# ARE TSETSE FLY POPULATIONS CLOSE

# TO EQUILIBRIUM?

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## ABSTRACT

Glossina or tsetse flies, the vectors of sleeping sickness, form a unique group of insects with remarkable characteristics. They are viviparous with a slow rhythm of reproduction (one larva approximately every 10 days) determined by the regular ovulation of alternate ovaries. This unusual physiology enables the age of the females to be estimated by examining the ovaries.

The resulting ovarian age structure of tsetse fly populations has been used to develop research into the demography of tsetse flies. Several authors have proposed methods of estimating population growth rates from ovarian age distribution data. However, such methods are applicable only when the growth rate ($\lambda$) is equal to 1 (i.e. the intrinsic rate of increase $r$ is equal to 0). In fact, in this type of estimation, the adult survival rate $a$ (or equivalently the mortality rate) cannot be dissociated from the growth rate.

Other independently determined demographic parameters must be used to remove this lack of identifiability. We have built a matrix model of the dynamics of tsetse fly populations which enables the growth rate to be calculated from the pupal survival rate, the pupal period and the adult survival rate. Assuming that the age-groups of the population studied have reached a stable distribution, it is possible to calculate the probabilities for the observed sample of belonging to each of the age-groups, to construct a likelihood function and thus to obtain an estimate of the 'apparent survival rate' $\beta = a/\lambda$. If the pupal survival rate and the pupal period are known, $a$ and $\lambda$ can then be calculated from $\beta$.

The application of this method to data collected for over two annual cycles in a savannah habitat (Burkina-Faso) showed a high overall stability in the populations of *Glossina palpalis gambiensis*. Seasonal fluctuations could be easily interpreted as being the result of climatic changes between the dry and rainy seasons.

## 1. INTRODUCTION

Because of their tendency towards sudden proliferation, insects (e.g. crickets, green fly, forest defoliator species) are often taken as examples of species with chaotic population

dynamics. This is not however a general rule, and well documented cases of chaos are rare (Pierre, 1993). In fact, the most striking feature in the insect world is rather the diversity of the population dynamics. Indeed, to use the terminology employed by Pianka (1970), not all insects are $r$-strategists. In this respect, the insect vector of sleeping sickness, the tsetse fly, could be classified with mammals rather than with insects (Glasgow, 1963; Gouteux, 1995). It presents a highly developed viviparity with a slow rhythm of reproduction (see § 2.1). The growth rate is thus considerably limited (Hargrove, 1988; Jarry *et al.*, 1996).

An age structure consisting of eight age-groups has been identified (Saunders, 1960, 1962; Challier, 1965) on the basis of the state of the ovaries. The first four age-groups can be determined precisely from the first ovarian cycle. Four older age-groups can be identified but since later cycles cannot be differentiated, these age-groups are imprecise (see § 2.1).

The ovarian age structure of female tsetse fly populations has been used by Taylor (1979), Ryan (1981), Allsopp (1985a) and Williams *et al.* (1990) to calculate a mean survival rate using the Euler-Lotka equations (Lotka, 1907) and classical life tables (Deevey, 1947; Andrewartha & Birch, 1956). Various approaches were used to overcome the difficulty with the four older age-groups. Saunders (1967), along with many other authors (Okiwelu, 1976; Phelphs & Vale, 1978; Ryan, 1981), assumed a constant mortality rate. Taylor (1979) and, later, Snow & Tarimo (1985) suggested that the four older age-groups could be determined more accurately by the wing fray technique described by Jackson (1946). These authors recognised that this method is subject to bias since the wear and tear of the wings depends on the activity of the individual fly and not on its true age (Challier, 1973; Allsopp, 1985b). However, they consider it preferable to assuming a constant mortality rate.

Other authors have developed different methods to that described by Saunders for estimating the survival rate. Challier & Turner (1985) used geometric means. Gouteux (1982) and Gouteux & Kiénou (1982) used a geometric progression formula for the four older age-groups, together with least squares fitting. The assumption of a constant mortality rate is first made only for the four older age-groups. These four estimated values and the observed values for the first four age-groups are then refitted using a negative exponential to determine a mean mortality rate. The geometric progression formula was used later by Rogers & Randolph (1984) and Rogers *et al.* (1984).

Most of these methods, however, raise another problem. As pointed out by Van Sickle (1988), the authors assume, explicitly or implicitly, that the populations are stationary (asymptotic growth rate $\lambda = 1$, or intrinsic rate of increase $r = 0$). In fact, in this type of estimation, the adult survival rate $a$ cannot be dissociated from the growth rate. Hargrove (1993) therefore obtained, by a maximum likelihood method, an estimate of a parameter depending on the mortality and on the growth rate.

The method proposed in the present paper assumes a constant adult survival rate as a first approximation. We first present a matrix model depending on only three demographic parameters: pupal survival rate, pupal period and adult survival rate. Assuming that the age structure of the population is stable, this model enables us to calculate the theoretical distribution of the ovarian age-groups. We show that an apparent adult survival rate ($\beta = a/\lambda$) can then be estimated by a maximum likelihood method. Given the pupal survival rate and the pupal period, $a$ and $\lambda$ can then be calculated from $\beta$.

This model has then been applied to field data and the various factors likely to regulate the tsetse fly populations discussed. Finally, the potential developments offered by this approach are discussed, in particular the possibility of taking into account an age-dependent adult survival rate.

## 2. TSETSE FLY DEMOGRAPHIC DATA

### 2.1 Biological Cycle

The tsetse fly belongs to the Glossinidae family which comprises about thirty African species (Moloo, 1993). The female 'delivers' a mature larva (ready for the pupal stage) after a gestation period of about ten days during which it is nourished in the uterus by maternal secretion. Once the larva is deposited it embeds itself in the ground and pupates almost immediately. The duration of the pupal stage varies according to the temperature (Jackson, 1949; Harley, 1968). For *Glossina palpalis gambiensis,* Challier (1973) observed a range of 26 to 50 days (mean 30-33 days at a mean monthly temperature of 25-26 °C). The newly emerged adults are called tenerals until they begin to feed (Jackson, 1933). Nearly all the females are fertilized in the first few days of life. The quantity of spermatozoa stored in the female's spermathecae is sufficient for her entire life (Glasgow, 1963).

The adults live for an average of 1 to 2 months, but flies marked six months previously in Côte d'Ivoire (Gouteux, 1985) and even nine months previously in Senegal (Challier, 1973) have been captured. The unusual physiology of the females enables their age to be estimated by examining the ovaries. The two ovaries (left and right) each comprise two ovarioles which are situated symmetrically on either side of the ovary. Ovulation occurs at regular intervals in
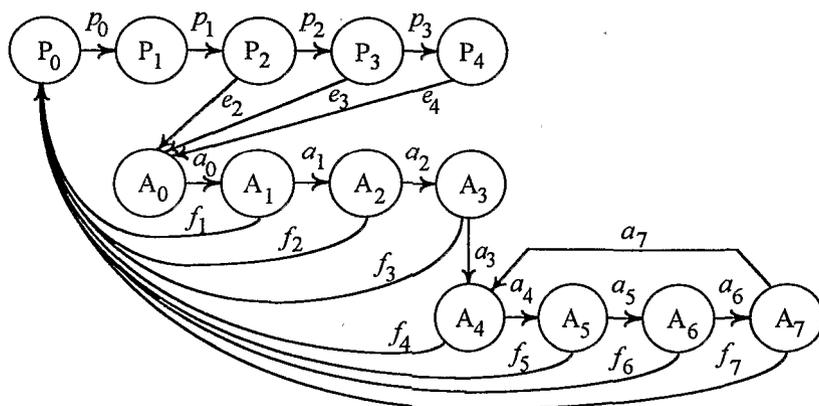


**Fig. 1.** The tsetse fly life cycle; the stages and the rates of passage from one stage to the next are described in the text.

the ovarioles of alternate ovaries. The initial observation of the regularity of the cycle of the four ovarioles (including the identification of the pre-reproductive phase and the three stages of larval development) enabled four age-groups ($A_0$, $A_1$, $A_2$ and $A_3$) to be determined (Saunders, 1960, 1962). Challier (1965) observed that each ovulation leaves a trace (follicular relic) and that only one relic persists, corresponding to the most recent ovulation. This enabled a further four age-groups ($A_4$, $A_5$, $A_6$ and $A_7$) to be determined. However, after the first four ovulations (i.e. a complete ovarian cycle) all four ovarioles present a follicular relic. It is therefore not possible to differentiate between later cycles, and these four age-groups remain imprecise.

The graph of the life cycle of the females is given in Figure 1. Each stage was assumed to be of equal duration of $h$ days, where $h$ corresponds to the mean interval between two ovulations (i.e. about 10 days). Since the free life of the larva is very short, this was not taken into account in the model. Since the pupal stage varies between 20 and 50 days according to the temperature (cyclic seasonal variations), it was subdivided into five fictitious stages ($P_0$, $P_1$, $P_2$, $P_3$ and $P_4$) to maintain a homogenous discrete representation. The coefficient $p_i$ represents the survival rate of a pupa at stage $P_i$ over a period of $h$ days and $e_i$ the emergence rate of pupae in stage $P_i$.

The adult stages $A_0$, $A_1$, $A_2$ and $A_3$ correspond to the first four ovarian age-groups and stages $A_4$, $A_5$, $A_6$ and $A_7$ correspond to the older age-groups. The path from $A_7$ to $A_4$ represents the indistinguishable cycle of the four older age-groups. The survival rate of a female in stage $A_i$ over a period of $h$ days is noted by $a_i$, and the fecundity by $f_i$.

## 2.2 An Example of Demographic Data

The data presented are from a population of *Glossina palpalis gambiensis* studied in the forest of Kou (Burkina Faso) from 1964 to 1967 (Challier, 1973 and personal communication). The pupal survival rate ($\bar{s}$) and the pupal period ($\bar{x}$) were determined by observing the emergence of adults from batches of young larvae distributed in small metal cases buried in the ground. When the normal emergence period was considered to have elapsed, the cages were unearthed and the number of empty, parasitized, hatched pupae were counted (Challier, 1973).

The ovarian age-group distributions were obtained from flies caught in a hand net. Since this method overestimates the nulliparous flies ($A_0$), the numbers of flies were adjusted using the results from a comparative study on the effectiveness of capturing by nets and biconical traps (Gouteux & Dagnogo, 1986). Such data were available from September 1964 to April 1967 at a rate of about one sample a month.

Table 1 provides an example of the data available for a complete annual cycle. Missing data on survival rates and the pupal period have been completed with data from the previous year. The pupal period reached a maximum in January (the middle of the dry season) and decreased rapidly in February-March to stabilise at around 30 days from March (beginning of the rainy season) to June (the middle of the rainy season). Overall, pupal survival appeared to be better

**Fig. 2. Opposite page.** Distribution of the ovarian age-groups of *G. palpalis gambiensis females* caught by hand-net from September 1964 to April 1967 in the Forest of Kou, Burkina Faso (Challier, 1973). The numbers are presented as frequencies in order to normalise the data.

1964 - 65     1965 - 66     1966 - 67

SEP. OCT. NOV. DEC. JAN. FEB. MAR. APR. MAY JUN. JUL. AUG.
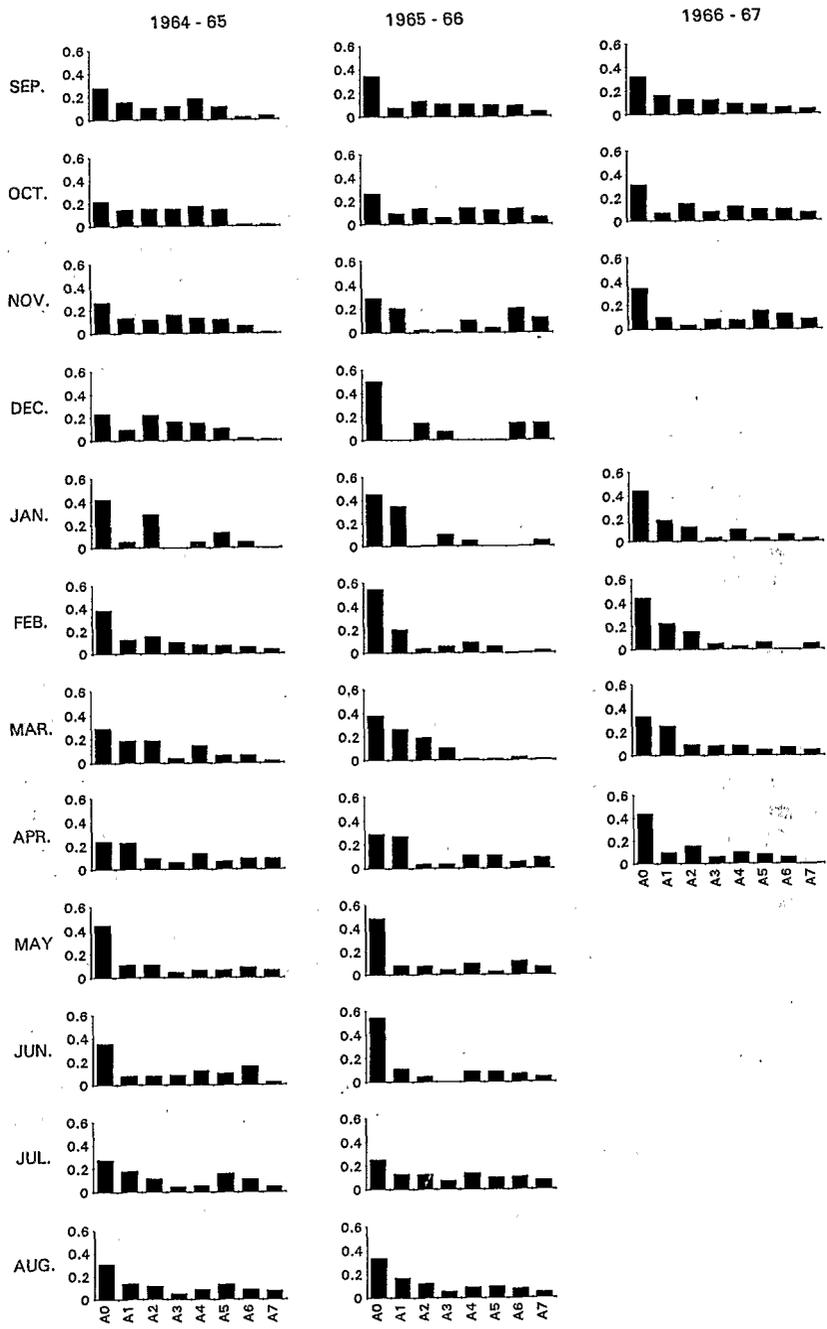
**Table 1.** Pupal survival rates ($\bar{s}$), pupal period ($\bar{x}$, in days) and distribution of ovarian age-groups ($n_0$ ... $n_7$ are the number of females of ovarian age $A_0$ ... $A_7$; $n$ is the size of the sample) of *G. palpalis gambiensis* females caught in a hand-net from September 1964 to August 1965 in the Forest of Kou, Burkina Faso (Challier, 1973).
* Missing data, replaced by weighted means of the values obtained in November and January.

| Month | $\bar{s}$ | $\bar{x}$ | $n_0$ | $n_1$ | $n_2$ | $n_3$ | $n_4$ | $n_5$ | $n_6$ | $n_7$ | $n$ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| September | .74 | 30.3 | 60 | 32 | 22 | 25 | 40 | 24 | 5 | 8 | 216 |
| October | .74 | 33.5 | 26 | 17 | 18 | 18 | 21 | 17 | 2 | 2 | 121 |
| November | .74 | 36.1 | 47 | 23 | 21 | 28 | 23 | 21 | 11 | 2 | 176 |
| December | .83* | 38.9* | 20 | 8 | 19 | 14 | 13 | 9 | 2 | 1 | 86 |
| January | .91 | 44.0 | 16 | 2 | 10 | 0 | 2 | 5 | 2 | 0 | 38 |
| February | .91 | 34.8 | 53 | 17 | 21 | 14 | 11 | 10 | 8 | 5 | 139 |
| March | .86 | 30.9 | 14 | 9 | 9 | 2 | 7 | 3 | 3 | 1 | 48 |
| April | .96 | 29.8 | 21 | 20 | 8 | 5 | 12 | 6 | 8 | 8 | 88 |
| May | .73 | 29.7 | 20 | 5 | 5 | 2 | 3 | 3 | 4 | 3 | 45 |
| June | .82 | 30.0 | 56 | 12 | 12 | 13 | 20 | 16 | 25 | 4 | 158 |
| July | .82 | 31.2 | 55 | 56 | 23 | 9 | 11 | 32 | 22 | 10 | 198 |
| August | .82 | 31.4 | 67 | 30 | 25 | 11 | 19 | 29 | 19 | 17 | 217 |

from January to April (dry season and beginning of the rainy season) but the differences were not significant ($\chi^2_{5df} = 7.46$ ; P = 0.19, Challier, 1973).

Figure 2 summarizes the trend in age structure during an annual cycle. Over the three annual cycles, the period of January-February (dry season) was characterized by a high proportion (40 % and over) of flies in the nulliparous stage ($A_0$). This occurred earlier in 1965-66, lasting from December to March. From July to November (rainy season), on average, the samples comprised older adults. The intermediate period (from March to June, the beginning of the rainy season) was less characteristic and varied according to the year, with, however, a new emergence of young flies in May 1965, May-June 1966 and April 1967.

## 3. BUILDING A MATRIX MODEL

A discrete model, with time steps $h$ days, can be derived from the life cycle diagram (Figure 1). It concerns only the female population and is expressed as:

$$X(t + 1) = M\,X(t) \qquad (1)$$

where $X(t)$ is a vector whose components represent the numbers of females in each stage at time $t$ and $M$ is the transition matrix associated with the life cycle:

$$
M = \begin{bmatrix}
0 & 0 & 0 & 0 & 0 & 0 & f_1 & f_2 & f_3 & f_4 & f_5 & f_6 & f_7 \\
p_0 & 0 & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & 0 \\
0 & p_1 & \cdot & & & & & & & & & & \cdot \\
0 & 0 & p_2 & \cdot & & & & & & & & & \cdot \\
0 & 0 & 0 & p_3 & \cdot & & & & & & & & \cdot \\
0 & 0 & e_2 & e_3 & e_4 & \cdot & & & & & & & \cdot \\
0 & \cdot & \cdot & \cdot & 0 & a_0 & \cdot & & & & & & \cdot \\
\cdot & & & & & \cdot & a_1 & \cdot & & & & & \cdot \\
\cdot & & & & & & \cdot & a_2 & 0 & \cdot & \cdot & \cdot & 0 \\
\cdot & & & & & & & \cdot & a_3 & 0 & 0 & 0 & a_7 \\
\cdot & & & & & & & & \cdot & a_4 & 0 & 0 & 0 \\
\cdot & & & & & & & & & \cdot & a_5 & 0 & 0 \\
0 & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & 0 & a_6 & 0
\end{bmatrix}
$$

The matrix $M$ is non-negative, irreducible and primitive. Under these conditions, it possesses a strictly positive and strictly dominant real eigenvalue $\lambda$ (Peron-Frobenius theorem; Caswell, 1989), which can be interpreted as the asymptotic growth rate of the population. The right eigenvector corresponding to the eigenvalue $\lambda$ gives the asymptotic stable distribution of the stages. When the asymptotic state is reached, we thus have:

$$Mw = \lambda w . \tag{2}$$

The values of the coefficients $e_i$ and $p_i$ can be derived from the pupal survival rate ($\bar{s}$) and the pupal period ($\bar{x}$) (Jarry $et$ $al.$, 1996). The values $f_i$ are calculated from the potential fecundity of the females ($f_p$) by applying a continuity correction (Caswell, 1989), since, for this species, there is no specific reproduction period during the year. Under the additional hypothesis of a constant survival rate among the adult females ($a_i = a$) and assuming $f_p$ to be constant and equal to 0.5, if we suppose a balanced sex ratio, we obtain a model which depends on only three parameters ($\bar{s}$, $\bar{x}$ and $a$). The dominant eigenvalue of the matrix $M$ cannot be expressed analytically, but can be calculated for fixed values of the demographic parameters. A study of the properties of this model can be found in Jarry $et$ $al.$ (1996).

# 4. ESTIMATION OF THE DEMOGRAPHIC PARAMETERS

## 4.1 Maximum Likelihood Estimation of the Apparent Survival Rate of the Females

In this section, we consider only the adult female tsetse flies. Following the notation adopted for the ovarian age-groups, let $N_0(t)$, $N_1(t)$, ..., $N_i(t)$, ..., $N_7(t)$ be the number of adults in age-group $A_0, A_1, ..., A_i, ..., A_7$. In terms of the matrix model $N_i(t) = X_{i+6}(t)$. Once the steady state is reached (asymptotic regime), the evolution of the numbers of adults in each stage can be described, using equation (1), in two ways:

$$N_i(t+1) = \lambda N_i(t) \text{ for } i = 0, 1 ... 7 \tag{3}$$

and

$$\begin{cases} N_i(t+1) = aN_{i-1}(t) \text{ for } i = 1...7 \text{ ; } i \neq 4 \\ N_4(t+1) = aN_3(t) + aN_7(t) \end{cases} \tag{4}$$

These equations describe the passage of the females flies from one age-group to another with a constant survival rate $a$, taking into account the uncertainty in the last four age-groups (see Figure 1 and the form of the matrix $M$ above). From (3), we have $N_i(t) = \frac{1}{\lambda} N_i(t+1)$. Substituting on the right-hand side of equations (4), we therefore obtain:

$$\begin{cases} N_i(t+1) = \frac{a}{\lambda} N_{i-1}(t+1) \text{ for } i = 1...7 \text{ ; } i \neq 4 \\ N_4(t+1) = \frac{a}{\lambda} N_3(t+1) + \frac{a}{\lambda} N_7(t+1) \end{cases} \tag{5}$$

Since equations (5) are time-independent, we can now write, for all time $t$,

$$N_1 = \frac{a}{\lambda} N_0$$

$$N_2 = \frac{a}{\lambda} N_1 = \left(\frac{a}{\lambda}\right)^2 N_0$$

$$N_3 = \frac{a}{\lambda} N_2 = \left(\frac{a}{\lambda}\right)^3 N_0$$

Putting $N_7 = \frac{a}{\lambda} N_6 = \left(\frac{a}{\lambda}\right)^2 N_5 = \left(\frac{a}{\lambda}\right)^3 N_4$ and substituting into equation (5) gives:

$$N_4 = \frac{a}{\lambda} N_3 + \left(\frac{a}{\lambda}\right)^4 N_4 \text{ and finally}$$

$$N_4 = \left(\frac{a}{\lambda}\right)^4 N_0 \Big/ \left[1 - \left(\frac{a}{\lambda}\right)^4\right].$$

The numbers $N_i$ in each stage can thus finally be expressed in terms of $N_0$:

$$\begin{cases} N_i = \left(\frac{a}{\lambda}\right)^i N_0 \text{ for } i = 0...3 \\[4mm] N_i = \left(\frac{a}{\lambda}\right)^i \Big/ \left[1 - \left(\frac{a}{\lambda}\right)^4\right] N_0 \text{ for } i = 4...7 \end{cases} \tag{6}$$

It may be noted that the case $\frac{a}{\lambda} = 1$ cannot occur in practical applications since this would imply $N_4 = N_7$ and hence, from equation (5), $N_3 = 0$. From equation (6), this would imply $N_0 = 0$, corresponding to the case of no females in the population.

The parameter $\beta = a/\lambda$ which appears clearly in equations (6) will be called the 'apparent survival rate' and may be estimated by maximum likelihood as follows.

Consider a simple random sample of size $n$ with ovarian age distribution $n_0, n_1,..., n_i,..., n_7$. Using equations (6), the probability of belonging to age-group $i$ is given by :

$$\begin{cases} P(X=i) = \beta^i(1-\beta) \text{ for } i = 0...3 \\[4mm] P(X=i) = \dfrac{\beta^i(1-\beta)}{1-\beta^4} \text{ for } i = 4...7 \end{cases} \tag{7}$$

The likelihood function $L(\beta) = \prod\limits_{i=0}^{7} P(x = i ; \beta)^{n_i}$ can thus be constructed, giving

$$\ln L(\beta) = w_1 \ln \beta + n \ln(1-\beta) - w_2 \ln(1-\beta^4) \tag{8}$$

with $w_1 = \sum\limits_{i=1}^{7} i\, n_i$ and $w_2 = \sum\limits_{i=4}^{7} n_i$.
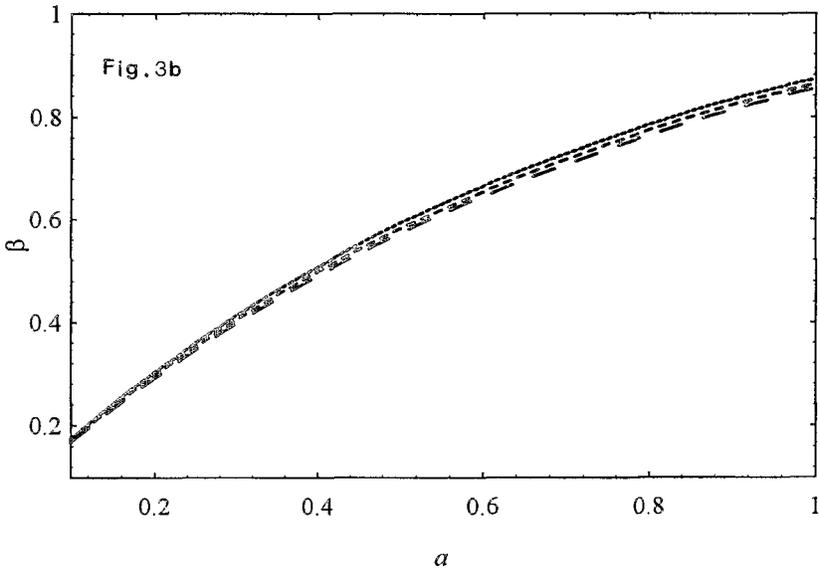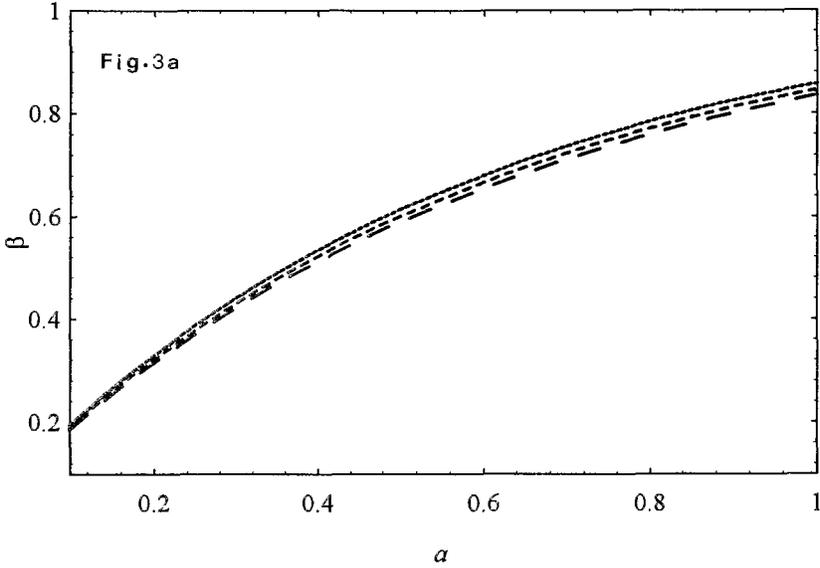
Fig. 3. Examples of functional relationships between 'apparent' survival rates of the females ($\beta = \lambda/a$) and 'real' survival rate $a$ for various values of pupal survival rate and pupal period ($\bar{s} = 0.7$ : ... ; $\bar{s} = 0.8$ : --- ; $\bar{s} = 0.9$ : _ _ ; $\bar{x} = 30$ days : Fig. 3a ; $\bar{x} = 40$ days : Fig. 3b).

Differentiating partially with respect to $\beta$ gives:

$$\frac{\partial \ln L(\beta)}{\partial \beta} = \frac{w_1}{\beta} - \frac{n}{1-\beta} + \frac{4w_2\beta^3}{1-\beta^4} \tag{9}$$

$$\text{or} \quad \frac{\partial \ln L(\beta)}{\partial \beta} = \frac{w_1 - n\beta - n\beta^2 - n\beta^3 + (4w_2 - w_1 - n)\beta^4}{\beta(1-\beta)(1+\beta+\beta^2+\beta^3)}$$

with $\beta \neq 1$ (see above).

For each sample, $\beta$ can be estimated by solving numerically the equation $\frac{\partial \ln L(\beta)}{\partial \beta} = 0$. The software Mathematica$^R$ was used and the goodness of the fit to the observed data tested by the $\chi^2$ test.

## 4.2 Deducing the Survival Rate of Females and the Growth Rate

A knowledge of the age structure of the females is not sufficient to estimate directly the survival rate, $a$, unless $\lambda = 1$, in which case $\beta = a$. This, *a priori* very strong condition of numerical equilibrium of the population, is not necessary if information is available concerning the pupal stages, namely the pupal period and survival rate. In this case, equation (1) provides a functional relationship between $\beta$ and $a$, which is illustrated in Figure 3 for selected values of $\bar{s}$ and $\bar{x}$. This function is monotonically increasing in the region of interest ($0.1 \leq a < 1$); to each value of $\beta$ corresponds one and only one value of $a$ and hence a single value of the growth rate $\lambda$. Estimation of these values is obtained by numerical computation.

## 5. APPLICATIONS TO FIELD DATA

The estimates of the female survival rate $a$ and the growth rate $\lambda$ corresponding to the 31 monthly recordings obtained by Challier (1973) for a population of *G. palpalis gambiensis* are presented in Figure 4. The close relationship between these two demographic parameters has already been shown (Jarry *et al.*, 1996). The fluctuations in the pupal survival rate seem to be less marked in this data set. A relatively low rate (October-November) did not prevent a growth rate of 1 or more. The effect of the duration of the pupal stage is more difficult to appreciate, since a shortening of this stage favours population growth when adult survival is high, but also increases the risk of extinction when adult survival is low (Jarry *et al.*, 1996). However, these effects only occur with extreme values which are beyond the fluctuations recorded for the population in this study.

Throughout the whole study period, the growth rate varied between 0.84 and 1.1 and generally fluctuated around 1. An unfavourable period of population growth was observed in each annual cycle from January to March (and, in 1967, even in April). During this unfavourable period (end of the dry season and beginning of the rainy season) the maximum temperature range was recorded. The following period (the rainy season) shows a less consistent
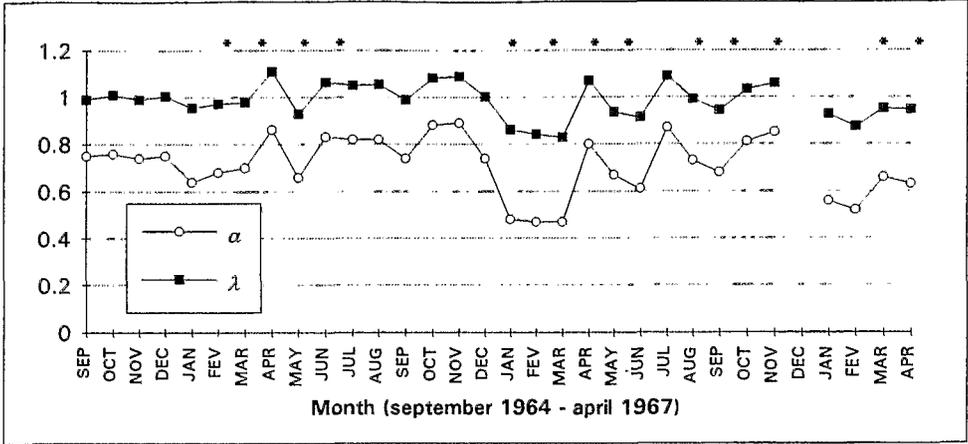
**Fig. 4.** Estimates of the survival rate *a* of *G. palpalis gambiensis* females and the growth rate λ of the population (Forest of Kou, Burkina Faso). Variations over more than two annual cycles from September 1964 to April 1967.
\* Acceptable fit to observed data ($\chi^2$ test at a threshold $\alpha = 0.05$)

growth rate, fluctuating rather strongly with fluctuations varying according to the year. The growth rate increased at the end of rainy season and at the beginning of the dry season, in particular in 1965 and 1966.

## 6. DISCUSSION

Using a maximum likelihood method, Hargrove (1993) estimated the quantity $\phi = \exp(-(\mu+\lambda))$, where μ is the adult mortality rate and λ is the growth rate, by solving the equation:

$$x_2(1-\phi^4)\,\mu\,x_1(1+\phi+\phi 2+\phi^3) + 4x_3\phi^4 = 0 \qquad (10)$$

with $x_1 = \sum_{i=1}^{7} n_i$, $x_2 = \sum_{i=1}^{7} i\,n_i$ and $x_3 = \sum_{i=4}^{7} n_i$, the $A_0$ flies being excluded since, according to this author, 'they are judged to be severely underrepresented in field sample'.

Our approach leads to the same result. Indeed, the implicit Hargrove's model is probably a continuous one, with μ and λ being instantaneous rates. Denoting *r* the growth rate of Hargrove (1993), the correspondence with our discrete model can be expressed as:

$$\begin{cases} r = \ln \lambda \\[2mm] \mu = -\ln a \end{cases} \qquad (11)$$

We can write $\phi = \exp(-\mu)/\exp(r) = a/\lambda = \beta$. If $A_0$ flies are excluded, we obtain a new estimation of $\beta$ by solving the equation:

$$w_1(1-\beta^4) - n(1+\beta+\beta^2+\beta^3) + 4w_3\beta^4 = 0 \qquad (12)$$

with $n = \sum_{i=1}^{7} n_i$, $w_1 = \sum_{i=1}^{7} i\, n_i$ and $\sum_{i=1}^{7} n_i$. It is clear that equations (10) and (12) are the same.

The method presented here provides estimates of the adult survival and growth rates if the pupal survival rate and the pupal period are known. The results are coherent and easily interpreted in terms of the variations in climatic conditions in the studied area. However, the fit of the model to the data, tested by $\chi^2$, was acceptable in only 13 cases out of 31 (Figure 3). The poor fits may be due to several causes, for example:

- It is assumed that the age-groups have reached a stable distribution for all sampling dates which are at intervals of approximately one month. This assumption is certainly not respected when major changes occur in the dynamics of the population. Certain samples probably correspond to a transitory phase. This is a major criticism which applies to most methods based on age structures. Our model should enable this point to be approached by studying the time required to return to a stationary phase after disturbance.

- Certain features of the biology of the tsetse flies, which are known but difficult to quantify, are not taken into account. For example, during the rainy season, strong storms may destroy the breeding grounds resulting in a sudden high larval mortality which is not taken into account in the field experiments since this type of situation is specifically avoided. This may result in gaps in the pyramid of ages which would spread over several months and delay the establishment of an asymptotic phase. Such 'empty' age-groups are quite visible in the raw data (Figure 2). Furthermore, field experiments take into account parasitism but not predation which can be quite considerable (Chorley, 1929; Kemps, 1951; Rogers, 1974).

- Several authors consider that the assumption of a constant adult mortality rate is not valid (Jordan & Curtis, 1972; Gouteux & Kienou, 1982; Hargrove, 1990, 1991; amongst others). Our model would be improved by introducing an age dependent mortality by distinguishing in the first instance the nulliparous flies ($A_0$), the young parous flies ($A_1$ to $A_3$) and the old parous flies ($A_4$ to $A_7$).

- The sampling was carried out by hand-netting which, despite correction, is biased by several uncontrollable human factors. It would be interesting to use data obtained by trapping which is a much more reliable method (Gouteux & Dagnogo, 1986).

Despite these limitations, the present study suggests that the tsetse fly natural populations have a growth rate remarkably close to 1. The stability of the tsetse fly populations, which is one of the basic assumptions of epidemiological model of sleeping sickness (Artzouni & Gouteux, 1996), finds a preliminary confirmation here. It should also be noted that this stability is deduced from a linear matrix model which therefore does not include any regulation such as density dependence. A relatively simple interpretation of the present results can be proposed as follows:

1. Given the characteristics of their reproduction, the maximum growth rate in tsetse fly populations is not very high. For an ideal survival rate of 1, the growth rate varies from 1.18

to 1.22 according to the pupal period, which corresponds to a production ranging from 457 to 1566 females per female per year (Jarry *et al.*, 1996). Hargrove (1988) gave values of the same order of magnitude, but slightly higher. By rearing tsetse flies, Curtis & Jordan (1968) obtained productions of 308-552 females per female per year for *G. austeni* and Jordan & Curtis (1972) obtained 400-500 females per female per year for *G. morsitans morsitans*.

2. The growth rate becomes less than 1 during unfavourable periods since the tsetse flies are sensitive to major changes in temperature and to drought. This affects mainly the adult survival rate.

3. These unfavourable periods do not last, and the population is able to recover as adult survival improves.

4. Over an annual cycle, favourable and unfavourable periods compensate each other and the overall situation remains in equilibrium.

This explanation is obviously too simplistic but provides a falsifiable explanatory model. It makes the assumption that the fly populations show extremely stable spatial patterns. This stability does exist to a certain extent (Gouteux & Lavassière, 1982) but population movements related to - amongst other factors - inter specific competition do occur (Gouteux, 1992).

From a practical point of view, this approach enables the growth rate of a population to be estimated from two demographic parameters related to the pupal stage and sample female age structures. Data on the pupal stage are relatively rare, but the example used shows that, for population dynamics, the fluctuations in the parameters related to this stage have less influence than those in the adult survival rate. If studies on the sensitivity of the model confirm this point, it would be possible to estimate the growth rate of the tsetse fly natural populations by using only the ovarian age distributions, assuming "reasonable" a priori values for the pupal survival rate and pupal period. Models describing the relationships between the pupal period and the temperature could also be used (see, for example, Potts, 1933; Buton & Lewis, 1934; Jack, 1939; Glasgow, 1963; Harley, 1968).

Our approach emphasizes the usefulness of determining the ovarian age of the females during control campaigns. It would enable the effectiveness of the protocol used in control campaigns to be tested. Trapping, which provides both a means of control and sampling, presents an unquestionable practical advantage.

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