability for different counting stages depends on the probability of recruitment between these stages. We showed that previous models used to estimate extinction probability for tsetse populations are special cases of the general model.

We can predict insect population persistence only if we count and calculate carefully, taking account of different stages. We caution that the basic reproduction number is not sufficient to accurately determine insect population persistence. Our results offer insights into population dynamics and provide tools that will help with more detailed models of insect populations. Finally, we advise that demographic studies of insects should be clear about life stages and counting points.

A limitation of the present study is that we do not consider density dependencies in the population. We are assuming situations where populations are well below their carrying capacities. Our results show that when the population is large enough to consider density dependent effects, the counting points may not matter.

Conflict of interest

The authors declare that they have no conflict of interest.

References