A Diffusion Model for *Glossina palpalis gambiensis* in Burkina Faso

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ABSTRACT The dispersal of *Glossina* species is of interest to pest control personnel since these flies are the biological vectors of human and animal trypanosomes in Africa. The design of control and/or eradication programmes requires an accurate knowledge of the ecological characteristics of tsetse flies and the geographic structure of their populations. The present study attempts to model the dispersal process of a riverine tsetse species, i.e. *Glossina palpalis gambiensis* Vanderplank in Burkina Faso along an apparent homogeneous gallery forest. While for savannah species, dispersal is usually modelled as a two-dimensional random walk (in time and space) or diffusion (its continuous analogue), for riverine species, dispersal can be viewed more simply as a one-dimensional random walk. The data reported here show that the topology of the habitat, which is a system of tributaries rather than a straight line, has a great impact on the dispersal process. Moreover, since only a part of the river system can be observed in practice, the effect of partial observation when estimating dispersal parameters can be quantified. The results reported here were obtained using a data set from a mark-release-recapture experiment carried out with *G. p. gambiensis* on a tributary of the Mouhoun River in Burkina Faso. The model was fitted to field data and used to estimate the displacement of a fly during 10% of its lifespan (13 kilometres) and the probability of it dispersing more than 10 kilometres from its initial position ($P > 0.1$). The analysis was carried out by either taking into account, or ignoring, the fact that only part of the river system was observed during the mark-release-recapture protocol.

KEY WORDS dispersal, tsetse fly, *Glossina palpalis gambiensis*, diffusion model, mark-release-recapture

1. Introduction

In West Africa, climate and land use pressures result in fragmentation of tsetse fly habitats, especially at the northern end of their distribution areas (Hendrickx et al. 2004). Residual subpopulations, surrounded by semi-permanent barriers (particularly cotton crops), are increasingly isolated and can become a priority target for sustainable control. If the tsetse population is not isolated, barriers of traps or screens impregnated with insecticides can be deployed, to prevent reinvasion (Cuisance and Politzar 1983, Politzar and Cuisance 1983, 1984), at least until the adjacent tsetse populations are suppressed. To establish these barriers, traps or screens are placed every 100 metres along five to ten kilometre river sec-

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tions. Control campaigns preferably target areas where agricultural barriers already exist, and the methods used vary in their cost effectiveness depending on their reliability and the overall objective, i.e. eradication or suppression (IAEA/FAO 2001). Information about the degree of isolation between populations can be very useful for the design, implementation and monitoring of area-wide integrated pest management programmes (AW-IPM), especially when resources are limited.

The cotton belt of Mali and Burkina Faso has been identified as a priority area for tsetse control because of the potential benefits associated with the removal of trypanosomosis (Hendrickx et al. 2004). In Burkina-Faso, riverine species (*Glossina palpalis gambiensis* Vanderplank and *Glossina tachinoides* Westwood) are the main vectors of African animal trypanosomosis, since the only savannah species (*Glossina morsitans submorsitans* Newstead) is now restricted to protected areas in the south of the country. Current studies on the population dynamics of vector species therefore focus on the valleys and riverine forests, using remote sensing and ecological data to evaluate the feasibility of an eradication campaign based on area-wide principles and in support of the Pan African Tsetse and Trypanosomiasis Eradication Campaign (PATTEC) recently initiated in Burkina Faso (IAEA/FAO 2001). In particular, researchers and programme managers are interested in the degree of isolation of vector populations, or conversely their ability to disperse as estimated by migration rates between favourable landscapes. For this purpose, both mark-release field experiments and population genetic analyses have proven to be very efficient tools (Solano et al. 2000, Krafsur and Endsley 2002, Krafsur 2003).

The methodology for estimating diffusion parameters by mark-recapture methods is now robust for species dispersing in two dimensions (Okubo and Levin 2001). For the savannah species of tsetse, such as *Glossina morsitans morsitans* Westwood, diffusion models have been successfully applied to model the dispersal process (Bursell 1970, Hargrove 1981, Hargrove and Lange 1989, Hargrove 2000). However, for tsetse flies dispersing along gallery forests, these are less well developed (Rogers 1977, Randolph and Rogers 1984, Cuisance et al. 1985).

Before addressing the problem of dispersal in fragmented landscapes, the present study analyses data obtained in a homogeneous riverine forest to understand the impact of river structure on the dispersal characteristics of riverine tsetse (Cuisance et al. 1985). In particular, account is taken of the fact that a river cannot be considered as a straight line but rather as a river system. As underlined by Buxton (1955):

> *The fly belt occupied by* G. palpalis *is nearly always along the waterside. [...] It is known that the insect moves very freely up or down stream or up a tributary. [...] Evidently then the width of the zones varies, but spontaneous movement of the insect is so closely confined to the vicinity of water that it is almost linear.*

2. Materials and Methods

2.1. Field Data

The mark-release-recapture data were collected in 1981 (Cuisance et al. 1985) on the Dienkoa River, a tributary of the Mouhoun River in Burkina Faso. Forty-three biconical traps were deployed at distances of approximately 500 metres over a distance of 20 kilometres along the main stream. The river section under study was bordered by a homogenous closed Guinean riparian forest. Trap locations (Fig. 1) were digitized from a Landsat Thematic Mapper image (pixel 30 metres x 30 metres) from December 2000 (cool dry season) using the original and very detailed field map (Cuisance et al. 1985).

For this study, the data obtained from the release of 8683 three-day-old male *G. p. gambiensis* were analysed. The flies were from the Centre de Recherche sur les Trypanosomoses Animales (CRTA) insectary and were fed once on a rabbit on the day before release. They were not irradiated before release. Ten weekly releases, which were not analysed by

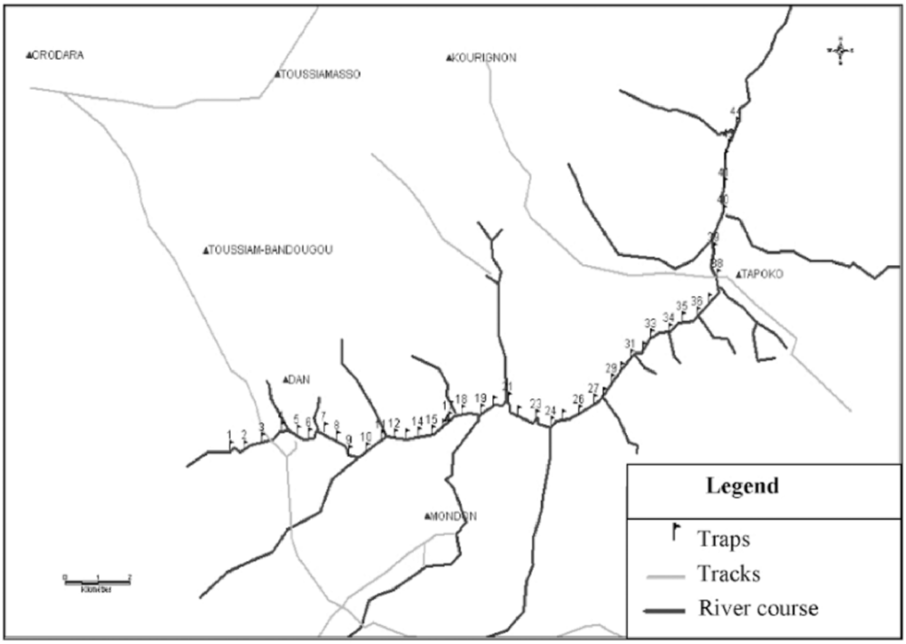

Figure 1. Location of the biconical traps of the 1981 study along the Dienkoa river.

Cuisance et al. (1983), were performed between May and August 1981. During these releases, the initial release point (Fig. 1) was located in the middle of the trapped section. Flies were marked on their pronotum with a dot of acrylic paint, the colour of which indicated the week of their initial release. Captures were performed three times per week with traps set from 08.00 hours to 16.30 hours each trapping day (On three days with heavy rain, traps could not be checked and only releases were carried out). Marked tsetse flies were released again at the location where they were captured.

Trapping was terminated at the same date for all cohorts so that data represent various times from the release of the cohorts (15 and four weeks for the first and last cohorts respectively). The data available are of two types: total trap catches by time elapsed from release cumulated over all ten cohorts (Cuisance et al. 1985), and a set of data obtained from Cuisance's diary corresponding to daily data cumulated for all traps.

2.2. Models

A discrete isotrope random walk (same probability of going up- or downstream one distance unit at each time unit), was used to model tsetse dispersal. It can be regarded as the simplest individual-based model of dispersal in one dimension. The model's assumptions are that, during one time unit (τ) a single fly will travel exactly one unit length (λ) either to the right or left with equal probability.

In this case, if the number of time steps n is large, and denoting:

$$x = m\lambda,\ t = n\tau$$

it can be shown that the probability density of the position at time t converges towards the density of a centred Gaussian random variable with variance $2Dt$, where D is the so-called diffusion coefficient and is equal to $\lambda^2/2\tau$ (Williams et al. 1992).

Since mortality appears as the main cause of the end of the diffusion process, zero diffusion was used to model the progress of fly dispersal. Such a model amounts to stopping an

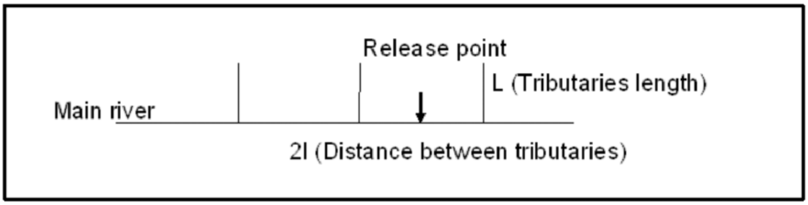

Figure 2. *Symmetric systems used for the simulations.*

individual's trajectory after a random time representing the individual's lifespan. Since the mortality rate between the first release and first recapture cannot be disentangled from the overall recapture rate, and since the mortality rate appeared almost constant during the later stages of the releases, a constant mortality rate, μ was used throughout (the model can however be easily extended to more accurate data on fly mortality). The parameter μ was roughly estimated as the log-regression coefficient of the number of recaptured flies against time. Based on the homogeneity of the gallery and trapping conditions, two strong assumptions had to be made, i.e. the time and space independence of capture and mortality rates.

The model was first applied on a theoretical system of tributaries, comprising an infinite main river where diffusion originates, and one or several tributaries connected to the main stream at definite locations (Fig. 2). Boundary conditions were isotropic at bifurcations (when a fly came to a junction between a tributary and the main river it had equal probability of going up the tributary, or up or down the main stream), and reflexive at the end of tributaries (when it reached the end of a tributary it always came back down at the next step). In order to assess the effects of geometry on the diffusion process, configurations with n = 2 and n = 10 tributaries were studied. To obtain a symmetrical process, the release was simulated in the centre of two tributaries distant of 2l (Fig. 2): the distance between the origin of the process and the next tributary was thus set to l = 1, and the diffusion coefficient was such that $2D = 1$. Several lengths of tributaries (L = 1, 3, 10) were used in the simulations.

The model's parameters (D, μ) were then estimated using the field data set and following two assumptions: (1) the trapping system allows a complete observation of the dispersal process which occurs only along the main river, and (2) the trapping system allows only a partial observation of the dispersal process which occurs throughout the whole river system (river basin with all its tributaries).

Finally, two "summary statistics" were calculated using the two-parameter estimations in a hypothetical case where two populations are ten kilometres apart on a straight river course without tributaries: (1) the distance to the origin exceeded during 10% of the fly's average lifespan, and (2) the probability of a fly travelling beyond a given distance to the origin. Details of the mathematical process will be described elsewhere (Sibert et al., in preparation).

3. Results

3.1. Theoretical Systems

The effects of considering only the main river for estimating D and μ while dispersal occurs throughout a river system was investigated using a variety of symmetric and asymmetric river systems. The results of the simulations depend on the complexity of the river system and the value of the diffusion coefficient. The results from the nine theoretical symmetric river systems (Fig. 3) are only illustrative but they use a realistic D, namely 0.5 square kilometres per day and a realistic river system,

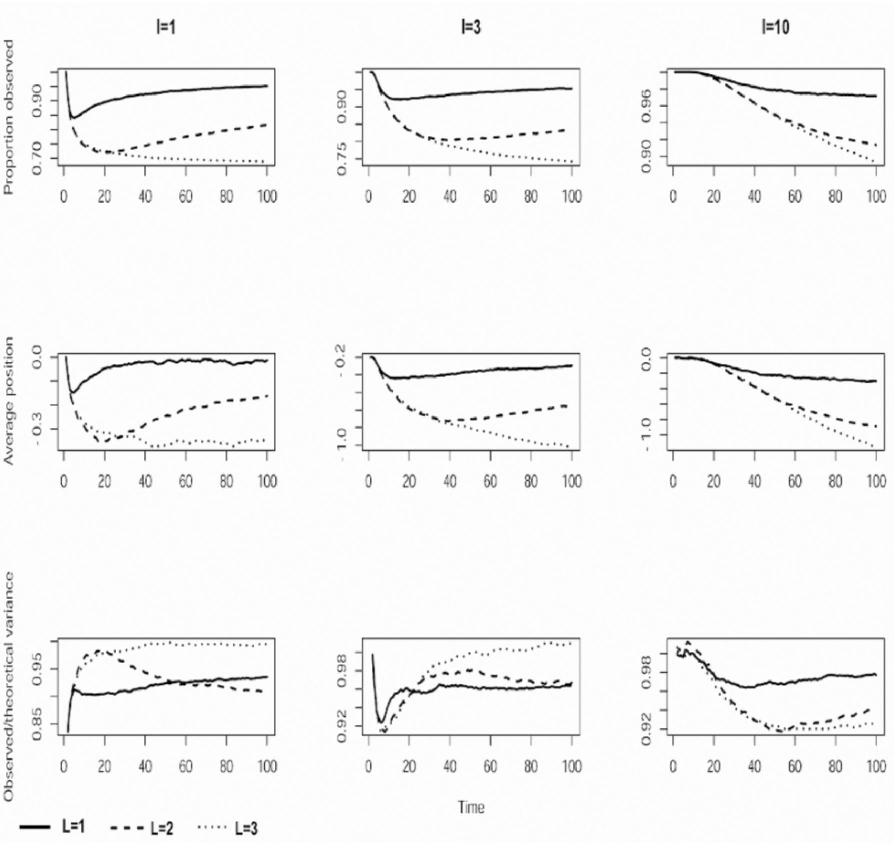

Figure 3. *(upper graphs) Proportion of flies observed on the main river, (middle graphs) average position in kilometres, and (lower graphs) ratio between observed and real variance in function of time (in days) in nine hypothetical river systems (n=10, L=1, 2 or 3 and l=1, 3 or 10).*

with ten tributaries. To appreciate the potential impact of partial observation on the estimation of D and μ, three variables are illustrated: (1) the proportion of flies observed on the main river (to illustrate the effect of partial observation on the estimation of mortality rates), (2) the average position of the population (to show that an isotropic random walk can lead to an apparent displacement of the population on the observed section), and (3) the ratio between observed and actual variance (to illustrate the impact of partial observation on the estimation of the diffusion coefficient (Fig. 3).

From the simulations, it is clear that spatial sampling, i.e. observing only the main river with traps while dispersal occurs on the whole river system, can lead to overestimation of mortality rates by up to 30% at day 40 (Fig. 3, first column, first line). The average position of the population on the main course can evolve up to one kilometre from the release position (Fig. 3, third column, second line), towards the centre of gravity of the system, leading to an apparent drift of the population, which would be impossible if the diffusion process occurred in an infinite symmetrical system. Finally, the variance in position (proportional to the diffusion coefficient) can be underestimated by 15% in the case of complex systems (Fig. 3, first column, third line).

3.2. Real Data Set

With the real data set presented above, D and μ could be estimated depending on two different assumptions: (1) dispersal occurs only on the main river and the trapping system provides complete information, and (2) dispersal occurs on the whole river system and the data set is thus spatially sampled.

If dispersal occurs only on the main river, a complete observation of a random walk on a straight line can be implied. Daily mortality rate estimated over the first month is then 6.5%, corresponding to a mean lifespan of 15.5 days. The corresponding diffusion coefficient is 0.29 km^2/day.

In the alternative hypothesis (partial observation of a random walk on a tree), the estimated mortality rate is only 4.4%, corresponding to a mean lifespan of 22.7 days. The diffusion coefficient is 0.46 km^2/day.

The two estimation errors due to spatial sampling demonstrate the same tendency, i.e. an underestimation of the probability of long-distance movement in the case of partial observation. When the model coefficients are corrected for the partial observation bias, the average distance covered by a fly during 10% of its lifespan increases from four to 13 kilometres. At the same time, the probability of a fly reaching a population located ten kilometres away increases from less than 0.01 to more than 0.1. In other words, the (apparent) displacement – and the (apparent) probability of reaching another population – is much lower than it is if only the data from the main river are included.

4. Discussion

The estimates of mortality rate obtained from the raw data are 30% lower when a partial system of tributaries is assumed (0.040 versus 0.065). However, mortality remains very high for this highly favourable environment (closed and conserved Guinean gallery forest). Density-dependent factors may induce an increase of mortality rates next to the release points due to increased local density (Rogers and Randolph 1984). The assumption of a constant mortality rate in space is then not valid as the fly density will be higher at the release point, at least during the releases and maybe during the following days. In all cases, taking into account the spatial complexity seems very important when estimating mortality rates, in the case of sterile insect releases for example. Moreover, dispersal over the entire available system (including the tributaries) may be considered as a way to reduce mortality density-dependent factors as much as possible.

The structure of a river system is not static in time, but evolves with macro-climatic variations through seasons. In the hot dry season, the small tributaries are drained and become unsuitable for tsetse survival, leading to their concentration in the moister section, i.e. in the main river. While dispersing with the same diffusion coefficient on either the entire system or the main course only, the probability of long-distance movements on the main river will increase, thereby enhancing long-distance dispersal during the dry season. Thus, on the one hand, tributaries can act as brakes to longitudinal movements particularly during the rainy season while, on the other hand, the mortality rate will decrease as relative humidity increases during the rainy season. These two parameters have thus opposing effects on long-distance dispersal.

In the model used, the two-dimensional structure of the system was not taken into account, and the possibility cannot be excluded that some flies escaped from the gallery (main stream or tributaries) and re-entered the system at some other point. However, during the release period (beginning of the rainy season), 145 traps were set in two circles located at one and two kilometres from the release point in the neighbouring savannah (Cuisance et al. 1983), and only 1.1% (36 from 3228) of the captured flies were caught outside the gallery. Moreover, as movement in the savannah is a two-dimensional diffusion, the latter environment can be considered less diffusive than the gallery itself and its contribution to long displacements along the main course can be neglected. During the rainy season however, riverine flies migrate into nearby savannah areas, especially while following their hosts, and their movement, perpendicular to the river systems, should be taken into consideration if attempting to estimate the probability of a river basin being "isolated" from another.

In the present work, the experimental site was chosen for its homogeneous, closed gallery. Provided that the spatial complexity is taken into account, a diffusion process was appropriate to describe tsetse fly dispersal. However, in fragmented landscapes, gallery forests are in fact very heterogeneous (Morel 1983). In such situations, a diffusion process may be unsuitable to describe fly dispersal, as the decision to disperse becomes a trade-off between a reduction in mortality-dependent factors and an increase in mortality-independent factors while moving from a favourable ecosystem (natural riverine forest) to a less favourable one (disturbed riverine forest) (Blondel 1995). Experimental releases integrating the lessons from the present work are presently being conducted in fragmented landscapes previously characterized by phytosociological analysis (Bouyer et al. 2005), to integrate spatial heterogeneity into dispersal models. In association with population genetics, these should be very useful in understanding the population structure within the Mouhoun river basin and may allow the identification of "natural" barriers in the planning of an AW-IPM programme in Burkina Faso.

5. Conclusions

A normal diffusion model can fit the data on riverine tsetse dispersal in homogeneous landscapes provided that the spatial complexity of the river system is taken into account. Daily mortality rate has an important effect on dispersal and especially on long-distance movements. Since they depend mainly on the season and the conservation status of the gallery forest, these elements may have a great impact on the tsetse dispersal process. Mark-release field experiments, supported by new techniques like dispersal models, remote sensing and geographic information systems (GIS) can be very useful in designing the sequential process of an AW-IPM project. They could also be used to optimize the releases of sterile flies during an eradication campaign.

6. References

Blondel, J. 1995. Biogéographie. Approche écologique et évolutive. Masson, Paris, France.

Bouyer, J., L. Guerrini, J. César, S. de la Rocque, and D. Cuisance. 2005. A phytosociological analysis of the distribution of riverine tsetse flies in Burkina Faso. Medical and Veterinary Entomology 19: 372-378.

Bursell, E. 1970. Dispersal and concentration of *Glossina*, pp. 382-394. *In* Mulligan, H. W. (ed.), The African trypanosomiases. George Allen and Unwin, London, UK.

Buxton, P. A. 1955. The natural history of tsetse flies. An account of the biology of the genus *Glossina* (Diptera). Lewis H. K. and Co. Ltd., London, UK.

Cuisance, D., and H. Politzar. 1983. Etude de l'efficacité contre *Glossina palpalis gambiensis* et *Glossina tachinoides* de barrières constituées d'écrans ou de pièges biconiques imprégnés de DDT, de deltaméthrine ou de dieldrine. Revue d'Elevage et de Médecine vétérinaire des Pays tropicaux 36: 159-168.

Cuisance, D., J. Février, J. Filledier, and J. Dejardin. 1983. Etude sur le pouvoir de dispersion des glossines. CRTA/IEMVT/OMS-83, Bobo Dioulasso, Burkina Faso.

Cuisance, D., J. Février, J. Dejardin, and J. Filledier. 1985. Dispersion linéaire de *Glossina palpalis gambiensis* et *G. tachinoides* dans une galerie forestière en zone soudano-guinéenne (Burkina Faso). Revue d'Elevage et de Médecine vétérinaire des Pays tropicaux 38: 153-172.

Hargrove, J. W. 1981. Tsetse dispersal reconsidered. Journal of Animal Ecology 50: 351-373.

Hargrove, J. W. 2000. A theoretical study of the invasion of cleared areas by tsetse flies (Diptera: Glossinidae). Bulletin of Entomological Research 90: 201-209.

Hargrove, J. W., and K. Lange. 1989. Tsetse dispersal viewed as a diffusion process. Transactions of the Zimbabwe Scientific Association 64: 1-8.

Hendrickx, G., S. de la Rocque, and R. C. Mattioli. 2004. Long-term tsetse and trypanosomiasis management options in West Africa. FAO, Rome, Italy.

(IAEA/FAO) International Atomic Energy Agency/Food and Agriculture Organization of the United Nations. 2001. Workshop on strategic planning of area-wide tsetse and trypanosomiasis control in West Africa. IAEA-63, Ouagadougou, Burkina Faso.

Krafsur, E. S. 2003. Tsetse fly population genetics: an indirect approach to dispersal. Trends in Parasitology 19: 162-166.

Krafsur, E. S., and M. A. Endsley. 2002. Microsatellite diversities and gene flow in the tsetse fly, *Glossina morsitans* s.l. Medical and Veterinary Entomology 16: 292-300.

Morel, P. C. 1983. Guide pour la détermination des arbres et des arbustes dans les savanes Ouest-Africaines. IEMVT, Maisons-Alfort, France.

Okubo, A., and S. A. Levin. 2001. Diffusion and ecological problems: modern perspectives. Springer-Verlag, New York, USA.

Politzar, H., and D. Cuisance. 1983. A trap-barrier to block reinvasion of a river system by riverine tsetse species. Revue d'Elevage et de Médecine vétérinaire des Pays tropicaux 36: 364-370.

Politzar, H., and D. Cuisance. 1984. An integrated campaign against riverine tsetse flies *Glossina palpalis gambiensis* and *Glossina tachinoides* by trapping and the release of sterile males. Insect Science and its Application 5: 439-442.

Randolph, S. E., and D. J. Rogers. 1984. Movement patterns of the tsetse fly *Glossina palpalis palpalis* (Robineau-Desvoidy) (Diptera: Glossinidae) around villages in the pre-forested zone of Ivory Coast. Bulletin of Entomological Research 74: 689-705.

Rogers, D. J. 1977. Study of a natural population of *Glossina fuscipes fuscipes* Newstead and a model of fly movement. Journal of Animal Ecology 46: 309-330.

Rogers, D. J., and S. E. Randolph. 1984. A review of density-dependent processes in tsetse population. Insect Science and its Application 5: 397-402.

Solano, P., S. de la Rocque, T. de Méeus, G. Cuny, G. Duvallet, and D. Cuisance. 2000. Microsatellite DNA markers reveal genetic differentiation among populations of *Glossina palpalis gambiensis* in the agropastoral zone of Sideradougou, Burkina Faso. Insect Molecular Biology 9: 433-439.

Williams, B., R. Dransfield, and R. Brightwell. 1992. The control of tsetse flies in relation to fly movement and trapping efficiency. Journal of Applied Ecology 29: 163-179.