Estimating tsetse population parameters:
Application of a mathematical model with density-dependence

Running title: Estimating tsetse population parameters

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ABSTRACT

A density-dependent model is used to describe the dynamics of an open population of tsetse flies (Glossina, Diptera: Glossinidae). Immigration (or emigration) takes place when the total population is below (or above) a biologically determined threshold value. The population is also subjected to birth and death rates, as well as to the risk of being trapped (continuously or intermittently). During trapping the population decreases toward a "low" equilibrium population and when trapping ceases the population starts recovering and increases toward a "high" equilibrium. The model is fitted using data collected on trapped flies in four experiments. The first one was conducted with "intermittent trapping" (i.e. several trapping-recovery cycles) on Glossina fuscipes fuscipes in the Central African Republic (Bangui area). In the next three experiments trapping data on Glossina palpalis palpalis was collected in "aggregate" form over several days at a time. Two of these were in Congo-Brazzaville (Bouenza area) and one in the Côte d’Ivoire (Vavoua focus). Estimates are derived for the low and high equilibrium values as well as the trapping rate. The estimated effect of sustained trapping is to reduce the population to low equilibrium values that are 85 to 87% lower than the levels without trapping. The effects of the natural intrinsic growth and of the migration flows cannot be estimated separately because in the model they are mathematically indistinguishable.

Key words: tsetse, density-dependence, migration, population dynamics, trapping.
1. Introduction

Estimating population parameters is a challenging and important task in entomology. This is particularly so in the case of tsetse flies, which are the "vectors" responsible for the spread of sleeping sickness. Indeed, to better understand the epidemiology of the disease and to devise optimal control strategies, it is important to assess population sizes and mortality rates obtained through various control methods.

Capture-recapture methods are commonly used to estimate animal populations. However, marking flies is a difficult and complex task that can result in increased mortality and biased results. Trapping techniques have long been used by entomologists to estimate tsetse populations (Harris, 1932, 1938; Morris and Morris 1949). Numbers trapped per day can decrease rapidly due to the added mortality, and various regression techniques can then be used to infer from this pattern the total population initially affected by the trap (Zippin, 1956; Southwood, 1972; Ryan et al., 1981).

Removal trapping techniques are typically based on the assumption that the population is closed, i.e. is not subjected to any migration. However, strong migratory flows have been observed in various control experiments (Rogers & Randolph, 1984a; 1984b). These flows have been found to be density-dependent, as documented a long time ago by Glasgow (1953) and more recently by Gouteux (1987) and Gouteux & Jarry (1998). In particular it was found that immigration increased as the fly population decreased.

In this paper we apply an existing density-dependent population dynamics model in conjunction with trapping data in order to estimate both total populations and trapping rates (Gouteux et al., 2001). The model has already been used under restrictive conditions, i.e. over short periods of time (typically 12 days) during which natural mortality and birth rates were ignored.

We will incorporate a natural growth rate and apply the model with trapping data spanning several weeks. Also, the model will be applied to situations with "intermittent trapping": such experiments involve cycles of several days of trapping (with either daily or aggregated trapping data) followed by days of "recovery" with no trapping (and therefore no data). Specifically, we will apply the model to the data obtained from four experiments, the purpose of which was to assess the effectiveness of various trapping strategies.

The first experiment was in the Central African Republic at Lake Gbalé (outside Bangui) with Glossina fuscipes fuscipes Newstead, 1910. Daily trapping data was collected over three alternating periods with and without trapping (Table 1). The model has already
been fitted to this data set, but for each period separately. Moreover, the recovery periods were not modeled (Gouteux et al., 2001).

The three other experiments were conducted with *G. palpalis palpalis* (Robineau-Desvoidy, 1830). The second and third were in Kimbaouka and Kimpalanga, two villages of the Republic of Congo-Brazzaville. The experiment in Kimbaouka was with continuous trapping, i.e. the experiment was uninterrupted. In Kimpalanga continuous "sampled" trapping was used, i.e. data from only three of 21 traps was collected. The third experiment was in Kaloufa (Ivory Coast) where continuous trapping was conducted with 30 traps. In these three experiments trapping data was collected only in "aggregate" form over several days at a time (e.g., numbers trapped the first five days, then the next three days, etc).

2. The model

i. Assumptions, equations and solutions

We assume a tsetse fly population with the following characteristics:

1. In the absence of trapping the natural growth rate is \( g = b - m \), where \( b \) and \( m \) are natural birth and mortality rates. During trapping the growth rate drops further to \( g - p \), where \( p \) is the trapping rate.

2. A density-dependent immigration (or emigration) takes place when the total population \( N(t) \) is below (or above) a biologically determined threshold value \( N^* \). The threshold value \( N^* \) for the migratory flows is determined by the individual interactions between the tsetse flies (at both the inter and intra-species levels). The "conflicting coexistence" observed between *Glossina palpalis* and *G. pallicera* Bigot, 1891, in pre-forested areas of Ivory Coast is one example of such interactions (Gouteux & Jarry, 1998). If one of these two species is decimated by trapping, the other will rapidly reinvade the area (See Gouteux & Jarry (1998) for a discussion of these regulatory mechanisms that structure a *Glossina* fly guild).

We formulate the density-dependent migratory mechanism by postulating that during each unit of time there is a *net migratory flow* of the form \( k[N^* - N(t)] \), where \( k \) is a positive parameter that expresses the force of this density-dependent migratory process. Therefore when \( N(t) \) is larger than \( N^* \) there are \(-k[N^* - N(t)]\) flies that *leave* the area per unit of time; when \( N(t) \) is smaller than \( N^* \) there are \( k[N^* - N(t)]\) flies that *enter* the area.

In the absence of trapping the differential equation satisfied by the total population \( N(t) \) is then
\[
\frac{dN(t)}{dt} = \frac{dN(t)}{dt} - gN(t) + k(N^* - N(t)) = -(k - g)N(t) + kN^* \\
\]

(1)

With trapping the growth rate \( g \) becomes \( g - p \) and the equation is

\[
\frac{dN(t)}{dt} = \frac{(g - p)N(t) + k(N^* - N(t)) = -(k - g + p)N(t) + kN^* }{1'}
\]

In the absence of trapping Eq. (1) shows that the solution \( N(t) \) would grow without bounds if \( k - g \) were negative or zero. In general however the population is "under control" in the sense that a sufficiently large feedback term \( k \), or a small (possibly negative) growth rate \( g \), render \( k - g \) positive. The solution \( N(t) \) to the differential equation (1) is then

\[
N(t) = (N(0) - K_H)\exp[-(k-g)t] + K_H \quad K_H = kN^*/(k-g) \\
\]

(2)

where \( K_H \) is the "high" equilibrium value (or "carrying capacity") in the absence of trapping. Indeed, Eq. (2) shows that \( N(t) \) approaches \( K_H \) as \( t \) becomes large; \( K_H \) is thus an equilibrium population of flies that is affected by the trapping devices.

When trapping takes place the term \( k-g+p \) in Eq. (1') is positive and the solution is

\[
N(t) = (N(0) - K_L)\exp[-(k-g+p)t] + K_L \quad K_L = kN^*/(k-g+p) \\
\]

(3)

where \( t = 0 \) is the time at which trapping starts; \( K_L \) is the "low" equilibrium value with trapping (indeed \( K_L < K_H \)).

With an initial population without trapping at its equilibrium value \( K_H \) (i.e. \( N(0) = K_H \)), then as trapping starts the population \( N(t) \) is given by Eq. (3) and decreases toward \( K_L \). If trapping ceases, then \( N(t) \) is given by Eq. (2) and during this "recovery" the population will increases toward \( K_H \). If trapping resumes, the population starts decreasing again, and so on. The function \( N(t) \) thus "seesaws" , alternating between Eqs. (3) and (2) when going from a trapping period to a "recovery" period.

### iii. Parameters and model fitting

Observed trapped flies on day \( t \) will be denoted \( T^*(t) \) while the fitted numbers trapped is \( T(t) = pN(t) \) with \( N(t) \) given by Eq. (3):

\[
T(t) = p\{(N(0) - K_L)\exp[-(k-g+p)t] + K_L \} \\
\]

(4)

In view of the expressions for \( K_L \) and \( K_H \) in Eqs. (2)-(3), the quantity \( k-g+p \) needed in Eq. (4) is given by

\[
k-g+p = pK_H/(K_H-K_L) \\
\]

(5)
This shows that the original model is overparameterized. Indeed, there are four parameters \((p, N^*, k, g)\) but only the three parameters \(p, K_L,\) and \(K_H\) are needed to express \(T(t)\) in a first trapping interval (recall that \(N(0) = K_H\)). We then have

\[
T(t) = p\{(K_H-K_L)\exp[-pK_H t / (K_H-K_L)]\} + K_L. \tag{6}
\]

If this trapping interval is then followed by a period without trapping, the total population during that period is given by Eq. (2) where everything is known (indeed, \(k\cdot g\) will be known since both \(k\cdot g + p\) and \(p\) are known). Equation (4) then provides fitted values for the next trapping interval with \(N(0)\) now replaced by the value \(N(t)\) in Eq. (2) at the end of the recovery period.

The three parameters \(p, K_L,\) and \(K_H\) are estimated by minimizing the sum of relative squared deviations between expected and observed numbers trapped over all the trapping intervals (the minimization was done with Excel®'s "Solver"). In all cases, whether trapping is continuous or intermittent, the model is completely determined by the knowledge of the three parameters \(p, K_L,\) and \(K_H\).

The effect of the overparameterization is to link the three parameters \(k, g\) and \(N^*\) in the following two equations

\[
k\cdot g = pK_H / (K_H-K_L) - p \tag{7}
\]

\[
kN^* = pK_L K_H / (K_H-K_L) \tag{8}
\]

Given values of \(p, K_L,\) and \(K_H,\) we can therefore estimate the quantities \(k\cdot g\) and \(kN^*\). However we cannot estimate \(k, g\) or \(N^*\) unless additional assumptions are made. One such assumption is that \(g\) is close to or equal to 0, which is often the case in normal situations (Jarry & Gouteux, 1996). If we make that approximation \(g = 0,\) Eq. (2) shows that \(N^*\) is equal to \(K_H.\) Therefore \(N^*\) is not only a threshold population but also the equilibrium population without trapping (i.e., without trapping the population is stationary and there is no migratory flow). If \(g\) is assumed 0, the parameter \(k\) is given by the right-hand side of Eq. (7) and the corresponding equilibrium reinvasion per day with trapping is

\[
k(N^*-K_L) = k(K_H-K_L) = pK_L \tag{9}
\]

The expression \(pK_L\) can easily be interpreted. With a natural growth rate \(g = 0,\) the only force that changes the population is trapping. Since the equilibrium population is \(K_L,\) the decrease per unit of time is \(pK_L\) and therefore \(pK_L\) flies must invade the area per unit of time in order for the population to be stationary.
iv. The long-run trapping rate

One can define a "long-run trapping rate" ($LRTR$), which is the percentage decrease from the high $K_H$ to the low carrying capacity $K_L$

$$LRTR = 1 - K_L/K_H$$

This rate expresses a theoretical maximum efficiency of the trapping devices were trapping to continue indefinitely with unchanging conditions.

v. Trapping rate per trap

When a trapping rate based on $n$ traps has been estimated, then under the usual independence assumptions a simple probability calculation yields a trapping rate $p_1$ for each trap, which is $p_1 = 1 - (1-p)^{1/n}$ where $p$ is the rate with $n$ traps. This allows comparisons between different experiments that use different numbers of traps.

3. Model fitting and interpretation

Estimated parameter values and other statistics are given in Table 3 for all four experiments.

i. Intermittent trapping experiment (G. fuscipes, Lake Gbalé)

A trapping experiment with four traps consisted of three 12-day trapping periods separated by periods of "recovery". Figure 1a depicts observed and expected values for trapped flies. Figure 1b depicts the fitted total populations $N(t)$, both during trapping and "recovery" periods. Also represented is the "imputed" total population $N'(t)$ during trapping that is obtained by dividing observed trapped flies $T^*(t)$ by the estimated value:

$$N'(t) = T^*(t)/\hat{p}.$$  \hfill (10)

The estimated pre-trapping equilibrium value $\hat{K}_H$ in the absence of trapping is $\hat{K}_H = 719$. A daily trapping rate $\hat{p} = 0.235$ tells us that 23.5% of flies are exterminated every day.

The estimated value of $LRTR$ is $1 - \hat{K}_L/\hat{K}_H = 0.85$. Therefore the "long-run" trapping effect is to decrease the equilibrium population by 85%. Figure 1a shows that in fact the limiting value is almost reached in less than two weeks.

The equilibrium reinvasion per day $pK_L$ is 26 when the intrinsic growth rate $g$ is assumed equal to 0. The reinvasion rate, as a percentage of the equilibrium population $K_L$, is therefore equal to the capture rate $p$: 26.0 flies (23.5% of the population) are trapped every day and the same number enters through reinvasion.
ii. Continuous trapping experiment (*G. palpalis*, Kimbaouka)

A continuous trapping experiment was conducted for 77 days in Kimbaouka. Flies caught in five traps were counted at irregular times over eight periods; 550 flies were trapped during the first five day, 393 during the next six days, etc. (Table 2).

As before, the model yields expected numbers trapped for each day from which one can calculate expected numbers trapped over each one of the eight periods. Figure 2a shows a good agreement between observed and expected average daily numbers caught over each one of the eight periods. Figure 2b depicts the rapidly decreasing fitted total populations \( N(t) \).

The equilibrium values \( K_L \) and \( K_H \) are comparable to those obtained at Gbalé for a slightly larger long-run trapping rate of 87%. This is in contrast with a trapping rate of 0.178 that is smaller than at Gbalé. This apparent discrepancy can be explained by a smaller value of \( k-g \), which is 0.032 instead of 0.043. If \( g \) is comparable in both cases (possibly close to 0) then the reinvasion parameter \( k \) is thus smaller for Kimbaouka. A smaller reinvasion rate thus explains why a smaller trapping rate was able to achieve a slightly better "long-run" result. Indeed, this village was part of a large-scale control campaign by trapping which explains why reinvasion may by smaller than at Gbalé (Gouteux & Sinda, 1990).

iii. Continuous "sampled trapping" experiment (*G. palpalis*, Kimpalanga)

A continuous trapping experiment was conducted for 55 days with a total of 21 traps. As in Kimbaouka, flies were counted at irregular intervals, but only those caught in the same three traps were counted - hence the term "sampled trapping". The fitted trapped population is then no longer \( pN(t) \) but \((3/21)pN(t)\):

\[
T(t) = (3/21)p\left[ (K_{H-L})\exp[-pK_H t/(K_{H-L})] + K_L \right]
\]

With 21 traps the affected population \( K_H \) of 2,432 is significantly larger than previously with a long-run trapping rate of 86%. Figure 3a presents the observed and expected average daily numbers caught. The observed data does not behave as well as previously, i.e. the daily observed averages should be decreasing. The worst offender is the third point, which is abnormally low and drove the algorithm to a poor solution. Such an outlier can arise from changing climatic condition, which can easily affect the results of an experiment (e.g. strong winds or rain can inhibit the flies' mobility and result in reduced numbers trapped). Also, ants can eat trapped flies if the trapping device is faulty. An abnormally low value could also be the result of a statistical deviation due to the fact that data
was collected from a small sample of only three traps out of 21. For all these reasons we decided to drop this outlier from the analysis.

**iv. Continuous trapping experiment (G. palpalis, Kaloufla)**

In view of the results for Kimpalanga one would have expected with 30 traps at Kaloufla a fairly large $K_h$. However, Table 3 shows that it is quite the opposite with the smallest value of $K_h$ at 607 (graphs are not shown as they are similar to previous ones). This is due to the fact that Kaloufla is a very small village in which a large number of traps did not increase trapping rates. In fact, about 85% of dead flies were found in the same four traps (Gouteux et al., 1986). Therefore 0.7% for the trapping rate per trap cannot be taken at face value since the calculation hinged on the assumption that all traps have the same efficiency and are independent of each other (0.7% can still be considered a crude measure of average efficiency over 30 traps).

A long-run trapping rate at 87%, again very close to previous values, is achieved with values of $p$ and $k$ at 0.187 and 0.034 respectively, that are similar to those obtained at Kimbaouka.

**4. Discussion**

A central issue when modeling a fly population affected by trapping devices is the absence of physical or natural boundaries that clearly define the population. In our model however, each member of the population is clearly defined as having the same probability of being trapped. This probability depends on the type, efficiency, spacing and number of traps as well as environmental conditions. Equally important are climatic conditions, which affect the activity of the flies (i.e. duration and speed of each displacement).

The value of the long-run trapping rates in the narrow 85-87% range provides useful information on the efficiency of trapping. This result is important in the context of control strategies aimed at reducing the prevalence of sleeping sickness. Indeed, Artzrouni and Gouteux (1996, 2001) have shown that the disease cannot spread if the fly population is below a certain threshold value. Therefore one way of controlling the spread of sleeping sickness is through a sustained trapping campaign that keeps the fly population below that threshold (see also Gouteux & Artzrouni, 1996, for a discussion of these issues).

A typology of trapping experiments can be summarized graphically in Figure 4 where the outcome for each one of the four experiments is depicted in the $(K_h, p_t)$ plane. The
population $K_H$ reflects environmental and geographic conditions as well as the effect of reinvasion; $p_1$ measures the average efficiency of the trapping devices. Figure 4 shows the four possible configurations with each one of the two parameters being either low or high. The ranges for $K_H$ and $p_1$ are quite plausible and in line with those obtained using capture-recapture methods (Gouteux and Buckland, 1984).

The most desirable situation is when $p_1$ is large, which is the case in Gbalé and Kimbaouka. The fact that $p_1$ is smaller for Kimpalanga and Kaloufia suggests that large number of traps may "dilute" their efficiency. As discussed earlier this dilution manifested itself in Kaloufia with only a small proportion of traps being efficent, which in turn resulted in a small affected population. In Kimpalanga the 21 traps were on average more efficient than in Kaloufia and the population affected larger. Having a small number of optimally located and efficient traps can thus reduce the cost of a control campaign.

5. Conclusion

A simple density-dependent model describes the dynamics of an open tsetse fly population subjected to different trapping experiments. Fitting the model to data in four experiments provided fairly wide but plausible ranges for numbers of flies affected by the traps and for trapping rates. These ranges reflect differing environmental conditions and trapping devices of varying efficiency. The results from Lake Gbalé are particularly striking as the fitted population $N(t)$ accurately captures the alternating trapping and recovery cycles.

One consistent finding concerns the long-term effect of a hypothetically sustained trapping campaign, which reduces the fly population by 85 to 87% in each one of the four experiments. This knowledge is relevant to the activities of the Pan African Tsetse and Trypanosomiasis Eradication Campaign (PATTEC) whose long term-goal is the eradication of tsetse borne trypanosomiasis from Africa through the elimination of tsetse flies using all available technologies (PAAT, 2001).

The question of the definition of the affected population remains somewhat unresolved, however. What determines that population, how is it affected by the number and positions of traps, are just some of the remaining issues. We plan to tackle these problems in the future using microsimulation models (or Agent-Based Simulations) in order to capture the detailed dynamics that exist in a small fly population subjected to migrations, individual interactions and different spatial layouts of traps.
References


**Legends for tables**

**Table 1**  Trapping data $T^*(t)$ on *Glossina fuscipes fuscipes* Newstead for three 12-day trapping cycles at Lake Gbalé near Bangui, in the Central African Republic.

**Table 2**  Trapping data on *G. palpalis palpalis* (Robineau-Desvoidy) for two continuous trapping experiments in the Republic of Congo-Brazzaville (Kimbaouka, Kimpalanga) and in the Ivory Coast (Kaloufia).

**Table 3**  Estimated parameter values for $p$, $K_L$, $K_H$, and $k$-$g$; $p_1$ is the estimated trapping rate per trap (see discussion; numbers of traps given in parentheses); $pK_L$ is the equilibrium reinvasion per day when $g$ is assumed 0; $R^2$ is the coefficient of determination The long-run trapping rate (LRTR) is the percentage decrease from $K_H$ to $K_L$, which measures the efficiency of the traps.
Table 1

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Table 3

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Legends for figures

**Figure 1** Results with *Glossina fuscipes fuscipes* Newstead at Lake Gbalé.
1a: Observed trapped flies T*(t) (points) and fitted numbers T(t) (line)
1b: Total imputed population N'(t) (points) and fitted population (thin descending line during trapping; thick ascending during recovery); lower and upper limits K_L, K_H.

**Figure 2** Results with *G. palpalis palpalis* (Robineau-Desvoidy) at Kimbaouka
2a: Observed (hatching), fitted (white) average daily number of trapped flies during each one of 8 periods.
2b: Modeled total population N(t) during the same period.

**Figure 3** Results with *G. palpalis palpalis* (Robineau-Desvoidy) at Kimpalanga
3a: Observed (hatching), fitted (white) average daily number of trapped flies during each one of 9 periods.
3b: Modeled total population N(t) during the same period.

**Figure 4** Typology of trapping experiments according to affected population K_H and the trapping rate per trap p_t
fig 1 a & b

a

b
Fig 2 a & b

a

![Graph showing trapped flies over periods 1 to 8.]

b

![Graph showing total population over dates from 8/5 to 17/7 with two curves, K_H and K_L.]

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Fig 3 a & b

a

b
Fig 4