A density-dependent model with reinvasion for estimating tsetse fly populations (Diptera: Glossinidae) through trapping

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Abstract

A simple density-dependent reinvasion model is described and used to estimate tsetse fly populations on the basis of removal trapping experiments. The model was tested on Glossina fuscipes fuscipes Newstead in the Central African Republic and G. palpalis palpalis (Robineau-Desvoidy) in the Republic of Congo (Brazzaville). The density-dependence is modelled by postulating that the inflow of flies each day is proportional to the deficit relative to the equilibrium population. Non-linear least square techniques were used to estimate the following parameters: the daily capture rate, the strength of the density-dependence, and the equilibrium fly population, at the beginning and at the end of the trapping experiment. The model ignores birth and death rates of flies and is applicable only when a rapid decrease in population occurs over a short period (between 10 and 20 days). Over longer periods one could not ignore the natural growth of the populations as well as other more complex density-dependent mechanisms.

Introduction

Estimating population size is a fundamental problem in ecology. It is a particularly critical one in the case of tsetse flies (Diptera: Glossinidae) which are responsible for the transmission of sleeping sickness. There is currently a resurgence of this disease in large areas of Central Africa, and control programmes require at least a rough knowledge of tsetse population density. Indeed, Geographic Information System (GIS) and epidemiological models require estimates that are more accurate than those obtained through apparent densities or trap indexes (ADT), which yield average numbers of flies per trap per day.

Several methods have been used to date. First, there are estimates which use apparent densities. Gouteux & Buckland (1984) have defined a relationship based on the equation \( N = a(ADT)^b \) where \( N \) is the estimated population and \( a, b \) are constants estimated by mark-recapture experiments. This model is used by Laveissière et al. (1994) to calculate an index of epidemiological risk for sleeping sickness. However these methods are very sensitive to the position and numbers of traps and thus \( a, b \) depend on local conditions (Gouteux & Buckland, 1984). Second, there are mark-recapture methods that suffer from theoretical and practical problems: tagging, low recapture rates, etc. (Hargrove, 1981a, 1988; Hargrove & Borland, 1994). Thirdly there are removal trapping techniques which use the decrease in numbers trapped to estimate total populations. Such decreases were observed in early trapping trials (Harris, 1932, 1938; Morris & Morris, 1949). In these methods regression analysis or maximum likelihood are used to estimate initial populations. The best known method in this category is due to Zippin (1956, 1958). The ‘Zippin method’ was later popularized by Southwood (1978) and used for...
tsetse flies by Ryan et al. (1981). These regression methods however, are often based on unrealistic assumptions, the main one being that populations are closed. This assumption is particularly problematic for tsetse flies, which are very mobile, particularly during the rainy season, when riverine tsetse flies have their maximum radial displacement (Glasgow & Duffy, 1961; Cuisance & Février, 1983). Migrations toward more open areas during the rainy season have also been documented for savanna species (Moggridge, 1956; Nash, 1937; Dransfield et al., 1990; Brightwell et al., 1992). Hargrove (1981b) describes a non-linear model used to fit observed numbers of flies trapped that takes into account migrations and temperature. His estimates are significantly lower than those obtained by mark-recapture methods (Phelps & Vale, 1978).

The reinvasion of flies in areas depleted by vector control has been well documented for quite some time (Randolph et al., 1984; Rogers et al., 1984). Dransfield & Brightwell (1989) emphasize the role played by fly movement in the development of control strategies. Almost half a century ago, Glasgow (1933) noted the strong density-dependence associated with this phenomenon: the more the population decreases, the stronger the reinvasion. Hargrove’s method takes reinvasion into account but he assumes that ‘Recruitment, mostly immigration from a pool of flies unaffected by the sampling, is independent of the number of flies N(t) in the sampling area’. Williams et al. (1992) propose a spatial model to study the diffusion of flies and the impact of trapping. Their model hinges on ‘Fisher’s equation’ (Murray, 1989) which relates the density of flies to time and distance. This model assumes a density-dependence of mortality but not of immigration. However density-dependence in the immigration of flies is a crucial, albeit complex phenomenon that cannot be ignored. This density-dependence was observed for a Glossina guild in the Côte d’Ivoire at both an intra- and inter-specific level (Gouteux, 1997; Gouteux & Jarry, 1998).

In this paper a simple density-dependent reinvasion model is described and used to estimate tsetse fly populations on the basis of removal trapping experiments. The model was tested with trapping experiments on Glossina fuscipes fuscipes Newstead in the central African Republic and G. palpalis palpalis (Robineau-Desvoidy) in the Republic of Congo (Bravazaville).

**Material and methods**

**Description of the model**

The model is applied to a sampling area in which a population of tsetse flies is subjected to a removal trapping experiment. The area is approximately 10,000 square metres. The target population is subjected to inward and outward migration. The population size on day $t$ is denoted $N_t$ and is assumed to be at an equilibrium at the onset ($t = 0$) of the trapping experiment. The daily capture rate $p$ (0 < $p$ < 1) is assumed constant and depends on the layout of traps, their number, their range, their radius of attraction and the mobility of flies potentially affected by the experimental trapping design. The number $C_t$ of flies captured on the $t$-th day is then $pN_t$. Birth and death rates are ignored because the experiments are conducted over a short period of time (10–20 days) during which the natural increase of the population is negligible compared to the mortality induced by trapping.

The density-dependent reinvasion is modelled by postulating that the inflow of flies each day is proportional to the deficit relative to the initial equilibrium population $N_0$, i.e. of the form $k(N_0 - N_t)$, $k > 0$ is thus a parameter that measures the strength of the density-dependence, and $N_{t+1}$ is given by:

$$N_{t+1} = N_t - pN_t + k(N_0 - N_t)$$  \(1\)

The parameter $k$ can be interpreted as a reinvasion rate that is equal to the number of immigrant flies per unit of time, for a one fly difference between the initial size $N_0$ and the current size $N_t$. In short, the total population changes through the combined effects of trapping and density-dependent reinvasion.

The continuous-time version of (1) yields the differential equation:

$$\frac{dN(t)}{dt} = kN(0) - (p + k)N(t)$$  \(2\)

which has the solution:

$$N(t) = k \frac{N(0)}{p + k} \left( \frac{N(0)}{p + k} \right)^{1 - p/2k + 1/2}$$  \(3\)

This classic equation of population dynamics is known as the ‘monomolecular’ (Lebreton & Miller, 1982) or the ‘Mitscherlich’ equation (Pavé, 1994). Equation 3, consisting of a constant plus a decreasing exponential, is also used by Hargrove (1981b) and Brightwell et al. (1997) for estimating and modelling fly populations.

Equation 3 shows that when $t$ becomes large the fly population decreases from $N(0)$ and approaches its equilibrium value $K = kN(0)/(p + k)$. The term $k/(p+k)$ is the ‘Trapping Survival Proportion’ (TSP) since it tells us the percentage of the initial population at which the population stabilizes under the assumption that trapping continues at the same rate $p$ and the flow of reinvading flies remains unchanged. The trapping survival proportion is really a ‘net’ survival rate that captures both the effects of trapping and reinvasion.

Two situations can occur. First, if the reinvasion rate $k$ is relatively large compared to the capture rate $p$, the trapping survival proportion is close to 1 and captured flies are very quickly replaced by immigrant ones coming in from a much larger population surrounding the one to be estimated. The total and trapped populations decrease only slightly and it is difficult or impossible to estimate the parameters $N(0), p$ and $k$. A second situation occurs when the density-dependence parameter $k$ is relatively small compared to $p$, in which case the trapping survival proportion is also small and the population decreases significantly. In this case the depletion due to trapping is larger than the reinvasion and the model can be fitted using the observed decrease in trapped populations. Indeed, if equation 3 is multiplied by $p$, the density of captured flies is $C(t) = pN(t)$, i.e.

$$C(t) = k \frac{N(0)}{p + k} + \left( \frac{N(0)}{p + k} \right)^{1 - p/2k + 1/2}$$  \(4\)

Non-linear least square techniques were used to fit equation 4 to the trapping data and estimate the parameters $N(0), p, k$. Two different software packages were used: Mathcad® which uses the Levenberg-Marquardt algorithm.
A density-dependent model for estimating tsetse populations

and STAT-ITCP® version 5 (ITCF, 91720 Boigneville, France) which uses the Gauss-Newton or Gauss-Marquardt algorithm (Huet et al., 1992) and gives approximate confidence intervals, coefficients of determination

\[ R^2 = 1 - \frac{\sum e_i^2}{\sum y_i^2} \]

and also tests whether the model is overparameterized.

The trapping data

The model was tested with data collected from G. fuscipesfuscipes at Lake Gbalé in the outskirts of Bangui in the Central African Republic in 1991-1992 (Gouteux et al., 1991; Gouteux, 1998). This small lake is surrounded by narrow wooded areas and is isolated in a man-made savanna. In this region the dry season lasts from December to March. Villagers come into this area for bathing and washing and women for the retting of manioc. Domestic pigs also move around the banks of lake. Data were collected daily at four traps during seven 12-day periods extending from December 1991 to September 1992.

Data were used from large-scale control trials when trapping G. palpalis palpalis in the Niari focus located in the grassland savanna region of Bouenza in Southern Congo (Brazzaville). In this region the dry season lasts from June to September. The data covered the period 1985-1986 (Gouteux & Sinda, 1990). Trapping was done with between three and 60 traps set in villages that were affected by sleeping sickness. Data were collected irregularly from these traps, every two to five days at the beginning, then once every month or fortnight.

Results

Model estimates for tsetse fly populations at Lake Gbalé

Dry season data

In table 1, the model was fitted for both sexes of G.f.fuscipes combined for each one of five 12-day periods from December 1991 to May 1992. The observed numbers trapped and corresponding fitted values C(t) are presented in fig. 1. There was a good fit with four of the five sets. The model was overparameterized for the February 1992 data which exhibited a linear as opposed to an exponential trend. The estimated values of k were between 2% and 5% while the estimated trapping rates p were in the relatively narrow and plausible 17% to 25% range. These estimated daily trapping rates were consistent with values obtained elsewhere with G. palpalis palpalis by mark-recapture methods (J.-P. Gouteux & S. Buckland, unpublished). The corresponding trapping survival proportions k/(k+p) were between 10 and 25% at the end of each 12-day period. If trapping continued the model predicted that the fly populations would stabilize at the lowered levels given by K. As fig. 1 shows, when trapping has been interrupted for a period of time, the number of trapped flies is larger once trapping resumes, which reflects at least a partial recovery of the total population. For example, table 1 shows a recovery from 207 estimated flies at the end of the first experiment to 798 at the beginning of the second experiment.

![Graph](image-url)
Table 1. Population parameter estimates of *Glossina f. fuscipes* at Lake Gbalé (Central African Republic); both sexes combined.

<table>
<thead>
<tr>
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</thead>
<tbody>
<tr>
<td>N(0)</td>
<td>997</td>
<td>798</td>
<td>542</td>
<td>309</td>
<td>183</td>
</tr>
<tr>
<td>K</td>
<td>207</td>
<td>139</td>
<td>104</td>
<td>67</td>
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<tr>
<td>p</td>
<td>0.17</td>
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<td>0.21</td>
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<td>0.25</td>
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<tr>
<td>k</td>
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<td>0.04</td>
<td>0.05</td>
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</tr>
<tr>
<td>TSP</td>
<td>19%</td>
<td>17%</td>
<td>19%</td>
<td>23%</td>
<td>17%</td>
</tr>
<tr>
<td>Total catch</td>
<td>941</td>
<td>793</td>
<td>582</td>
<td>295</td>
<td>196</td>
</tr>
<tr>
<td>R²</td>
<td>0.95</td>
<td>0.98</td>
<td>0.98</td>
<td>0.87</td>
<td>0.92</td>
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<td>no</td>
<td>no</td>
<td>yes</td>
<td>no</td>
<td>no</td>
</tr>
</tbody>
</table>

*N(0)*, initial population; K, equilibrium population at the end of the trapping experiment; p, daily capture rate; k, daily reinvasion rate; TSP, Trapping Survival Proportion; R², coefficient of determination.

The observed and fitted numbers trapped per day for males and females and both sexes combined with 95% confidence intervals for December 1991 are shown in fig. 2. In table 2 separate parameter estimates for both sexes of *G. f. fuscipes* are given for four of the five sets (the overparameterized model for February 1992 is omitted from the table). The sum of fitted initial populations N(0) for each sex was close to the sum obtained with both sexes combined. For December 1991, the initial combined total was 536 + 397 = 933 flies when both sexes were estimated separately (table 2) and 997 flies when the model was fitted for both sexes together (table 1). The numbers were closer for the other months (tables 1 and 2). The parameter k was always greater for females than for males. It was slightly larger in January, about double for December and April-May, and almost ten times larger for March. The trapping survival proportion for females was between 5% and 17%, and significantly higher for females, between 19% and 24%. Higher estimated values of k (and K) for females confirmed previous observations concerning the greater reinvasion propensity of female flies (Gouteux, 1983; Williams, 1995). This pattern was also reflected in a higher estimated sex ratio (percentage of females) at the end of each 12-day period (population given by K than at the beginning (N(0)). Over the four periods, this sex ratio increased from 61% to 73%.

**Rainy season data**

In July (fig. 1) the data showed little or no decline in numbers of *G. f. fuscipes* trapped, because fly populations were less concentrated near the lake and climatic conditions favoured a greater dispersion in open areas (R² = 0.77, k = 0.08, p = 0.18, K = 98 and N(0) = 257). In September (data not shown) there was only a slight decrease in the trapped population over time, with an estimated value of k (the reinvasion rate) equal to 0.10 (R² = 0.58, k = 0.10, p = 0.17, K = 131 and N(0) = 356). These values of k, which are double the values 0.04 and 0.05 obtained for the dry season, reflected the stronger reinvasion that takes place during the rainy season.

**Model estimates from control trials in Bouenza**

**Dry season data**

The model for *G. p. palpalis* was overparameterized in three of the six dry season data sets (table 3, first six columns). This could be due to variable numbers of traps,
and variable durations between counts of trapped flies. Estimated daily capture rates varied from 12% to 21% for the three data sets for which the model was not overparameterized. In those cases, as above, the total numbers captured were close to the estimated initial population. The relatively low estimates of $k$ (between 0.001 and 0.021) were due to large-scale control efforts, which significantly depleted the external reservoir of flies (Gouteux & Sinda, 1990). The trapping survival proportion was consequently low in those trials, ranging from 1 to 3% in three villages, 7% in two others, and 22% at Kimpalanga.

Rainy season data

Only one data set, was available for $G. \ p. \ palpilis$ in the rainy season and in this case the model was overparameterized, despite a high value of $R^2$ (table 3, last column). The high humidity favoured reinvasion with the highest estimated value of $K$ (946 flies) and of the reinvasion rate ($k = 0.30$). The estimated trapping survival proportion, 53%, was the highest estimate obtained and reflected the greater mobility of flies during the rainy season and probably the proximity of an important reservoir of flies nearby.

Discussion

In this paper a simple density-dependent model of the decrease in tsetse populations caused by trapping experiments is described. The estimated parameters $p$, $k$, $N(0)$ and $K$ provide information on the efficacy of trapping, the strength of reinvasion and the equilibrium fly population affected by the traps, at the beginning and at the end of the experiment. With the data used here, the model shows that the total captured population in our 12-day experiments was approximately equal to the estimated initial population. It may be of interest to explore this relationship with other experimental designs. Hargrove’s (1981b) model, which assumes a constant inflow of immigrant flies and a constant rate of loss and capture, has four parameters, one of which is temperature. Our model, which assumes attrition through trapping only and a density-dependent reinvasion, has three parameters. Both models yield the same monomolecular equation for the total population $N(0)$, but are constructed in different ways. The parameters and their interpretation as well as the conclusions that can be drawn are thus quite different. Hargrove’s model incorporates temperature, which is an important parameter but not more important than wind-speed and rainfall. Other parameters such as humidity and light are as, or even more, important in some cases (Gouteux & Monteny, 1986). Our model ignores climatic effects but these are reflected in the estimated values of $p$ and $k$ (e.g. $k$ is larger during the rainy period, thus reflecting an increased ‘radial reinvasion’ that is known to occur during the rainy season). In addition, the density-dependent reinvasion introduced here captures in a simplified manner the reaction of the external population to the localized decrease in the density of flies caused by a large removal of flies. There is a ripple effect in the low density of flies into the ‘depressed’ area: the flies just outside the focus react to the depression by entering the focus, and in turn create another depression, which causes populations further afield to be attracted to the focus. Although the model is arguably a reasonable approximation of reality, there may be delays in this ripple effect.

Table 2. Population parameter estimates of Glossina f. fusca at Lake Gbâlé males and females separately.

<table>
<thead>
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<th></th>
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<th></th>
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<tr>
<td></td>
<td>female</td>
<td>male</td>
<td>female</td>
<td>male</td>
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<tr>
<td>$N(0)$</td>
<td>536</td>
<td>397</td>
<td>538</td>
<td>281</td>
</tr>
<tr>
<td>$K$</td>
<td>132</td>
<td>66</td>
<td>101</td>
<td>38</td>
</tr>
<tr>
<td>$p$</td>
<td>0.21</td>
<td>0.16</td>
<td>0.18</td>
<td>0.23</td>
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<tr>
<td>$k$</td>
<td>0.07</td>
<td>0.03</td>
<td>0.04</td>
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<tr>
<td>TSP</td>
<td>25%</td>
<td>17%</td>
<td>19%</td>
<td>13%</td>
</tr>
<tr>
<td>Total catch</td>
<td>589</td>
<td>352</td>
<td>511</td>
<td>282</td>
</tr>
<tr>
<td>$R^2$</td>
<td>0.96</td>
<td>0.93</td>
<td>0.97</td>
<td>0.96</td>
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<tr>
<td>overparam.</td>
<td>no</td>
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<td>no</td>
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</tr>
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</table>

*See table 1 for explanation.

Table 3. Population parameter estimates of Glossina p. palpalis for control trials in the Bouenza region (Congo); February 1986 (rainy season) for Biyoki and May-June 1989 (dry season) for the other villages.

<table>
<thead>
<tr>
<th>Parameters*</th>
<th>Dakar</th>
<th>Kissi</th>
<th>Pambou</th>
<th>Gouala</th>
<th>Langa</th>
<th>Baouka</th>
<th>Biyoki</th>
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<td>$N(0)$</td>
<td>3573</td>
<td>6975</td>
<td>2323</td>
<td>2930</td>
<td>234</td>
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<td>2006</td>
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<tr>
<td>$K$</td>
<td>179</td>
<td>446</td>
<td>70</td>
<td>47</td>
<td>49</td>
<td>21</td>
<td>946</td>
</tr>
<tr>
<td>$p$</td>
<td>0.21</td>
<td>0.30</td>
<td>0.51</td>
<td>0.33</td>
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<td>0.12</td>
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<tr>
<td>$k$</td>
<td>0.015</td>
<td>0.021</td>
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<td>0.009</td>
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<td>7%</td>
<td>3%</td>
<td>2%</td>
<td>22%</td>
<td>1%</td>
<td>53%</td>
</tr>
<tr>
<td>Total catch</td>
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<td>1572</td>
<td>1279</td>
<td>296</td>
<td>1294</td>
<td>4129</td>
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<td>No. of traps</td>
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<td>21</td>
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<td>5</td>
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<tr>
<td>No. of days</td>
<td>30</td>
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<td>no</td>
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<td>yes</td>
</tr>
</tbody>
</table>

*See table 1 for explanation.

effect that are not accounted for (i.e. it takes a while for the effect of the ‘depression’ to cause the reinvasion). The ‘jumpy’ data (going up and down rapidly from day to day after the first few days of trapping – see graphs) could be an effect of this delay.

Any model based on removal trapping techniques will be inapplicable when the capture rate is small and/or there is a high reinvasion rate (5) because there is no noticeable removal of flies (with a TSP that remains close to 1). This is often the case in rainforest areas and elsewhere during the rainy season when flies are very scattered and/or mobile. Such circumstances limit the applicability of the model, even though in some cases the removal trapping techniques can be used if the number of traps is increased, which can cause a noticeable decline in the fly populations. In contrast, during the dry season, flies in some cases are concentrated around waterholes. A few traps are sufficient to cause a large decrease in trapped populations, in which case the estimation technique described here becomes relevant and applicable and yields estimated total populations that also decrease rapidly. The model documents the differential behaviour between the two sexes by showing that females have a greater reinvasion propensity. This behaviour may be a result of natural selection by which inseminated parous female flies colonize new areas, for the good of the species (Couteux, 1983).

It should be noted that over the six-month period when the trapping experiments were conducted at Lake Gbalé, the initial population N(0) showed a decreasing trend from 997 to 183 between the first and the last of the five 12-day trapping periods. This decrease occurred because the fly population did not have time to recover to its original estimated level (of approximately 1000 in December) between the various trapping experiments. With an estimated trapping survival proportion that remains around 18%, the estimated values of K also decreased over the six-month period to reach an estimated low of 29 in May 1992.

The cases when the model does not fit the data well are difficult to interpret (e.g. Lake Gbalé, February 1992). The trend is clearly linear in these cases, and the high correlation between the estimated parameters shows that the model is inadequate and needs to be improved in order to capture other phenomena that may influence the trapping experiment. For example, human or animal hosts are known to reduce the attractiveness and efficacy of the traps, or a bushfire will impede the reinvasion of flies.

Finally, it should be emphasized that our model ignores birth and death rates of flies and is applicable only when a rapid decrease in population occurs over a short period (10–20 days). Over longer periods one cannot ignore the natural growth of the populations as well as other more complex density-dependent mechanisms described by Rogers & Randolph (1984).

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References


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