Bulletin of Entomological Research (1999) 89, 515–521

Estimation of age-dependent survival rates of female tsetse flies (Diptera: Glossinidae) from ovarian age distributions

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Abstract

Existing attempts to estimate the survival rate of tsetse flies from ovarian age distributions generally assume that the population is stationary. The fact that the survival rate cannot be dissociated from the growth rate by these methods poses a problem. Under the assumption of a stable age distribution, we propose a maximum likelihood method to estimate the 'apparent survival rate' for three categories of females: nulliparous (β_0), young parous (β_1) and old parous flies (β_2). The rate depends both on 'real survival rates' a_0, a_1 and a_2, and a growth rate λ: $\beta_0 = a_0/\lambda$, $\beta_1 = a_1/\lambda$, and $\beta_2 = a_2/\lambda$. We used a matrix model, which can be parameterized if the pupal survival rate and the pupal period are known. Replacing a_0, a_1 and a_2 by $\beta_0\lambda$, $\beta_1\lambda$, and $\beta_2\lambda$ in the projection matrix, the problem amounts to calculating its dominant eigen-value λ, and hence a_0, a_1 and a_2. The application to a field population of *Glossina palpalis gambiensis* Vanderplank in Burkina Faso showed there was a marked difference in survival rate according to age category. The average survival rate increased with age with decreasing variability. The results suggested that sampling (by trapping) may have had an effect on the dynamics of this tsetse population by ageing it artificially. This method may be a useful tool for monitoring tsetse control.

Introduction

Tsetse flies *Glossina* spp. (Diptera: Glossinidae), the vectors of sleeping sickness, are insects with the unusual characteristics of being viviparous, and having a low reproduction rate (about one larva every 10 days). The ovarian (or physiological) age of the female flies can be determined by examining the dissected ovaries under a microscope (Saunders, 1960). Several attempts have been made to estimate the survival rates of females from their ovarian age distribution (Saunders, 1962; Gouteux, 1982; Gouteux & Kiénou, 1982; Rogers & Randolph, 1984; Rogers *et al.*, 1984; Challier & Turner, 1985).

However, as pointed out by Van Sickle (1988), these authors assume, more or less explicitly, that the population is stationary (asymptotic growth rate $\lambda = 1$, or intrinsic rate of increase $r = 0$). In fact, without additional information adult survival (or mortality) cannot be dissociated from the growth rate. Hargrove (1993) consequently estimated, by a maximum likelihood method, a parameter depending on the mortality and the growth rate. To solve this problem, Van Sickle (1988), proposed an alternative method using the Euler-Lotka equation. It was necessary to assume only the population had a stable age distribution, and that an independent estimate of the survival rate could be obtained for one age class. Unfortunately, this author also showed that this method was very sensitive to sampling error and he recommended that the growth rate should be estimated independently from, for instance, data based on regular captures (Van Sickle & Phelps, 1988).

Here we propose a method similar to that of Van Sickle (1988), but derived using a matrix model adapted for studying *Glossina* populations (Jarry *et al.*, 1996a). The model

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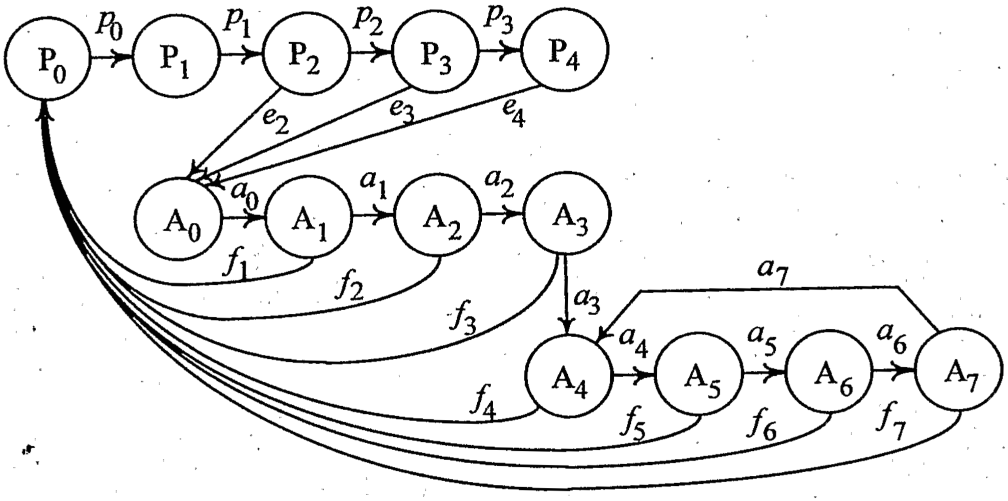
assumes that data are available on pupal survival rate, mean pupal period and ovarian age distribution.

Materials and methods

Life cycle of the female tsetse fly

The regular ovulation alternating between two ovaries, each of which contains two ovarioles, enables eight age-groups to be determined in tsetse flies. The first four age-groups correspond to the first ovarian cycle and can be distinguished precisely. Subsequent cycles cannot be distinguished from one another and the four older age-groups therefore correspond only to age within a cycle (Challier, 1965; Jarry *et al.*, 1996a) (fig. 1). Each stage corresponding to the mean duration between two ovulations lasts for h days (generally $h \approx 10$). Since the duration of the pupal stage varies between 20 and 50 days according to the temperature (cyclical seasonal variation, Jackson, 1949; Harley, 1968), it was subdivided into five hypothetical stages (P_0, P_1, P_2, P_3 and P_4) to maintain a homogenous discrete



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

Fig. 1. Graph of the life cycle of female *Glossina* and associated transition matrix.

representation. The coefficient p_i represents the survival rate of the pupa in stage P_i over a period of h days and e_i the emergence rate of pupae in stage P_i. The path from A_7 to A_4 represents the indeterminacy associated with the four older age-groups. The survival rate of a female in stage A_i over h days is noted by a_i and her fecundity by f_i.

Matrix modelling

The matrix model is derived from the life cycle and involves only the female population:

$$N(t+1) = M\,N(t) \tag{1}$$

where the components of the vector $N(t)$ represent the number of females in a given stage at date t and M is the transition matrix associated with the life cycle graph.

The matrix M is non-negative, irreducible and primitive. Under these conditions, it possesses a strictly positive and strictly dominant real eigen-value λ (Peron-Frobenius in Caswell, 1989) which can be interpreted as the asymptotic growth rate of the population. The right eigen-vector associated with this eigen-value gives the stable distribution of the stages.

If we assume that the survival rate is constant about the pupal period life, the values of the coefficients e_i and p_i can be derived from pupal survival rate ($\bar{s}$) and mean pupal period ($\bar{x}$) (Jarry *et al.*, 1996a, see Appendix 1). The values f_i are calculated from the potential fecundity of the females ($f_{pmax} = 0.5$ if we assume a balanced sex ratio) by applying a continuity correction (Caswell, 1989), since, for this species, there is no specific reproduction period during the year.

In the first instance, we will assume a constant survival rate among the adult females ($a_i = a$). The model now depends on only three parameters ($\bar{s}$, $\bar{x}$ and a) if we consider f_{pmax} to be constant and if the inter-larval period h is constant at 10 days, the mean value estimated by Challier (1973) for the example treated.

Results

Estimation of a constant survival rate of the female flies

The complete development of the estimation process is given in Jarry *et al.* (1996b). In this section, we simply produce the principal results necessary to understand the extension to the case of age-dependent survival rates. We consider only the adult population of tsetse flies and we modify slightly the notation of the indices of the vector $N(t)$ so that it is coherent with the notation adopted for the physiological age-groups. Let $N_0(t), N_1(t), \ldots, N_i(t), \ldots, N_7(t)$ be the number of adults in age-groups $A_0, A_1, \ldots, A_i, \ldots, A_7$.

Assuming that the age structure of the population is stable, the numbers N_i in each stage at any time t can be expressed in terms of N_0 as:

$$\begin{cases} N_i = (a/\lambda)^i N_0, & \text{for } i = 0,\ldots 3 \\ N_i = \left[\dfrac{(a/\lambda)^i}{1-(a/\lambda)^4}\right] N_0, & \text{for } i = 4,\ldots 7 \end{cases} \tag{2}$$

with $a/\lambda \neq 1$, which corresponds to a non-zero population size (Jarry *et al.*, 1996b).

The 'apparent survival rate' $\beta = a/\lambda$ which appears clearly in equations (2) can be estimated by maximum likelihood. For each sample of size n, with $n_0, n_1, \ldots n_7$ in each of the physiological age-groups $A_0, A_1, \ldots A_7$, β may be estimated by solving numerically the equation:

$$\frac{\partial \ln L(\beta)}{\partial \beta} = \frac{w_1}{\beta} - \frac{n}{1-\beta} + \frac{4 w_2 \beta^3}{1-\beta^4} = 0 \tag{3}$$

with $w_1 = \sum_{i=1}^{7} i\, n_i$, $w_2 = \sum_{i=4}^{7} n_i$ and $\beta \neq 1$ (see above).

Knowing the age structure of the adults is not in itself sufficient to estimate directly the survival rate a of the adults unless $\lambda = 1$, in which case $a = \beta$. 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 the survival rate. Replacing a by $\beta\lambda$ in matrix M, all other elements being defined, $M - \lambda I$ is a matrix with only one unknown λ. The problem is to solve an equation of degree p (the dimension of the matrix M) and the Perron Fronenius theorem guarantees that one real solution exists. In practice, we used Mathematica® software for solving the equation:

$$\det(M - \lambda I) = 0 \tag{4}$$

Extension to the case of age-dependent survival rates

Female tsetse flies may be classified into three broad categories: nulliparous (A_0), young parous (A_1, A_2 and A_3) and old parous flies (A_4, A_5, A_6 and A_7). Let a_0, a_1 and a_2 be the survival rates in these three categories, and β_0, β_1 and β_2 the corresponding apparent survival rates ($\beta_i = a_i/\lambda$). Equations (2) then become:

$$\begin{cases} N_i = \beta_0 {\beta_1}^{i-1} N_0, & \text{for } i = 1,\ldots 3 \\ N_i = \dfrac{\beta_0 {\beta_1}^3 {\beta_2}^{i-4}}{1-{\beta_2}^4} \mathrm{N}_0, & \text{for } i = 4,\ldots 7 \end{cases} \tag{5}$$

and the probabilities of belonging to each age-group become:

$$\begin{cases} P(X=0) = u/v \\ P(X=i) = \dfrac{u\,{\beta_0}^{i-2}{\beta_1}^{i-1}}{v}, \text{ for } i = 1,\ldots 3 \\ P(X=i) = \dfrac{\beta_0 {\beta_1}^3 {\beta_2}^{i-4}}{zv}, \text{ for } i = 4,\ldots 7 \end{cases} \tag{6}$$

where $u = 1-\beta_2$; $v = (1-\beta_2)\left(1+\beta_0\left(1+\beta_1+{\beta_1}^2+{\beta_1}^3\right)\right)$ $+\beta_0{\beta_1}^3$ and $z = 1+\beta_2+{\beta_2}^2+{\beta_2}^3$.

The likelihood function $L(\beta_0, \beta_1, \beta_2)$ is then given by:

$$\ln L(\beta_0, \beta_1, \beta_2) = w_0 \ln \beta_0 + w_1 \ln \beta_1 + w_2 \ln \beta_2 + w_3 \ln(1-\beta_2) - n \ln v - (n - w_3) \ln z \tag{7}$$

with $w_0 = \sum_{i=1}^{7} n_i$; $w_1 = n_2 + n_3 + 3\sum_{i=4}^{7} n_i$; $w_2 = n_5 + 2n_6 + 3n_7$ and $w_3 = \sum_{i=1}^{3} n_i$.

The estimates of β_0, β_1 et β_2 are solutions of the system:

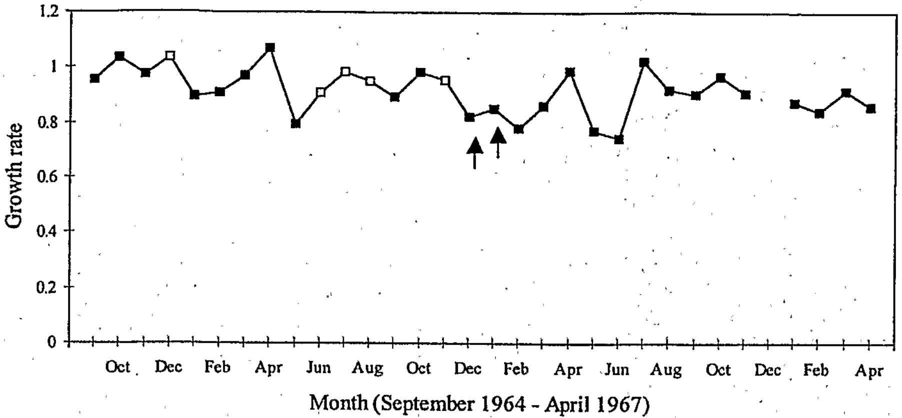


Fig. 2. Variation in the estimated growth rate λ of a population of *Glossina palpalis gambiensis* in the Burkina-Faso forest, assuming age-dependent survival rates of female. ■, acceptable fit to observed data (χ^2 test, $\alpha = 0.05$); □, fit rejected; ↑, fit not tested, sample too small.

$$\begin{cases} \dfrac{\partial}{\partial \beta_0} \ln L(\beta_0, \beta_1, \beta_2) = 0 \\ \dfrac{\partial}{\partial \beta_1} \ln L(\beta_0, \beta_1, \beta_2) = 0 \\ \dfrac{\partial}{\partial \beta_2} \ln L(\beta_0, \beta_1, \beta_2) = 0 \end{cases} \qquad (8)$$

and may be obtained numerically.

The coefficients p_i and e_i of the matrix M being known, it is sufficient to replace a_0, a_1 and a_2 by $\beta_0\lambda$, $\beta_1\lambda$ and $\beta_2\lambda$ to solve, as before, the equation:

$$\det(M - \lambda I) = 0 \qquad (9)$$

Numerical solution of this equation gives λ, and hence a_0, a_1 and a_2.

Applications to G. palpalis gambiensis *in the Burkina-Faso forest*

The data used were obtained from a population of *Glossina palpalis gambiensis* Vanderplank (Diptera: Glossinidae) studied in the forest of Kou, Burkina-Faso, from 1964 to 1967 (Challier, 1973 and personal communication). The survival rates of the pupae ($\bar{s}$) and the pupal period ($\bar{x}$) were determined by monitoring the emergence of the adults from batches of young larvae distributed in small metal cages buried in the ground. When the normal emergence period was considered to have elapsed, the cages were unearthed and the dead (parasitized) or hatched pupae were counted (Challier, 1973). The physiological age-group distributions were obtained from flies caught by hand nets. Since this method overestimates the nulliparous flies (A_0), the numbers were adjusted using results from a study comparing the efficacy of trapping in nets and in biconical traps (Gouteux & Dagnogo, 1986). Such data were obtained from September 1964 to April 1967 with approximately one sampling per month (for details, see Jarry *et al.*, 1996b).

Under the hypothesis of constant adult survival rate, the fit of the model to the data, as tested by χ^2, is acceptable only for 12 samples out of 29 (two samples were too small for this type of test). The growth rate λ is obviously closely related to the survival of the adults. The growth rate fluctuated around 1 over the study period, varying between 0.84 and 1.1. An unfavourable period for population growth was observed every year between January and March (April in 1967), which corresponds to the end of the dry season and beginning of the rainy season, when the maximum temperature range is recorded. In the following period (the rainy season), the growth rate was less homogenous, with relatively strong fluctuations depending on the year. The growth rate increased at the end of the rainy season and at the beginning of the dry season, in particular in 1965 and 1966. Thus, although subject to seasonal fluctuations, the overall dynamics of the growth rate were considered to be stable (Jarry *et al.*, 1996b).

The introduction of age-dependent survival rates modifies markedly the interpretation of these data (fig. 2). There is a clear improvement in the model fit (χ^2 acceptable for 24 samples out of 29), but there are only four values of λ over 1 and overall there is a decreasing trend in the growth rate. The trend in the different survival rates (fig. 3) shows marked differences according to the age of the flies. The average survival rate increases with age (0.456, 0.649 and 0.715 for nulliparous, young parous and old parous flies respectively), but the variability decreases (the variances are respectively 0.051, 0.040 and 0.016). In fact, for the old parous flies, the survival rate increased from around 0.60 at the beginning of the study to fluctuate around 0.70 at the end of the study period.

These results suggest that sampling by trapping may have had an effect on the dynamics of this population. The decreasing trend in population size did not clearly appear on the trap data, because it was masked by seasonal fluctuations (Challier, 1973). However, this decrease can be observed during unfavourable periods. The catches in December 1964 and January 1965 were higher than in December 1965 and January 1966 (too small for χ^2 test, see fig. 2). In December 1966 the catches were about zero.

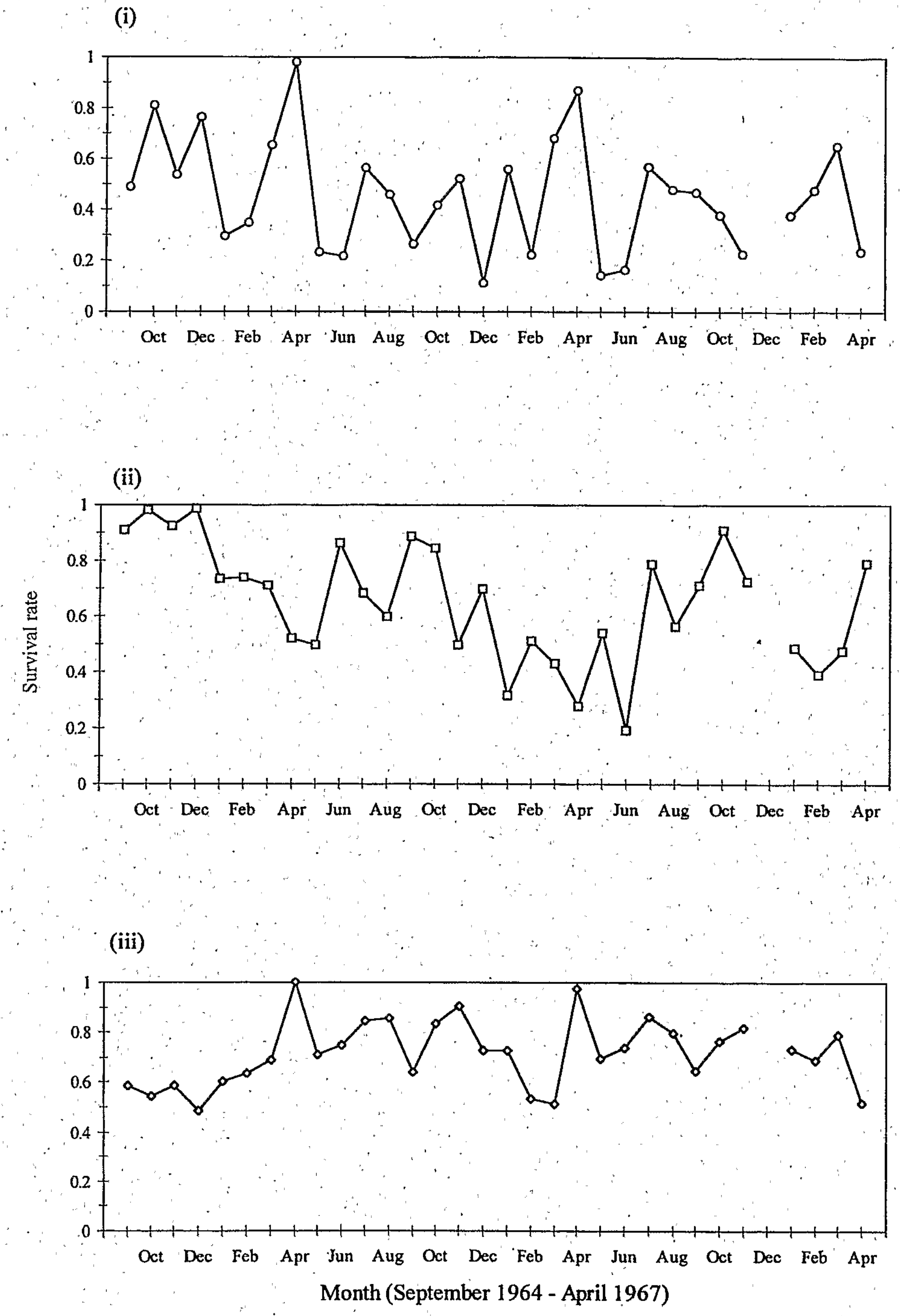


Fig. 3. Variation in the survival rate for three categories of female *Glossina palpalis gambiensis*: (i) nulliparous (a_0); (ii) young parous (a_1); and (iii) old parous (a_2).

Discussion

Several authors (e.g. Jordan & Curtis, 1972; Gouteux & Kienou, 1982; Hargrove, 1990, 1991) consider that the assumption of constant mortality rates of adult flies is not valid. Both in the laboratory and in the field, the mortality graph was U-shaped. However, our results showed that the mortality decreases continuously with age. The high variability of the nulliparous females confirms that sampling this age-group is problematic, to the extent that several authors prefer to exclude these females when analysing data. The likelihood equation given by Hargrove (1993) is a good illustration of this. Survival rate of old parous is surprisingly high. We hypothesize that this is caused by a scale effect. Challier's catching design covered a limited area (a few hundreds of square metres) and the local removal might be compensated by the displacement of parous females, especially the old ones, emigrating from surrounding areas. This addition of old parous flies was insufficient to keep the population at an equilibrium, but explains the ageing of the population. The application of our method to other data sets (in preparation) will enable this point to be examined in more detail.

Certain aspects related to the use of numerical methods for solving equations should be noted. The stability of numerical estimates of the apparent survival rates depends on the structure of the samples. In some cases, values of $\beta > 1$ were obtained, which is probably impossible in the context of the proposed matrix model. Indeed, graphs of the relationships between λ and a (Jarry *et al.*, 1996b) suggest that the condition $\lambda > a$ is always fulfilled.

It should also be noted that although a poor model fit may indicate that the population is in a transitory stage, a good fit does not necessarily imply that the population is stationary. The relatively large fluctuations in the estimated growth rate between two successive months (e.g. April–May 1965 or July–August 1966), when the fit to the data was correct, pose a problem. In the future, a method of calculating the confidence intervals of the growth rate could be developed, but it seems quite clear, from a biological point of view, that these strong variations in growth rate are due to the migration of young parous flies. Thus, taking into account spatial aspects in this model of population dynamics would be an important subject for future research.

This contribution is an optimist's reply to the pessimist conclusion of Van Sickle (1988). This optimism is due to the good fit obtained with Challier's data, allowing a very consistent interpretation of these data. It will be necessary to test our method with other data sets. We will have also to demonstrate its robustness against sampling errors, but, in conclusion, the present approach offers many possibilities for future development both in terms of analysing demographic data on tsetse flies and, more generally, with respect to the properties of matrix population models.

Acknowledgements

The authors thank A. Challier for permission to use his data and J.W. Hargrove for helpful comments on the manuscript. These studies were supported by GDR-CNRS no 1107 CoReV (Modèles et Théories pour le Contrôle de Ressources Vivantes et la Gestion de Systèmes Écologiques) and IRD (ex ORSTOM, UR 41, Maladies Infectueuses et Parasitaires).

References

Caswell, H. (1989) *Matrix population models.* 328 pp. Sunderland, Sinauer Associates Inc.

Challier, A. (1965) Amélioration de la méthode de détermination de l'âge physiologique des glossines. Etudes faites sur *Glossina palpalis gambiensis* Vanderplank, 1949. *Bulletin de la Société de Pathologie Exotique* 58, 250–259.

Challier, A. (1973) Ecologie de *Glossina palpalis gambiensis* Vanderplank, 1949 (Diptera – Muscidae) en savane d'Afrique occidentale. Mémoire ORSTOM no 64, Paris.

Challier, A. & Turner, D.A. (1985) Methods to calculate survival rate in tsetse fly (*Glossina*) populations. *Annales de la Société Belge de Médecine Tropicale* 65, 191–197.

Gouteux, J.P. (1982) Analyse des groupes d'âge physiologique des femelles de glossines. Calcul de la courbe de survie, du taux de mortalité, des âges maximale et moyen. *Cahiers ORSTOM, série Entomologie Médicale et Parasitologie* 20, 189–197.

Gouteux, J.P. & Dagnogo, M. (1986) Ecologie des glossines en secteur pré-forestier de Côte d'Ivoire. 11. Comparaison des captures au piège biconique et au filet. Agressivité pour l'homme. *Cahiers ORSTOM, série Entomologie Médicale et Parasitologie* 24, 99–110.

Gouteux, J.P. & Kiénou, J.P. (1982) Observations sur les glossines d'un foyer forestier de trypanosomiase humaine en Côte d'Ivoire. 5. Peuplement de quelques biotopes caractéristiques: plantations, forêt et galerie forestière, en saison des pluies. *Cahiers ORSTOM, série Entomologie Médicale et Parasitologie* 20, 41–61.

Hargrove, J.W. (1990) Age-dependent changes in the probabilities of survival and capture of the tsetse fly *Glossina morsitans morsitans* Westwood. *Insect Science and its Application* 11, 323–330.

Hargrove, J.W. (1991) Ovarian ages of tsetse flies (Diptera: Glossinidae) caught from mobile and stationary baits in the presence and absence of humans. *Bulletin of Entomological Research* 81, 43–50.

Hargrove, J.W. (1993) Age dependent sampling biases in tsetse flies (*Glossina*). Problems associated with estimating mortality from sample age distributions. pp. 549–556 in *Management of insect pests: nuclear and related molecular and genetic techniques*. Vienna, International Atomic Energy Agency.

Harley, J.B.M. (1968) The influence of the temperature on reproduction and development in four species of *Glossina* (Diptera: Muscidae). *Proceedings of the Royal Entomological Society of London* 43, 170–177.

Jackson, C.H.N. (1949) The biology of tsetse flies. *Biological Review* 174.

Jarry, M., Khaladi, M. & Gouteux, J.P. (1996a) A matrix model for studying tsetse fly populations. *Entomologia Experimentalis et Applicata* 78, 51–60.

Jarry, M., Gouteux, J.P. & Khaladi, M. (1996b) Are tsetse fly populations close to equilibrium? *Acta Biotheoretica*, 44, 317–333

Jordan, A.M. & Curtis, C.F. (1972) Productivity of *Glossina morsitans* Westwood maintained in the laboratory, with particular reference to the sterile-insect release control. *Bulletin of the World Health Organization*, 46, 33–38.

Rogers, D.J. & Randolph, S.E. (1984) From a case study to a theoretical basis for tsetse control. *Insect Science and its Application* 5, 419–423.

Rogers, D.J., Randolph, S.E. & Kuzoe, F.A.S. (1984) Local variation in the population dynamics of *Glossina palpalis palpalis* (Robineau-Desvoidy) (Diptera: Glossinidae) I. Natural population regulation. *Bulletin of Entomological Research* 74, 403–423.

Saunders, D.S. (1960) The ovulation cycle in *Glossina morsitans* Westwood (Diptera: Muscidae) and a possible method of age determination for female tsetse flies by examination of their ovaries. *Transactions of the Royal Entomological Society of London* 112, 221–238.

Saunders, D.S. (1962) Age determination for female tsetse flies and the age composition of samples of *Glossina pallidipes* Aust., *G. palpalis fuscipes* Newst. and *G. brevialis* Newst. *Bulletin of Entomological Research* 53, 579–595.

Van Sickle, J. (1988) Invalid estimates of the rate of population increase from *Glossina* (Diptera: Glossinidae) age distributions. *Bulletin of Entomological Research* 78, 155–161.

Van Sickle, J. & Phelps R.J. (1988) Age distribution and reproductive status of declining and stationary populations of *Glossina pallidipes* Austen (Diptera: Glossinidae) in Zimbabwe. *Bulletin of Entomological Research* 78, 51–61.

(Accepted 15 September 1999)

Volume 89(6) 485–602 December 1999 ISSN 0007–4853

BULLETIN *of* ENTOMOLOGICAL RESEARCH

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