A matrix model for studying tsetse fly populations

M. Jarry[1], M. Khaladi[2] & J.-P. Gouteux[3]

[1] *Département de Mathématiques Appliquées, URA-CNRS 1204, IPRA-UPPA, Avenue de l'Université F-64000 Pau, France;* [2] *Department of Mathematics, Cadi Ayyad University, Marrakech, Morocco;* [3] *ORSTOM, Département de Mathématiques Appliquées, URA-CNRS 1204, IPRA-UPPA, Avenue de l'Université F-64000 Pau, France*

Abstract

Some characteristics of tsetse fly population dynamics were investigated using a matrix model. To take into account the peculiarities of the tsetse fly life cycle, the classic Leslie model was modified. Our model integrated the physiological age group of *Glossina* females, the pupal and adult survival rate and the pupal life span. The limit of the growth rate was studied and the results were satisfactory when compared with data of tsetse fly mass rearing. The effect of adult and pupal survival rates on the growth rate was examined and confirmed the importance of adult survival. The sensitivity analysis showed that the growth rate was particularly sensitive to change in the survival rate of young nulliparous females. This matrix model, directly accessible to the experimenter, enhanced our understanding of tsetse population dynamics.

Introduction

Several authors have used mathematical modelling to study vector populations (Bailey, 1975; Anderson & May, 1982; Gettinby, 1989; De Muynck & Rogers, 1989). These models contribute to a better understanding of biological and epidemiological processes and enable various methods of control to be investigated. However, modelling tsetse fly populations is at a preliminary stage and few studies have been carried out.

Two main modelling approaches have been published. One uses age groups of the female tsetse flies determined by the sequential and alternate ovulation of the four ovarioles. The other uses the variations in apparent density of the flies estimated from the number of flies caught in traps (or previously in hand-nets) per unit time.

The first approach follows studies by Saunders (1960, 1962) and Challier (1965) on the physiological age, using mainly the Euler-Lotka equations (Lotka, 1907) to construct life-tables (Deevey, 1947; Andrewartha & Birch, 1956). Such studies have been carried out by Taylor (1979), Ryan (1981), Allsopp (1985) and Williams *et al.* (1990). Other authors have developed original methods for integrating the eight age groups. Challier & Turner (1985) used geometric means to estimate survival rates and Gouteux (1982) used the formula of geometric progression with the least squares method. This formula, slightly modified, was used later by others (Rogers & Randolph, 1984; Rogers *et al.*, 1984). Hargrove (1993) recently provided an estimation for mortality using the maximum likelihood estimation method.

The second approach was developed by Rogers (1979, 1990) and Dransfield & Brightwell (1989). It consists of first using the fluctuation in apparent density to estimate the mortality rates by auto regression (so-called 'Moran curves', Rogers, 1979), then introducing these mortality rates in order to model these fluctuations. This method uses the apparent densities both as explicative and explained variables which results in an obvious bias (Maelzer, 1970; Ito, 1972). These difficulties led Lebreton (1982) to write '... that currently all studies aiming to detect the density-dependence by regression are suspect'. The use of biased parameters

to interpret data from which these same parameters are obtained, raises a further problem of acceptability.

A third approach consists of using matrix models (Caswell, 1989). To date, Hargrove (1988) is the only author to have investigated this method, using the Leslie model (1945). However, Timischl (1981) did implicitly use this model to calculate various demographic parameters. Models using projection matrices are directly accessible to the experimenter. They have already been used to study populations of parasites (Gettinby & McClean, 1979). Furthermore, these models can easily be adapted for numeric simulation and provide clear interpretation. The matrix model was developed by Leslie (1945, 1948) for describing the growth of populations from one age group to the next. Changes in numbers are expressed in terms of survival and fecundity rates, and the matrix structure was used to predict the dynamic trend to the population. The populations studied must, however, have easily identifiable age groups and be available for periodic follow-up as in the case of human populations. This is not the case for many plant (Jarry et al., 1995; Khaladi et al., 1995) or animal species. For the tsetse fly populations, as well as the pupal and imaginal stages present in all diptera, females can be classified into eight age groups by the ovarian dissection method. However, one difficulty is the impossibility to distinguish the precise ovarian cycles after the first four age groups (Challier, 1965).

In order to build a matrix model which best expresses the dynamics of a given population, the key stages in the biological cycle must be identified (i.e., the most significant stage in the life cycle of the species studied). The time-step of the model is of prime importance and must correspond to a significant period for both the age groups and the stage of the life cycle. Hargrove (1988) chose a time-step of one day, and used a matrix with large dimensions (200 × 200); this model represents a discrete form of the continuous model of Williams et al. (1990). Using a time-step of one day, this model does not take explicitly into account the specificity of the tsetse fly cycle characterised by a 9–11 days inter-larval cyclic period (see Fig. 1).

We present here a new matrix model which is a modification of the Leslie model, and enables us to integrate the eight physiological age groups. In this paper, we will particularly use this model to study the relationships between some demographic parameters and the sensitivity of the growth rate to small change in these parameters. The problem of the parameter

estimation from field data will just be briefly tackled in the discussion and will be presented in a later work.

Materials and methods

Life cycle and biological rhythm of the tsetse fly. The demographic strategy of *Glossina* differs from that of other fly species. Whereas the latter reproduce by laying hundreds of eggs, the tsetse gives birth to a single mature larva (i.e., ready for the pupal stage) after gestation of about ten days (Fig. 1). This rhythm of reproduction – one larva every ten days – is particularly slow, resembling the small mammal reproduction rate, rather than that of an insect. It thus represents a K-strategy (Pianka, 1970), relatively rare in invertebrates and exceptional in Diptera (Grassé, 1951).

The tsetse larva is laid on the soil where it buries itself in a few minutes and becomes a pupa. The pupal period varies, mainly according to the temperature. The extreme values observed in the field by Challier (1973) for *Glossina palpalis gambiensis* are between 26 and 50 days (between 30–33 with an average monthly temperature of 25–26°C).

The newly emerged adults are described as 'teneral' until their first meal because of their soft cuticle (from the latin *tener* = tender, Jackson, 1993). Nearly all females are inseminated in the first days of their life. The spermatozoa stocked in the female's spermathecae are generally sufficient for her entire life (Glasgow, 1963). The adult females live one to two months on average, but individuals have been found living after six months in the forest area (Gouteux, 1985) and even nine months in Senegal (Challier, 1973). The particular physiology of the females enables their age to be estimated by dissecting their ovaries. Both ovaries (the right and the left) contain two ovarioles, one on the inside and one on the outside of the axis of symmetry of insect (Fig. 1). The regularity of the cycle of these four ovarioles enabled four age groups to be determined initially (Saunders, 1962). Subsequently, with more accurate observations, eight groups were determined by Challier (1965). A follicular relic was produced after each ovulation, but only one remains visible on the ovariole, irrespective of the number of ovulations. After four ovulations (i.e., the first ovarian cycle) each ovariole presents this relic and subsequent ovarian cycle cannot be distinguished. Thus, age classes 4 to 7 cannot be distinguished from age classes $4+4n$ to $7 + 4n$, where n is the number of complete ovrian cycles.
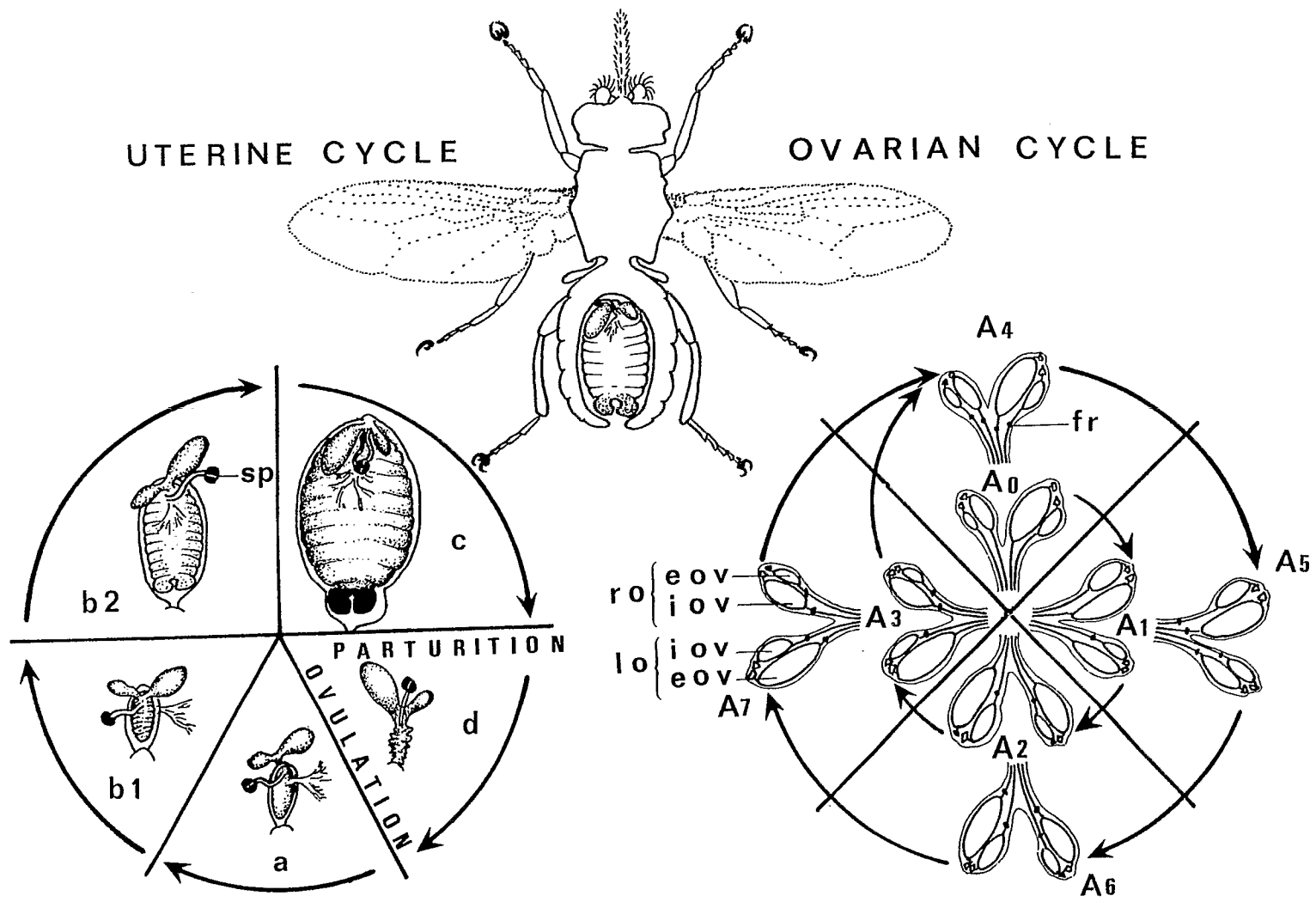
Fig. 1. Uterine and ovarian cycles of *Glossina*. Determination of physiological age. Uterine cycle: a: egg; b_1, b_2, and c: first, second and third instar larva; sp: spermatecea. Ovarian cycle: ro and lo: right and left ovary; i ov and e ov: internal and external ovarioles; fr: follicular relic.
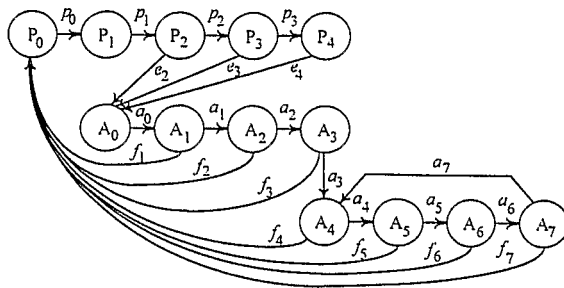
Fig. 2. Graph of the life cycle of Glossinae showing 5 pupal stages P_0, P_1, P_2, P_3, P_4 and 8 adults stages (A_0, A_1, A_2, A_3, A_4, A_5, A_6, A_7) corresponding to the physiological ages. The coefficients p_i represent the survival rate of pupae in class P_i and the coefficients a_i the survival rate of adults in class A_i over a period of h days. e_i is the emergence rate of pupae in stage P_i and f_i is the average fecundity of females in class A_i.

The matrix model. This model has been designed to study the dynamics of the female population. It is structured in stages of the life cycle determined according to data obtained in the field. Each stage in the model has an equal duration of h days. So that the stages would correspond to the physiological ages described above, the chosen step h corresponds to the average period between two ovulations (i.e., about 10 days).

Since the free life of the larva is short, this was not taken into account in the model. The pupal varies between $2h$ and $5h$ days depending on the temperature, and thus showing cyclic seasonal variations. According to the matrix model, the pupal period was divided into five classes: P_0, P_1, P_2, P_3 and P_4 (Fig. 2). The coefficient p_i represents the survival rate of pupae of class P_i over a period of h days and e_i is the emergence rate of P_i pupae. By modifying the rates of survival and emergence it is thus possible to model the variability of the pupal period.

The first four physiologically definite adult classes with precise age groups are represented as A_0, A_1, A_2, A_3 and the four following stages with indefinite ovarian cycles are A_4, A_5, A_6, A_7. Let a_i be the probability of survival of the class A_i fly for a period of h days. The path from A_7 to A_4 indicates logically that females of class A_7 will return to class A_4 after h days. The average fecundity of A_i female is noted as f_i.

The matrix of projection A corresponding to the graph of Fig. 2 is as follows:

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

and the corresponding model is:

$$X(t+1) = A \cdot X(t),$$

where $X(t)$ is a vector of dimension 13, each component of which represents the number of flies at a given stage at date t, with a time-step of h days.

The parameterization of the model (how to calculate the constant coefficients of matrix A from demographic parameters) is presented in Appendix 1.

Results

Limits to the growth rate. The matrix A is nonnegative and primitive and thus allows an eigenvalue λ, real, positive, simple and dominant (Péron-Frobenius theorem, Caswell, 1989), which represents the growth rate by unit of time (h days).

Under the best conditions (survival rate of adults $a_i = 1$; survival rate of pupae $\bar{s} = 1$; larviposition of a potentially female larva by a female every h days, which leads to $f_i = 0.5$), the maximum potential growth rate approximately linearly decreases when pupal period $\bar{x}$ increases, from 1.22 for $\bar{x} = 25$ days to 1.18 for $\bar{x} = 45$ days. With an inter-larval period (h) of 10 days, these rates correspond to the production of 457 and 1566 females per female per year, respectively.

The effect of adult survival. This demographic parameter is important for the determination of a_i and f_i (see Appendix 1). In the first instance, we shall assume a constant survival ($a_i = a$; $\forall i$). Figure 3 represents the trend in growth rate according to a for three
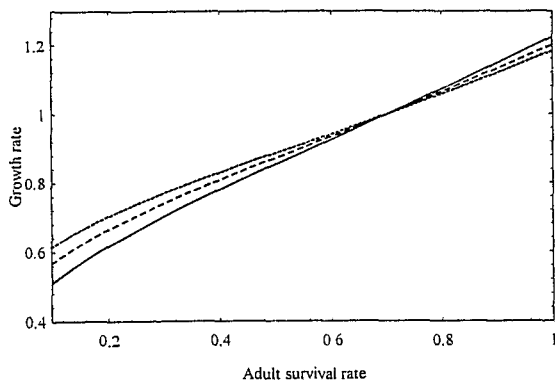
Fig. 3. Influence of the adult survival rate (a) on the growth rate (λ) for three pupal life span: short ($\bar{x} = 25$ days [—]), medium ($\bar{x} = 35$ days [- - -]) and long ($\bar{x} = 55$ days [...]) when the larval survival rate is maximal ($\bar{s} = 1$).
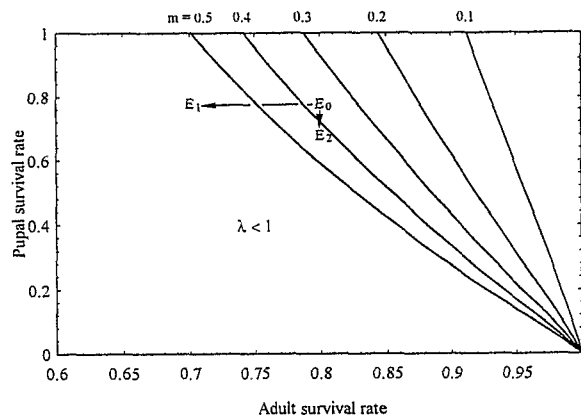

Fig. 4. Values of pupal and adult survival rates giving a demographic equilibrium (growth rate $\lambda = 1$) with different values of potential female fecundity by unit of time (h days) and pupal life span of 35 days. The arrows illustrate an example of change in the population dynamics from E_0 to E_1 (decrease in the adult survival rate of 0.1) or from E_0 to E_2 (decrease in the pupal survival rate of 0.1). Note that only the situation E_1 corresponds to a clearly negative growth rate.

pupal periods (short, medium, long) without pupal mortality ($\bar{s} = 1$) and with a constant potential fecundity $m = 0.5$ (see Appendix 1 for calculation of f_i). When adult survival is low, an increase in the pupal period increases the growth rate of the population. On the contrary, when the adult survival is high, the relationship is inverted and the maximum value of λ is obtained for the shortest pupal period ($\bar{x} = 25$ days). The reason is that long pupal development slows down both population growth (for high adult survival) and population extinction (for low adult survival). As a result, long pupal development decreases the slope of the lines in Fig. 3, bringing the lines to cross exactly for $\lambda = 1$.

It can be seen that the value a corresponding to $\lambda = 1$ (population numerically stable) does not depend on the pupal period. In this case, a is equal to 0.70, which corresponds to a daily survival of 0.965 (with $h = 10$ days). Near this equilibrium, the pupal period does not have much effect on the growth rate.

This global effect of adult survival is conserved for values of m and $\bar{s}$ inferior to the maximum values ($m = 0.5$ and $\bar{s} = 1$), but the influence of pupal period is less when m and $\bar{s}$ decrease.

Relationships between average pupal survival ($\bar{s}$) and adult survival (a) for various values of potential fecundity over h days (m). Figure 4 summarizes the relationship between the various parameters to obtain a growth rate $\lambda = 1$, with the pupal period fixed at 35

days. The area enabling demographic growth ($\lambda > 1$, part above the graphs $\lambda(a) = 1$ for each given value of m) is relative limited even if m is at its maximum value (0.5). For example, for $\bar{s} = 0.80$ and $m = 0.5$, a must be larger than 0.75 to get a population growth. This value of a represents a daily survival of over 0.971. This daily survival must be over 0.976 for $m = 0.4$ to maintain $\lambda > 1$.

Sensitivity analysis of the growth rate λ. The calculation of the sensitivity of the growth rate λ to changes in the coefficients of matrix A is given in Appendix 2.

The global sensitivity to a constant survival rate of adults a (see equation A.9) is equal to 0.77 in the theoretical case of maximal growth ($\bar{s} = 1$; $\bar{x} = 25$; $a = 1$) and equal to 0.69 with estimations of Challier (1973; $\bar{s} = 0.82$; $\bar{x} = 31.4$; $a = 0.776$).

Global sensitivity of λ to pupal survival rate is more complex because of the variability of pupal duration and the relationships between p_i and e_i. However, equation A.8 can be used for classes P_0 and P_1, where they are not emergences. The sensitivity of λ to these two classes is about 0.18–0.19 and 0.12–0.13 for the two data sets considered (Fig. 5).

Figure 5 also shows the changes in the sensitivity of λ according to the age classes. The overall pattern of the curves is the same for the two data sets. It clear-
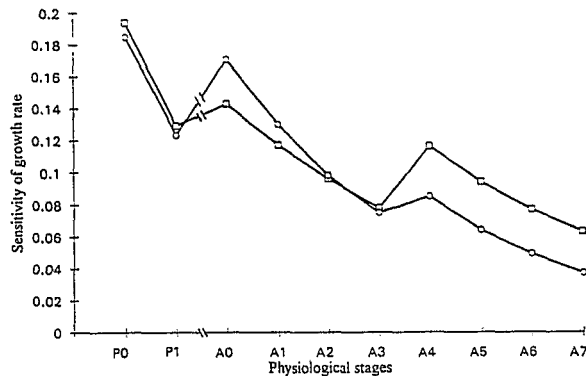
Fig. 5. Sensitivity of the growth rate λ to fluctuations in survival rates of various physiological stages. □: maximal growth ($\bar{s} = 1$; $\bar{x} = 25$; $a = 1$; $\lambda = 1.2233$) o: estimations of Challier, 1973 ($\bar{s} = 0.82$; $\bar{x} = 31.4$; $a = 0.776$; $\lambda = 1.0232$).

ly shows the importance of the A_0 class (nulliparous females) and increase in class A_4 which corresponds to an accumulation of females of different ages $(4 + 4n)$ in this class (see Materials and methods).

Discussion

Our results do not differ significantly from those obtained by Hargrove (1988). This author found that in the absence of pupal mortality and with the highest possible fecundity, the adult daily survival was 0.96. The results obtained with this model are 0.965. This slight difference probably occurs from the approximation made on the fecundity (see Appendix 1, equation A.1) which Hargrove (1988) did not carry out. Indeed, if the correction is not done, our model provides exactly the same value as that obtained by Hargrove (1988).

The correction on fecundity also affects the estimates of the annual production of females per female, which is important information for assessing the levels obtained in mass production of tsetse fly (mass rearing for control by the sterile-male technique, for example). Our estimations (between 457 and 1566 females per female per year depending on the pupal period) are lower than those given by Hargrove (1988) but are comparable to the data of mass rearing (400–550 females per female per year for G. morsitans morsitans Westwood (Jordan & Curtis, 1972); 308–552 females per female per year for G. austeni Newstead (Curtis & Jordan, 1968)).

The possibilities of strong growth of Glossina populations seem therefore relatively limited as shown in Fig. 4. This figure also suggests that it is more effective to modify adult mortality than pupal mortality, but this impression is biased by the fact that adult survival is established over about ten days whereas pupal survival represents the whole precise information. An equal decrease of adult survival rate in all the age classes can effectively limit the growth rate. For example, with the field data of Challier (1973), a decrease of survival rate a from 0.776 to 0.740 is enough to obtain a growth rate lower than 1.

However, Fig. 5 shows that the growth rate λ is particularly sensitive to changes in the survival rate a_0 of young nulliparous females in relation to older ones. If this age class escapes a given method of control, the effectiveness of the method will be strongly reduced. Gouteux (1987) pointed out that the spatial occupation of females varies according to their age; so, the effectiveness of trapping control will depend on the precise location of the traps (Gouteux et al., 1986). For example, in the pre-forested area of Ivory Coast during the rainy season, Gouteux & Laveissière (1982) showed that nulliparous females represented 4% of the total number of females of G. p. palpalis caught by biconical traps in sunny sites. In shaded sites near water holes, this proportion reached 22%. During the dry season, these proportions were respectively 20 and 40%. Nevertheless, traps and targets catching pattern are generally biased against young females (see Hargrove 1990, 1991 and 1993), for savannah species G. m. morsitans and G. pallidipes).

Concerning the control of tsetse pupae, Hargrove (1988) states: 'At inter-larval periods of 10 days, a tsetse population could still have a positive growth rate with 60% pre-adult losses as the adult mortality is kept at not more than about 1.5% per day ...' and concluded: 'Tsetse control by way of killing the pre-adult phases, for instance by release of larval/pupal parasites, would thus seem to be a very difficult proposition'. Our theoretical results (Fig. 5) nevertheless show that pupal control could be envisaged if most young females escape trapping. Indeed, the sensitivity of λ for P_0 and P_1 classes is of the same order as for young females classes (A_0 and A_1). The question remains, how to kill the pupae.

This model is currently being developed as a tool for the prediction and control of Glossina and the preliminary conclusions need to be confirmed. Its usefulness is not limited to the theoretical study of the possibility of growth of a tsetse fly population. Subject

to a suitable procedure for estimating the parameters, it seems to be well adapted to several types of data. It should enable the seasonal fluctuations of the growth rate to be monitored, and imporve the understanding of the factors which regulate the populations dynamics. The matrix approach is extremely flexible. For example, the number of pupal stages can be increased to obtain pupal periods of over 45 days. Formally, these matrix model are based on the same principals as the model using life tables (Ryan, 1980; Taylor, 1979; Allsop, 1985; Williams *et al.*, 1990). They provide a more convenient tool for field workers. For these reasons and because of the unacceptability of models using the fluctuation in apparent density to estimate the mortality rates by auto regression, we consider them to be more promising.

The remaining problem is that of the identifiability of our model in relation to the ovarian age data. Most estimation methods available in the literature assume a population in equilibrium ($\lambda = 1$ or r, intrinsic rate of increase, $= 0$). It is thus incorrect to use these methods to calculate the growth rate later. This problem, explained clearly by Van Sickle (1988), is not easy to avoid. Hargrove (1993), using the maximum likelihood method, gave an estimation of $(\lambda + \mu)$ where μ is the adult mortality. This mortality can be estimated if the growth rate λ is known. In the same way, Van Sickle & Phelps (1988) proposed a solution based on an independent estimation of the intrinsic rate of increase r.

Moreover, these methods assume a constant adult survival. We ourselves put forward this hypothesis to facilitate our theoretical approach, but it is clear that adult survival depends on the age (Gouteux & Kienou, 1982 and Hargrove, 1990, in fields; Jordan & Curtis, 1972, in laboratory). This simplification is thus not entirely satisfactory and we are currently working on this problem particularly taking into account the difference between nulliparous (A_0), young (A_1 to A_3), and older (A_4 to A_7) female survival rates.

Another way is to estimate survival rates, which ensures total independence of these estimations and demographic models. The Jolly-Seber model (Jolly, 1965) used by Gouteux & Buckland (1984) can be improved (see Lebreton *et al.*, 1992). Capture-recapture is particularly interesting, given the characteristics of the tsetse fly (easy to mark, relatively long life span) and the development of simple trapping techniques which are more reliable than hand-net catching (Gouteux & Dagnogo, 1986). Recent progress in data analysis (Anderson *et al.*, 1993) further support this alternative.

References

Allsop, R., 1985. Variation in the rates of increase of *Glossina morsitans centralis* and their relevance to control. Journal of Applied Ecology 33: 91–104.

Anderson, D. R., M. A. Wotawa & E. Rexstad, 1993. Trends in the analysis of recovery and recapture data. In: J. D. Lebreton & Ph. M. North (eds), Marked Individuals in the Study of Bird Population, Birkhaüser, Verlag, Base: 373–386.

Anderson, R. M. & R. M. May, 1982. Population biology of infectious diseases. Report on the Dahlem Workshop on population biology agent. Berlin. Springer-Verlag, 14–19.

Andrewartha, H. G. & L. C. Birch, 1956. The Distribution and Abundance of Animals. University of Chicago Press, Chicago.

Bailey, N. T. J., 1975. The Mathematical Theory of Infectious Diseases and its Application. London, Griffin.

Caswell, H., 1989. Matrix Population Models. Sinauer Associates Inc., Sunderland.

Challier, A., 1965. Améloriation 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. & D. A. Turner, 1985. Methods to calculate survival rate in tsetse fly *(Glossina)* populations. Annales de la Société Belge de Médecine Tropicale 65: 191–197.

Curtis, C.F. & A. M. Jordan, 1968. Calculations of the productivity of *Glossina austeni* Newst., maintened on goats and on lop-eared rabbits. Bulletin of Entomological Research 59: 651–658.

De Muynck, A. & D. J. Rogers, 1989. Towards a quantiative epidemiology of Human Sleeping Sickness. In: A. De Muynck & D. J. Rogers (eds), Workshop on modelling sleeping sickness epidemiology and control, Antwerp, 25–29 January 1988, Annales de la Société Belge de Médecine Tropicale, 69, Suppl. 1: 11–13.

Deevey, E. S., 1947. Life tables for natural populations of animals. Quarterly Review of Biology 22: 283–314.

Dransfield, R. D. & R. Brightwell, 1989. Problems of field testing theoretical models: a case study. Annales de la Société Belge de Médecine Tropicale, Supplément 1: 147–154.

Gettinby, G., 1989. Understanding infectious diseases: modelling approaches for the trypanosomiases. Annales de la Société Belge de Médecine Tropicale 69: 21–30.

Gettinby, G. & S. McClean, 1979. A matrix formulation of the life cycle of liver fluke. Proceedings of the Royal Irish Academy, 79B: 155–167.

Glasgow, J. P., 1963. The distribution and abundance of tsetse. International Serie Monography of Pure and Applied Biology, Division of Zoology, 20. Pergamon Press, Oxford, 241 pp.

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 de l'ORSTOM, Série Entomologie Médicale et Parasitologie 20: 189–197.

Gouteux, J. P., 1985. Ecologie des glossines en secteurs pré-forestier de Côte d'Ivoire. Annales de Parasitologie Humaine Comparée 60: 329–347.

Gouteux, J. P., 1987. Ecodistribution de Glossina palpalis (Rob.-Desv.) en secteur pré-forestier de Côte d'Ivoire. Sexe, rythmes ovaro-utérins et utilisation de l'espace. Acta Oecologica, Oecologia Applicata 8: 27–38.

Gouteux, J. P. & J. P. Kiénou, 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 de l'ORSTOM, Série Entomologie Médicale et Parasitologie 20: 41–61.

Gouteux, J. P. & C. Laveissière, 1982. Ecologie des glossines en secteur pré-forestier de Côte d'Ivoire. 4. Dynamique de l'écodistribution en terroir villageois. Cahiers de l'ORSTOM, Série Entomologie Médicale et Parasitologie 20: 199–229.

Gouteux, J. P. & S. T. Buckland, 1984. Ecologie des glossines en secteur pré-forestier de Côte d'Ivoire. 8. Dynamique des populations. Cahiers de l'ORSTOM, Série Entomologie Médicale et Parasitologie 22: 19–34.

Gouteux, J. P. & M. Dagnogo, 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 de l'ORSTOM, Série Entomologie Médicale et Parasitologie 24: 99–110.

Gouteux, J. P., J. Lancien, F. Noireau & D. Sinda, 1986. Lutte antivectorielle par piégeage et impact sur la transmission de la maladie du sommeil dans une zone à forte densité de Glossina fuscipes quanzensis (Rivière Léfini, République populaire du Congo). Tropenmedizin und Parasitologie 37: 101–104.

Grassé, P. P., 1951. Traité de Zoologie. 10, Masson, Paris, 1940 pp.

Hargrove, J. W., 1988. Tsetse: the limits to population growth. Medical and Veterinary Entomology 2: 203–217.

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: Glosinidae) 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. In: Management of Insect Pests: Nuclear and Related Molecular and Genetic Techniques, International Atomic Energy Agency, Vienna, pp. 549–556.

Ito, Y., 1972. On the methods for determining density-dependence by means of regression. Oecologia 10: 347–372.

Jackson, C. H. N., 1933. The causes and implications of hunger in tsetse flies. Bulletin of Entomological Research 24: 443–482.

Jarry, M., M. Khaladi, M. Hossaert-McKey & D. McKey, 1995. Modeling the population dynamics of annual plants with seed bank and density dependent effects. Acta Biotheoretica 43: 53–65.

Jolly, G. M., 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika 52: 225–2247.

Jordan, A. M. & C. F. Curtis, 1982. Productivity of Glossina morsitans Westwood maintained in the laboratory, with particular reference to the sterile-insect release control. Bulletin of World Health Organisation 46: 33–38.

Khaladi, M., M. Jarry & M. Hossaert-McKey, 1995. A model for annual plant dynamics with seed bank and density dependent effects. Journal of Biological Systems 3(2), in press.

Lebreton, J. D., 1982. Modèles dynamiques déterministes définis par des équations de récurrence, In: J. D. Lebreton & C. Millier (eds), Modèles Dynamiques Déterministes en Biologie, Masson, Paris, pp. 58–98.

Lebreton, J. D., K. P. Burnham, J. Clobert & D. R. Anderson, 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62(1): 67–118.

Leslie, P. H., 1945. On the use of matrices in populations mathematics. Biometrika 33: 182–212.

Leslie, P. H., 1948. Some further notes on the use of matrices in population mathematics. Biometrika 35: 213–245.

Lotka, A. J., 1907. Relation between birth rates and death rates. Science 26: 21–22.

Maelzer, D. A., 1970. The regression of $Log(N_{n+1})$ on $Log(N_n)$ as a test of density-dependence: an exercise with computer constructed density independent population. Ecology 51: 810–822.

Pianka, E. R., 1970. On r- and K-selection. American Naturalist 104: 592–597.

Rogers, D. J., 1979. Tsetse population dynamics and distribution: a new analytical approach. Journal of Animal Ecology 48: 825–849.

Rogers, D. J., 1990. A general model for tsetse populations. Insect Science and its Application 11: 331–346.

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

Rogers, D. J., S. E. Randolph & F. A. S. Kuzoe, 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.

Ryan, L., 1981. Glossina (Diptera: Glossinidae) growth rates. Bulletin of Entomological Research 71: 519–531.

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. Transaction 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.

Taylor, P., 1979. The construction of a life-table for Glossina morsitans morsitans Westwood (Diptera: Glossinidae) from seasonal age-measurements of a wild population. Bulletin of Entomological Research 69: 553–560.

Timischl, W., 1981. Optimization of productivity in the rearing of tsetse flies (Diptera: Glossinidae). Zeitschrift für Angewandte Entomologie 3: 301–309.

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. & R. J. Phelps, 1988. Age distributions and reproductive status of declinary and stationary populations of *Glossina pallidipes* Austen in Zimbabwe. Bulletin of Entomological Research 78: 51–61.

Williams, B. G., R. D. Dransfield & R. Brightwell, 1990. Tsetse fly (Diptera: Glossinidae) population dynamics and the estimation of mortality rates from life-table data. Bulletin of Entomological Research 80: 479–485.

Appendix 1: Parametrization of the model

In this Appendix we will not tackle the problem of parameters estimation from field data, which will be the object of a later work. The question is here how to calculate the coefficients of matrix A from demographic parameters, chosen a priori or available in the literature.

Adults survival rate

Various methods of estimating the adult survival rate have been put forward (Gouteux, 1982; Rogers & Randolph, 1984; Rogers *et al.*, 1984; Challier & Turner, 1985; Hargrove, 1993). The data available in the literature will be taken as an example, without discussing the validity of these methods.

Potential and approximated fecundity

Each female lays one larva every h days. Thus, potential fecundity on this period is 0.5 females/female. However, because of the adult mortality between times t and $t + 1$, the fecundity of a female of class i is approximated by:

$$\frac{m_i + a_i m_{i+1}}{2}$$

where m_i is the mean potential fecundity of females aged x, $i \leq x < i + 1$, on a period of h days.

Besides, at time $t + 1$, the number of pupae P_0 is not quite equal to the sum of larvae laid by the females during the interval $t, t + 1$; some of these will not survive during this interval of h days. Those laid just after t must survive almost h days to be included in P_0 class at time $t + 1$. Those laid just before $t + 1$ will be almost certainly included in P_0 class. An average larva must survive for one-half interval h, the probability of which is $(p_0)^{1/2}$, if we consider that the survival rate of a larva during h days is the same as the pupal survival rate p_0. Including this correction for the parameterization of the fecundity parameters, we obtain:

$$f_i \approx p_0^{\ 0.5} \left(\frac{m_i + a_i m_{i+1}}{2} \right). \qquad \text{(A.1)}$$

This equation has been adapted from those given by Caswell (1989, p. 11).

Pupal survival rate

Given the difficulty of obtaining suitable field data to compute the coefficients p_i and e_i, we propose to compute them from the mean pupal survival rate $(\bar{s})$ and from the mean pupal life span $(\bar{x})$.

The structure of the graph (Fig. 2) requires the following constraints:

$$\begin{cases} p_0 \leq 1; p_1 \leq 1; \\ p_i + e_i \leq 1 \text{ for } i = 2 \text{ and } 3; \\ e_4 \leq 1. \end{cases} \qquad \text{(C.1)}$$

If we assume that survival rate is constant about the pupal period life, we have:

$$p_0 = p_1 = p_2 + e_2 = p_3 + e_3 = e_4 = p. \qquad \text{(A.2)}$$

Thus, $\bar{s}$ and $\bar{x}$ can be related to p_i and e_i by:

$$\begin{cases} \bar{s} = p_0 p_1 (e_2 + p_2(e_3 + p_3 e_4)) \\ \bar{x} = \frac{25 e_2 + p_2(35 e_3 + 45 p_3 e_4)}{e_2 + p_2(e_3 + p_3 e_4)}. \end{cases} \qquad \text{(A.3)}$$

With $\alpha = \bar{x} - 25$, $\beta = \bar{x} - 35$, $\gamma = \bar{x} - 45$, equations (A.2) can be written:

$$\begin{cases} p_0 p_1 (e_2 + p_2(e_3 + p_3 e_4)) = \bar{s} \\ \alpha e_2 + \beta p_2 e_3 + \gamma p_2 p_3 e_4 = 0. \end{cases} \qquad \text{(A.4)}$$

Expressing p_0, p_1, e_2, e_3 and e_4 in function of p, p_2 and p_3, we obtain:

$$\begin{cases} ((1-p)p_2 + (1-p)p_2 p_3)p^2 = p^3 - \bar{s} \\ (\alpha + \beta p)p_2 + (\beta - \gamma p)p_2 p_3 = \alpha p \end{cases} \qquad \text{(A.5)}$$

and

$$\begin{cases} p_2 = \frac{\alpha p^3(1-p) - (\beta - \gamma p)(p^3 - \bar{s})}{10 p^2 (1-p)^2} \\ p_3 = \frac{10(p^3 - \bar{s})(1-p)}{\alpha p^3(1-p) - (\beta - \gamma p)(p^3 - \bar{s})} - 1 \end{cases} \qquad \text{(A.6)}$$

Constraints on $p(\bar{s} < p^3 < 1)$, due to (A.5), and those on p_2 and p_3 $(0 \leq p_2 \leq 1, 0 \leq p_3 \leq 1)$ lead us to frame p by $p_{\min}$ and $p_{\max}$, compute $p = \frac{p_{\min} + p_{\max}}{2}$, p_2 and p_3 by (A.6) and p_0, e_2, e_3 and e_4 by (A.2).

A program, written using *Mathematica*[R] language, allows to compute these different coefficients and the

dominant eigenvalue λ of matrix A from values of a, $\bar{s}$ and $\bar{x}$.

An example

Data from Challier (1973) concern *Glossina palpalis gambiensis*. Survival rate and pupal life span ($\bar{s}$ and $\bar{x}$) have been determined from controlled fields experiments in Kou forest (Burkina Faso, August 1966). Adult survival rates have been estimated from ovarian age distribution of sampled females by geometric mean method (Challier & Turner, 1985), and $h = 10$ days.

Input data:

Pupal survival rate: $\bar{s} = 0.82$;

Pupal life span: $\bar{x} = 31.4$ days;

Adult survival rates: $a = 0.776$ (daily survival rate $= a^{1/h} = 0.975$).

Parameterization of the model:

$p_{\min} = 0.947028$, $p_{\max} = 0.947284$

$p_0 = p_1 = e_4 = p = 0.947156$;

$p_2 = 0.468442$, $e_2 = 0.478714$;

$p_3 = 0.337299$, $e_3 = 0.609857$;

Fecundity ($f_i = f$, $\forall i$); $f = 0.4321$

These values give a growth rate $\lambda = 1.0232$.

Appendix 2: Sensitivity analysis

A simple formula to calculate the sensitivity of the growth rate λ to small changes in the matrix elements a_{ij} is given by Caswell (1989, p. 121):

$$\frac{\partial \lambda}{\partial \alpha_{ij}} = \frac{v_i w_i}{\langle v, w \rangle} \qquad (A.7)$$

where w and v are the right and left eigenvectors corresponding to λ and $\langle v, w \rangle$ is their scalar product.

However, this formula can be used if only one element a_{ij} is subject to change, while all the others are held constant. To take into account the relationships between f_i and a_i (see Appendix 1) we must use the general formula given by:

$$\frac{\partial \lambda}{\partial \alpha_{ij}} = \frac{1}{\langle v, w \rangle} \left(\sum_{p,q=1}^{n} v_p w_q \frac{\partial \alpha_{pq}}{\partial \alpha_{ij}} \right). \qquad (A.8)$$

Thus, the global sensitivity to survival rate of adults a (with $a_i = a$; $\forall i$) is:

$$\frac{\partial \lambda}{\partial a} = \frac{1}{\langle w, v \rangle} \left(\sum_{k=7}^{13} w_k v_1 \frac{m p_0^{1/2}}{2} + \sum_{k=6}^{13} w_k v_{k+1} + w_{13} v_{10} \right). \qquad (A.9)$$