LIVESTOCK PRODUCTION PROGRAMME

TSETSE MUSE: AN INTERACTIVE PROGRAMME TO ASSESS THE IMPACT OF CONTROL OPERATIONS ON TSETSE POPULATIONS.

Final technical report

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TABLE OF CONTENTS

Executive Summary

Animal trypanosomiasis, transmitted by tsetse flies, is a major constraint to livestock health and production over more than 10 million square kilometres of sub-Saharan Africa, resulting in annual losses worth an estimated ~US$4.5 billion. Recognising the enormity of the problem, the African Union established the Pan African Tsetse and Trypanosomiasis Eradication Campaign (PATTEC) to promote large-scale control operations using all available tsetse control techniques including bait technologies, ground- and aerial application of insecticides and the sterile insect technique. Towards this end, tsetse-affected countries are preparing and/or implementing national strategies to eliminate tsetse and there is a need for decision support tools to support this process.

This project developed a general simulation model to assess the efficacy and impact of any vector control technique, applied singly or in combination, against a population of tsetse. The model was incorporated into a user-friendly and interactive programme ('*Tsetse Muse*') which enables users without modelling expertise to compare the cost-effectiveness of strategies to control tsetse and undertake various 'what-if' analyses. Users of *Tsetse Muse* can define values for various parameters controlling both the dynamics of the tsetse population and the efficacy and cost of the control methods. To facilitate use, the programme can suggest appropriate values for these parameters based on results from published studies of tsetse biology and control. The programme was disseminated via the world-wide web (www.tsetse.org) and the distribution of ~350 CD-ROMs at dissemination workshops and meetings with potential users in Botswana, Ethiopia, Kenya, Tanzania, Uganda and Zimbabwe.

The value of the model was exemplified by using it to compare: 1) the sterile insect technique (SIT), involving weekly releases optimised at three sterile males for each wild male, and 2) insecticide-treated cattle (ITC) at 3.5/km^2. If SIT or ITC were used against an isolated population of tsetse, comprising 2500 males and 5000 females/km^2, then the population was eliminated within 187 days by ITC compared to 609 days for SIT. If ITC was used for 87 days to suppress the population by 99%, subsequent control by SIT alone took 406 days; the female population increased by 48% following the withdrawal of ITC and remained above the immediate post-suppression level for 155 days; the vectorial capacity initially increased seven times and remained above the immediate post-suppression level for 300 days. Combining SIT and ITC after suppression was a little faster than ITC alone provided the population had not been suppressed by more than 99.7%. Even when SIT was applied under favourable conditions, the most optimistic cost estimate was 20-40 times greater than for ITC. Modelling non-isolated unsuppressed populations showed that tsetse invaded ~8 km into the ITC area compared to ~18 km for SIT. There was no material improvement by using a 3-km barrier of ITC to protect the SIT area. In general, the simulations show that tsetse control by killing flies is more appropriate than reducing births. Tsetse Muse was also used to (i) assess the best use of baits to prevent reinvasion of areas cleared of tsetse, (ii) show how residual pockets of infestation arise and can be tackled, and (ii) address the risks associated with mosaics of contrasting control measures.

Articles demonstrating the use of *Tsetse Muse* and summarising some of the policy implications of the programme's outputs were published in *Medical and Veterinary Entomology* and *Trends in Parasitology* and presented at a meeting of the International Scientific Council for Trypanosomiasis and Control.

Background

Animal trypanosomiasis is a major constraint to agricultural production over more than 10 million square kilometres of sub-Saharan Africa. The disease is a serious constraint to livestock health and production, resulting in annual losses worth an estimated ~US$4.5 billion (Budd, 1999).

Progress in eliminating tsetse (*Glossina* spp.) and trypanosomiasis has been disappointingly slow (Maudlin *et al.,* 2004). The chief causes of this are debatable, but they include: wars and socio-economic instability, African governments being too poor to implement national control schemes and a dearth of adequately experienced veterinarians and entomologists. Thus, despite the development of new and improved tools to control tsetse, there has actually been a resurgence in trypanosomiasis in large parts of Africa: currently, an epidemic of Gambian sleeping sickness is sweeping across a swathe of Central Africa and the animal trypanosomiasis situation is deteriorating in southern Africa.

In the absence of help from governments or donors, farmers in tsetse-infested regions take action themselves, by administering trypanocides to their cattle and undertaking small-scale tsetse control operations using bait technologies. Such initiatives can have considerable local impact. A community-based control operation in the Kagera region of Tanzania for instance seems to have eliminated tsetse and trypanosomiasis from an area of 2500 km^2 where, prior to control, there were ~16000 cases of trypanosomiasis annually (Hargrove *et al.*, 2000). However, in many cases these local initiatives are often undertaken with inadequate – if any – expert guidance and thus the control method selected for a particular situation is often not the most appropriate, or is used incorrectly. Consequently, the scant resources of poor farmers are squandered on ineffective control operations (Brightwell *et al.,* 2001).

A means of improving the efficacy of community-based operations is suggested by the fact that tsetse control can be modelled convincingly (Hargrove, 2001; Hargrove, 2003; Hargrove *et al.*, 2003). Indeed, such models have been used to guide operations in Tanzania and Ethiopia. However, the models have generally been used only by the persons who produced them and the outputs are generally confined to specialist scientific lierature. It would be better to make available some models that are readily useable by non-specialists, and are generalised to offer wider ranges of inputs and outputs. Accordingly, DFID has supported the development of an interactive computer programme called 'Tsetse Plan'. This programme, which can be downloaded from the world-wide web (www.tsetse.org), offers help to NGOs and other agencies on the planning, budgeting and implementation of bait techniques, *ie*, the methods that are suitably cheap and simple for small-scale use by non-specialists.

Improving the efficacy of community-based operations will benefit local farmers. However, the number and size of these operations is tiny in comparison to the 10 million km^2 of Africa affected by trypanosomiasis. Recognising the enormity of the problem, the African Union launched the Pan African Tsetse and Trypanosomiasis Eradication Campaign (PATTEC) in 2001. This initiative aims to increase the impact on trypanosomiasis by promoting large-scale control operations supported by national and donor agencies. The campaign's proponents envisage using all available tsetse control techniques including bait technologies, ground- and aerial application of insecticides and the Sterile Insect Technique. Towards this end, tsetse-affected countries are currently being encouraged to prepare national stategies for eliminating tsetse

(Kabayo, 2004). In formulating these plans, it is necessary to assess the likely impact and cost of various control methods. Tsetse Plan can provide this for operations using bait technologies and the planners at the ADB have been using Tsetse Plan for this purpose. However, Tsetse Plan does not have a facility for assessing the impact of ground spraying, aerial spraying or SIT.

Assessing the impact of SIT is especially important. PATTEC has frequently stated that this technique will be used to eradicate tsetse following a period of suppression by more traditional techniques such as aerial spraying. The proposed use of SIT has generated considerable controversy. On the one hand, its proponents state that SIT is the 'most appropriate method for the final phase of eradication' (P. Holmes quoted in Taverne 2001) and '... not only takes care of the last fly in integrated campaigns, but also deals with newcomers in a clean area so that the pest cannot establish itself as a problem.' (U Feldmann & R. Mattioli quoted in Ahmed, 2003). On the other hand, opponents of the technique question its cost (Rogers & Randolph, 2002) and efficacy (Hargrove, 2003) or judge it to be 'inappropriate, unaffordable, unsustainable and irrelevant' (Molyneux, 2001).

An objective, quantitative model of the likely cost and impact of all the techniques, including SIT, would help the PATTEC initiative move from rhetoric to reality. In particular, an interactive programme that allowed users to consider the underlying biological and socio-economic processes is required. In this regard, the model should be widely and freely available in the public domain, the questions and input/output facilities should meet the requirements of the vast majority of tsetse workers, and the modelling methods and outputs should be available for scrutiny. Moreover, the modelling methods should be modified in the light of feedback from users, to ensure that the methods and outputs get a broad base of credence for policy decisions. By making the model, and a summary of its main implications, widely available, users could make different inputs, inspect the calculations and outputs, and so see if credible alternative implications are possible. Ultimately it should emerge more confidently, clearly and publicly what is and is not a sensible set of tsetse control options, with the opportunity to consider quickly the importance of new developments as they arise.

A prototype of such a programme was developed by Professor Vale and colleagues at the Natural Resources Insitute. Building on the methods and outputs from previous DFID-funded (AHP, LPP) projects, this project developed the model further to provide a means of assessing the impact and cost of any control intervention on tsetse populations. The model was incorporated into an interactive, user-friendly programme ('Tsetse Muse') that enable users to assess the outcome of various control campaigns given various assumptions specified by the user. The programme includes a user friendly interface so that users need not be specialist modellers.

To promote the programme, 'Tsetse Muse', supporting instructions and summaries were disseminated via the tsetse.org website and CD-ROM, in-country workshops and presentations at international scientific meetings.

Project Purpose

The project's purpose was to develop and disseminate a rational approach to supporting livelihoods of poor livestock-keepers through scaling-up of tsetse and trypanosomiasis control strategies. This was achieved by developing a decision support system to assist national (government veterinary departments) and regional institutions (PATTEC, ADB, UN agencies) to plan large-scale operations to control tsetse-borne trypanosomiasis.

Research Activities

Activity 1. Developing a quantitative model

Building on earlier work, a general simulation model of the impact of control operations on tsetse populations was developed.

The model

The tsetse population comprised: 1) pupae, 2) wild adult males, 3) sterile adult males, 4) virgin females, 5) breeding females, ie, fertile-mated in time to produce the next larva, 6) sterile-mated females, and 7) females that were fertile-mated, but too late to breed in the present larval cycle. The numerical and spatial distribution of each of these components was tracked deterministically in spreadsheets of Microsoft's Excel 2000. To do this, each component was covered by a life table (Focks *et al.*, 1993a,b). Rows were daily age classes, with the oldest flies at the top, and columns were different bands along a transect. The numbers displayed in each cell were determined by a formula behind the cell. Each of these formulae referred to the numbers displayed in cells below, ie, the numbers of flies one day younger, and calculated the daily changes due to natural and imposed deaths and losses or gains due to transfers between bands and population components. The spreadsheet was set to iterative mode so that the calculations moved in repeated waves down the tables, with each wave updating the displays by one day. After each wave the displayed data were summarised and plotted against time.

Values for the parameters controlling all calculations can be specified by the user. The default values, largely reflecting a savannah species of tsetse such as *G. pallidipes*, were as follows.

Standard population

The baseline tsetse population, pre-intervention, was stable at an average daily temperature of 25^{o}C (Table 1). Females mated only once and lived for up to 178 days, *ie*, just long enough to produce 19 larvae. Males had half the life span of females and mated with effectiveness independent of age after maturity. Females found a mate with daily probability of 0.10 if there was only one mature male per square kilometre. Females mated less than five days, *ie*, about half an interlarval period, before the due date for larval deposition did not produce a larva until the next due date.

Adult death rates, *ie*, the proportion dying each day, followed the pattern suggested by the mark and recapture data of Hargrove (1990), after allowing that the observed death rate for older flies was enhanced by frequent handling, especially for males (J. Hargrove, personal communication). Death rates were high during the first day of life, declining linearly to a minimum on the tenth day. For females this minimum was 10 % of the initial level and was maintained until day 50; for males the minimum was 20% of the initial level and was maintained until day 15. Thereafter the death rates increased linearly, to treble at maximum age, and were 1.00 when the maximum lifespan was exceeded. The absolute death rates required for stability were found by Excel's Goal Seek.

For males the daily random displacement was 100 m on the first day after emergence, increasing linearly to a maximum of 300 m at age 10 days, when flight muscles were regarded as fully developed. The maximum was maintained until age 25 days and then declined linearly, due to wing damage, to be 200 m at maximum age. For females the rate of displacement was greater (Vale *et al*, 1984), being 200 m on the first day, 600 m at age 10-50 days and declining to 400 m at maximum age.

Table 1. Features of the standard stable population, assumed to occur an average daily temperature of 25oC, before any intervention. All ages and periods are in days.

			Males	Females	Source [4]
Adult flies per square kilometre			2500	5000	G
Mean adult age			24	44	M
Pupal period			28	26	H
Age at sexual maturity			5	3	G
Age at first larval production			-	16	H
Interlarval period			-	9	H
Maximum adult lifespan			89	178	G
Death rate	Pupae, per pupal period		0.2500	0.2500	H
	Eggs/larvae, per larval period		0.0500	0.0500	H
	Adults, per day	Average[1]	0.0614	0.0307	M, H
		First day	0.1942	0.1362	M, H
		Young adult [2]	0.0194	0.0136	M, H
		Last full day [3]	0.0583	0.0409	M, H
Daily displacement, km, average[1]			249	367	M, V, L

[1] Rates vary with age, as discussed in the text.

[2] Days 10-25 for males, 10-50 for females.

[3] All remaining flies died at the start of the next day.

[4] G = Glasgow (1963). H = Hargrove (2004). L = Leak (1999). M = Model's calculations. V = Vale et al. (1984). References suggest values at or near those adopted.

Density dependence

It was assumed that field populations stabilise due to density dependent predation and parasitism (Rogers, 1974) and feeding success (Vale, 1977). Death rates for adults, pupae, and eggs/larvae were taken as minimal when population densities are 0-10% of the stable density, and to increase linearly with density above 10%. For death rates of adults and eggs/larvae the density reference was the abundance of all adults, *ie*, females plus wild and sterile males. For pupal mortality the reference was the daily rate of larval deposition, *ie*, 409/km^2/day at stability. It was assumed that the percentage contributions of density dependent factors to the stable standard rates of death were the same for each component of the population. It then remained to decide what this percentage contribution should be. The higher the contribution the greater the rate of growth when the population density is low enough for only density independent deaths to apply. If it is allowed that the contributions are 15, 20, 25, 30 and 35%, then in the absence of mating difficulties the annual growth of the population is 3.6, 5.5, 8.4, 12.9 and 19.6 times, respectively. The growth rate of 8.4 is close to the geometric mean of rates suggested by Hargrove (2004). Hence, it was taken that 25% of the deaths at standard stable density are density dependent.

Operational areas

The programme allowed consideration of tw types of area. The first was an isolated habitat with a uniform distribution of the standard population. The second was immediately next to an invasion source, separated from the operational area by an imaginary line called the invasion front. Most mainland situations are like this. For example, in Zimbabwe many operational areas are next to an invasion source provided by a wilderness or game reserve; the populations in the operational area are dense near the front but lower further away where heavy cultivation creates unsuitable habitat (Reid *et al.*, 2000). The model's map (Fig. 1) contained adjacent bands, 1 km wide and of effectively infinite length, running parallel to the invasion front. Although tsetse were considered to move in two dimensions, the habitat was assumed to change in only one, ie, between bands, not along them. This meant that the population could be modelled over a single transect, so ensuring that the calculations of tsetse movement were simple enough to be handled by most desktop computers. The transect ran from 20 km inside the invasion source to 40 km inside the operational area. To allow that the transect entered unfavourable habit in the distal parts of the operational area, all death rates were increased by 5% for every kilometre increase in distance beyond 5 km, to be 200% of the standard values at or beyond 25 km.

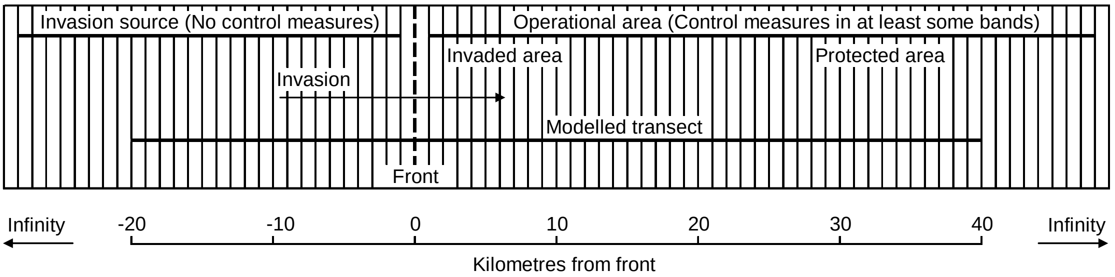


Fig. 1. Modelled transect though the non-isolated operational area and its invasion source. The whole of the mapped area consists of imaginary bands, 1 km wide, extending for many kilometres up and down the page. Other bands were present to an effectively infinite distance to the left and right, but they are not shown. The invaded area is where an invasion barrier operates to prevent further invasion.

Control measures and costs

The model allowed consideration of all available vector control techniques applied in an temporal and/or spatial combination specified by the user. Similarly, the user can specify the direct and indirect costs of any of the techniques.

Given the current practical interests and contrasts of using either the Sterile Insect Technique (SIT) and/or insecticide-treated cattle (ITC) to control tsetse, the project undertook a study to compare the cost and efficacy of these particular techniques using the following conditions and costs.

SIT. Sterile males, three days old, were released weekly. The number released per wild adult male was termed the release rate. This should be distinguished from the sterile:wild ratio which refers to the numbers of each type of adult male in the simulated field population. Unless stated otherwise, the release rate was constant so that the number released declined as the abundance of wild males dropped. To allow for the poor field performance of sterile males (Vreysen *et al.*, 2000, Hargrove, 2003), they were considered to die at rates 25% greater than for wild males, and to have daily displacements and mating capabilities that were 25% lower. Hence, the proportion of fertile matings was taken as $w/(w + 0.75s)$ where w and s are the numbers of sexually mature males in the wild and sterile categories, respectively. As suggested during the modelling, the present assumption of mild impairment of sterile male performance seems insufficient to account for the very poor competitiveness of sterile males on Unguja Island (Vreysen *et al.*, 2000), but it is allowed that research might result in fitter sterile flies.

The cost of rearing a tsetse at the Tsetse Research Laboratory, Bristol was about £1 a decade ago (Hargrove, 2003). Economies of mass production might have outstripped greatly the inflation since then, so the cost of rearing and sterilising a male was taken as £0.05. This ensures that the costs of SIT modelled in the most favourable conditions are compatible with those suggested by the proponents of the technique (Feldmann, 2004).

Costs of sterile males must be supplemented by the expense of releasing them, to be calculated per square kilometre covered each week by the release plane. Flying costs are £0.64/km (personal communication, T. Theron, Central Air Transport Services Ltd, Harare) so that the release cost is £0.45/km^2/week, assuming a flight plan similar to that of Vreysen *et al.* (2000). This means that the cost per sterile male increases with reduction in the number released, to be £0.50 per male when releases are only 1/km^2.

While it is usually envisaged that SIT be employed only after insecticides have suppressed the population by about 99% (Feldmann, 2004), SIT and ITC were modelled with and without suppression to highlight basic principles more clearly. In particular, SIT effects are potentially confusing if modelled only after suppression.

ITC. It was assumed that insecticide was sprayed only on the largest cattle, killing tsetse of each sex and age at the same rate. The daily kill rate was related to the number (**n**) of treated animals per square kilometre, using the formula $1\text{-}0.97^{\mathbf{n}}$ (Vale & Torr, 2004), which indicates a rate of 0.1 when 3.5 cattle/km^2 are treated. To check this, let us say that there are a total of 40 cattle/km^2. Such a density usually implies heavy settlement and few wild hosts, suggesting that almost all tsetse feed on the cattle. Allowing that tsetse feed every 2-3 days and that only 40% of visits to cattle result in feeding (Vale, 1977), the daily kill rate would be about 0.08 if representative cattle were treated. However, since treatments are on the largest and hence most attractive animals (Torr *et al.*, 2001) the death rate would be up to twice as great, provided all treatments are not in one small herd. Where there are fewer total cattle the abundance of wild hosts could be expected to increase in compensation.

The insecticide was taken to contain 20% alphacypermethrin, purchased and shipped at a cost of £14 per litre (personal communication, F. O'Shea, Appropriate Applications Ltd, Berkhamstead). With dilution at 2000:1 and spraying at two litres per animal per fortnight, the cost becomes £0.001/animal/day. This was multiplied by ten in generous allowance for import duty, equipment and labour, so that the total daily cost was £0.01/animal. The contribution of the equipment and labour to this cost would alter with any gross change in the number of treated animals per square kilometre, as with the change in flying costs per male released when the number of flies released changed during SIT. However, during any one operation with ITC the number of treated animals was constant, and changed by only six-fold between the various operations simulated, compared to 375,000-fold changes in weekly releases of sterile males. Hence, it seemed acceptable to take the cost per animal per day as fixed.

Vectorial index

It was assumed that the probability of disease transmission depends on the abundance of flies in each potentially infective age class, and the probability that each class is infective. The proportion of tsetse that carry mature infections of the common bovine trypanosome *Trypanosoma vivax* rises steadily with increasing age above 14 days (Woolhouse *et al.*, 1993). The rise is not quite as steady with *T. congolense* (*loc. cit.*). Nevertheless, the trypanosomiasis risk to stock is roughly proportional to the number of flies/km^2 in each potentially infected age class, multiplied by age minus 14 days, and summed over all age classes and both sexes. This was termed the vectorial index. It is unclear whether sterile males should be included in this since released males might be fed trypanocides (Msangi *et al*, 2000), a procedure that reduces vectorial capacity in the laboratory (Moloo & Kamunya, 1987; Zongo *et al.*, 2004). However, the procedure is not fully effective and awaits field confirmation. Hence, the vectorial index is quoted as a maximum and minimum*, ie*, with and without including the sterile males. The reader must decide which index to regard, although it involves no material difference to conclusions. Where sterile males are included, they first became infective at release age plus 14 days, *ie*, 17 days.

Activity 2. Dissemination and promotion.

To facilitate use by non-specialist users, the model was incorporated into an interactive programme called ‘Tsetse Muse’. The programme has a user-friendly interface and is accompanied by explanatory notes and facilities to assist the checking of the calculations. Tsetse Muse allows users to enter various inputs related to their particular circumstances. These inputs include all the general biological parameters (eg, mortality rates of wild flies, sexual competitiveness of sterile flies) used in the simulation of the tsetse population, as well as parameters that specify the local conditions (eg, fly density, extent and type of control method). Where highly specialised inputs are required, “Suggest” buttons are provided to offer the user the opportunity to have the inputs entered automatically. The interactive nature of the programme not only facilitates use by non-specialists but also allows the user to undertake various ‘what-if’ analyses.

Test versions of the programme were run on a variety of computers and operating systems to identify ‘bugs’. Documentation on the installing Tsetse Muse system were produced in html format, suitable for use on a CD-ROM and website and an ‘installation wizard’ for convenient downloading and installation of the programme from a CD or via the tsetse.org website.

Preliminary versions of the programme were circulated via CD-ROM and the world-wide web to obtain feedback from target users. Workshops to demonstrate the programme were undertaken in Botswana, Ethiopia, Kenya, Tanzania, Uganda, Zimbabwe and the UK. Feedback from these workshops and users were used to rectify programming bugs, improve the user interface and make modifications as necessary.

The project team modelled a number of scenarios to derive general principles regarding the impact of various control techniques on tsetse and trypanosomiasis and the outcomes of these activities were presented at the workshops.

Activity 3. Lessons learned

Two articles summarising the policy implications of model outputs were produced for publication in the peer-reviewed journals *Medical and Veterinary Entomology* and *Trends in Parasitology*. In addition, an oral presentation on Tsetse Muse (presented by

Vale), and a poster on the tsetse.org website, were presented at the ISCTRC meeting in Addis Ababa (Sep 2005).

In collaboration with Drs Alex Shaw (consultant livestock economist) and Tim Robinson (FAO Pro-poor livestock Initiative), comparisons were made of the impact and cost of using (i) insecticide-treated cattle, (ii) targets, (iii) aerial spraying and (iv) the SIT to control tsetse in Uganda. The results of this study were presented at FAO headquarters (Dec, 2005; presentation by Alex Shaw) and at an IFAD-supported meeting held in Kampala (December, 2005; separate presentations by Torr and Robinson) for stakeholders concerned with developing a national programme to control tsetse-borne trypanosomiasis in Uganda.

At the meetings in Addis Ababa and Kampala, ~350 CD-ROMs of the tsetse.org CD-ROM which included the latest version Tsetse Muse were distributed to all participants.

Application of Tsetse Muse to the use of aerial spraying to control tsetse were developed in collaboration with Patrick Kgori, a scientist from the Botswana Tsetse Control Division, and an oral presentation on this work was made, by Patrick Kgori, at the annual meeting of the Royal Entomological Society at the University of Sussex, UK (Sep 2005).

Outputs

Output1: A general simulation model of the cost and efficacy of tsetse control

The use and value of the model developed by this project is best exemplified by demonstrating, in detail, its application to assess the cost and efficacy of various control interventions against tsetse.

During the course of this project the model was used to:

(i) Compare the cost and efficacy of SIT and ITC.

(ii) Assess how variation in the spatial distribution of baits affected the outcome of tsetse control operations.

(iii) Assess the efficacy of various aerial spraying strategies.

The results of the first study were published as a paper in *Medical and Veterinary Entomology* and the second will be published in the proceedings of the ISCTRC meeting. The last study will form a component of a paper being prepared for submission to the *Journal of Medical Entomology*. For the purposes of this report, extracts from these three papers are presented below.

1. Application to sterilising and insecticidal techniques

Mating difficulties and halting control

The sustainability of sparse populations is crucially dependent on the probability of mating. This was investigated by instantly reducing the abundance of all age groups of adults and pupae, and allowing the population to grow naturally over the next 1000 days (Fig. 2). With reductions to 10, 1 and 0.1% the population increased by 10, 84, and 305 times, respectively. None of these reductions limited seriously the ability of females to find mates. When the initial reduction in population was more severe, to leave only 0.01%, growth was rapid initially since most of the females then extant had already mated. However, when these females died their replacements had difficulty in finding a mate so that the population growth slowed until density increased sufficiently to facilitate mating. When the population reduction was almost complete, leaving only 0.001%, the population declined markedly and permanently after brief growth. The low or negative rates of modelled growth at densities of less than about one or two males/km^2 accord with field observations of mating difficulties at or near such densities (Glasgow, 1963).

Since the modelled population eventually expires naturally when the density of wild adult males drops below 0.2/km^2 there is little benefit in continuing control much beyond that. Hence, all modelled control was stopped where the wild adult males declined to <0.1/km^2. The population was considered to be eradicated in such places, albeit that the combined density of adult males and females was then usually several times greater than 0.1/km^2.

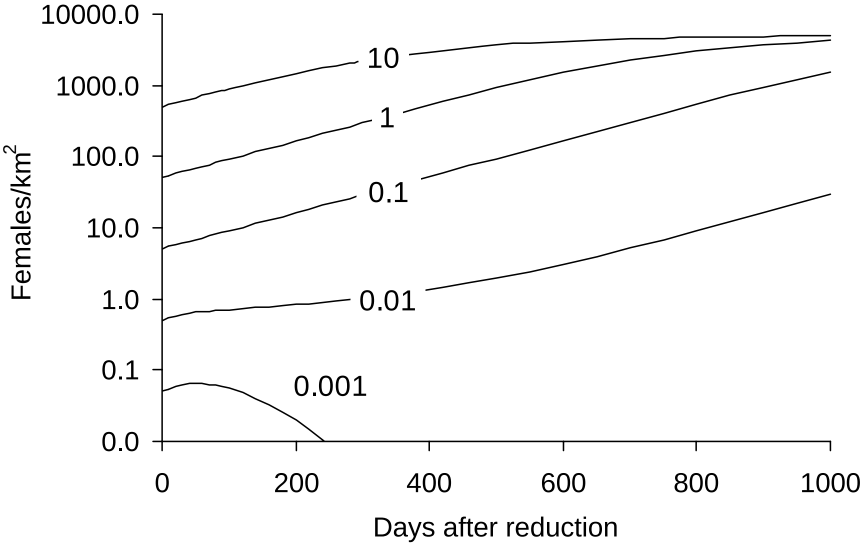


Fig. 2. Numbers of adult females per square kilometre in days following various instant reductions in population density, to levels of 10%, 1%, 0.1%, 0.01% and 0.001% of stable density. The reductions applied equally to pupae and adults of each age and sex, so that the sex ratio and age structure of the population were not immediately changed.

Control of isolated populations

Optimisation of control rates. Calculations were made of the required duration of control, and the costs per square kilometre, for various death rates imposed by ITC and various release rates with SIT (Fig. 3), used against the unsuppressed population. While the costs and durations would be less if the population had been suppressed, the pattern of results would be similar. Two features are important. First, the costs for ITC change little with an increase in the rate of imposed death, but with SIT the cost curve rises markedly with increasing release rate. Second, with SIT the duration of control bottoms out at about a year, whereas with ITC the control period can be only a few months. The fact that the required duration of SIT soon bottoms is because SIT does not directly kill the flies, albeit that the many males released for SIT do have a slight affect by enhancing the density dependent deaths when the population density of wild and released flies is above 10% of its initial level.

The fact that the costs of SIT rise steeply with an increase in release rate is because high rates give little compensatory reduction in the required duration (Fig. 3, B). The long duration of SIT is in turn due to the fact that SIT, unlike insecticidal techniques, does not kill the flies. The principles in this are illustrated by considering what would happen if SIT or any insecticidal technique were applied with perfect efficiency. With perfect insecticidal control, all flies would be killed when the last pupa had hatched*, ie*, after 26 days for females. With perfect SIT the females mated just before the first releases would continue producing pupae up to age 178 days, and although all newly emerging females would be sterile-mated they would still survive for 178 days. Hence, perfect SIT would take 379 days (175+26+178) to show its perfection. Even if recently mated females copulated again immediately after producing their first larva the population would not be completely gone before 217 days (16-3+26+178).

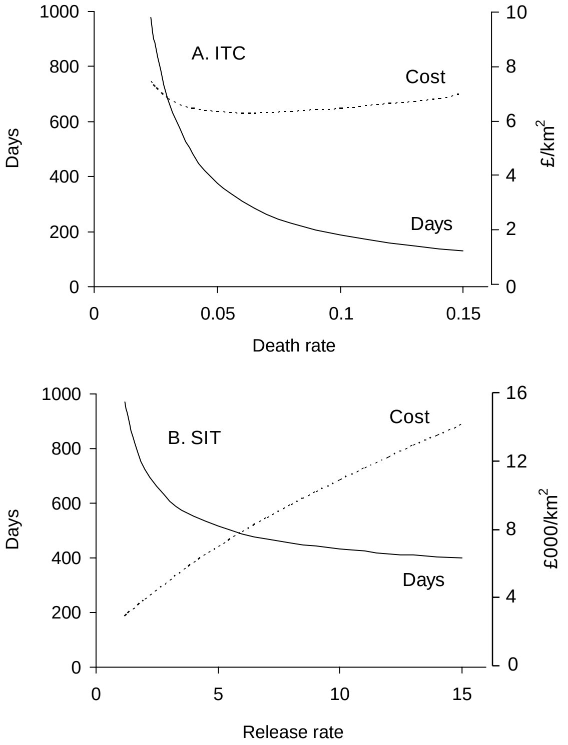


Fig. 3. Days required for eradication (solid line), and costs (broken line), at various daily death rates imposed by ITC or various release rates with SIT. Each technique was used alone against an isolated population, without prior suppression. Cost scales use units for ITC and thousands for SIT.

In selecting the optimum rates for each technique it is important to consider not only the costs but also the time involved -- the control personnel need to see something happening quickly, and there are benefits in rapidly reducing the disease risk. The daily death rate of 0.1 with the cattle alone seems adequate. Given that raising the release rate with SIT increases the costs much more than it reduces the time required, it is sensible to err towards low release rates: a rate of three sterile males released for every one fertile male present seems about optimal. Such a rate produces from a month onwards an average sterile:wild ratio of 13:1 in the simulated field population. This ratio is within the range evident in the actual operations on Unguja Island, *ie*, around 5:1 initially, rising to about 400:1 after two years (Vreysen *et al.*, 2000).

Rising release rates could smooth the demand for sterile males and reduce the overall requirement; the first males released would produce a useful effect at a time when a much greater effect would require very much greater numbers. To investigate the effects of rising release rates, the rate was taken as 1.0 initially, rising by 0.1 for each week thereafter. The duration for SIT was then 573 days at a total cost of £4,420. This cost is 22% lower than the cost £5,640 when the release rate was steady at 3.55, *ie*, sufficient to require the same duration of control. In the fifth week of rising rates the sterile: wild ratio in the simulated field population averaged 2.4:1, increasing to 54.4:1 in the final week. Although these ratios are half to an eighth of those actually produced on Unguja Island, the required duration of control was a few months less than the actual, presumably because the model assumed only slight impairment of the competitiveness of sterile males.

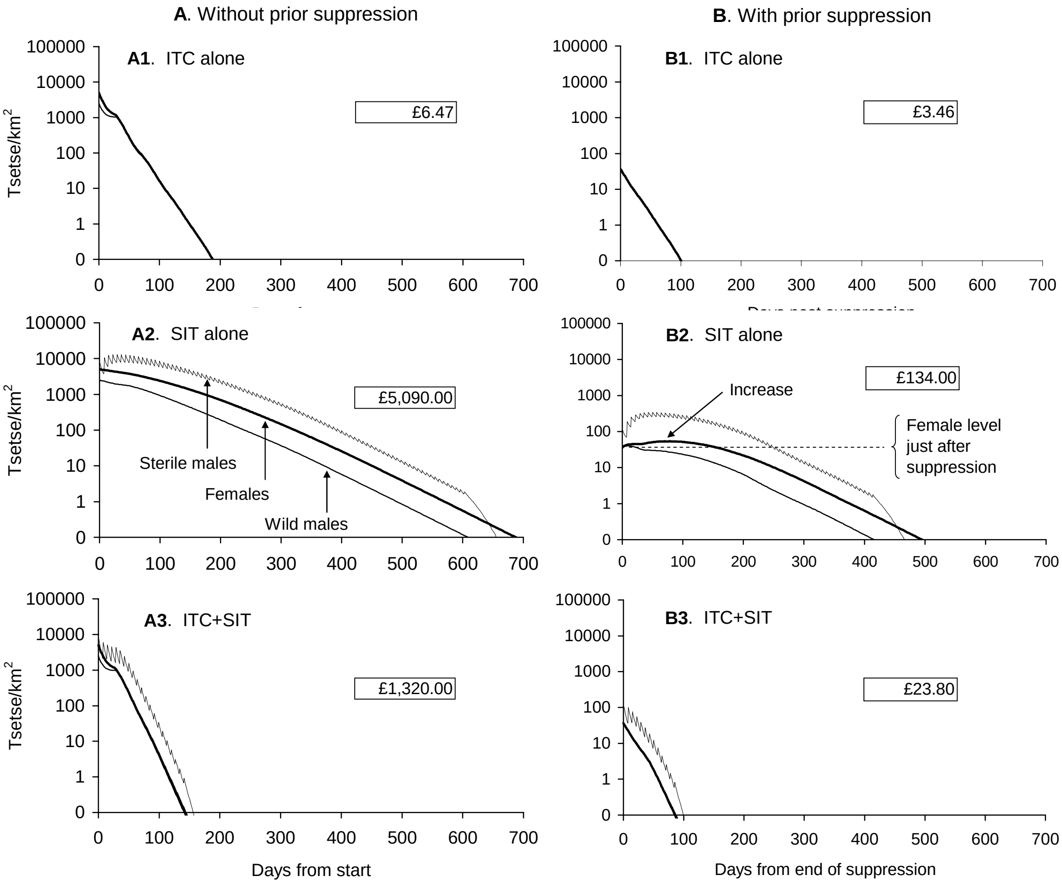


Fig 4. Abundance of females (bold line), wild males (line of medium thickness) and sterile males (fine line), in an isolated population at various times after the start of ITC alone, SIT alone and ITC+SIT, applied without (A) and with (B) the prior use of ITC to produce population suppression to 1% of the pretreatment level of adult males plus females. Eradication costs of per square kilometre are shown to three significant figures, exclusive of any suppression costs.

Greater rises in release rate are implied in a policy of keeping constant the *absolute number* of released flies. For example, the initial release rate of three requires the release of 7500 sterile males. If this number is maintained each week, until the population is eradicated on day 346, the final release rate is ~ 69,000 sterile males for each wild male. Provided this policy is applied against an unsuppressed population its main strength is the inflation of density-dependent deaths, so hastening control, but it is hugely expensive at £18,800. Hence, it seems that the alternatives to a steady release rate of three produce little or no improvement in the cost-effectiveness of SIT, so they were not considered further.

Population change without prior suppression. With ITC alone (Fig. 4, A1), the abundance of males and females declined quickly, with the curves for both sexes being close. The rate of decline was not perfectly even, especially in the first few weeks when the death of many adults was partly offset by steady emergence. This perturbed the age structure of the population and hence affected future emergence rates. The regularly occurring but ever-diminishing changes in later rates of decline reflect the movement towards a new stable age structure. However, the modelled variations in rates of decline were slight, so the results accord with the linear decline in the logged catches of actual bait campaigns in effectively isolated areas (Hargrove, 2003; Hargrove *et al.*, 2000).

With SIT alone (Fig. 4, A2), the wild population declined slowly, especially in the first few weeks. This is because SIT does not kill the flies; the effect on breeding cannot take hold until all pupae initially present have emerged and the new adult females have lived long enough to have normally bred. The curves for males and females are widely separated since SIT does not level the death rates of the sexes. The curve for sterile males is jagged due to the weekly releases, and rises rapidly in the first few weeks as flies from several releases accumulate. The sterile male curve dropped sharply when the density of wild males declined to <0.1/km^2, *ie*, when releases stopped. With the simultaneous combination of ITC and SIT (ITC+SIT) (Fig. 4, A3) the abundance of wild males and females initially dropped at much the same rate as for ITC alone, due to the fact that ITC, not SIT, produces the first impact.

With prior suppression. In the present model, suppression to 1% occurs after operating ITC alone for 87 days, when the population consists of 35.2 males and 36.3 females/km^2, making 71.5/km^2 in all. A variety of techniques was used immediately after such suppression, *ie*, from day 88 onwards (Fig.4, B). If SIT was *not* introduced to replace ITC at this stage (Fig. 4, B1), the population decline was merely a continuation of that during the suppression. If ITC was halted and SIT now used alone (Fig. 4, B2) the population actually *increased* by 48% at first, due to SIT not killing the flies and not reducing the productivity of females that were already breeding – when low abundance encouraged maximum growth. It took 156 days of SIT before female abundance dropped below the immediate post-suppression level.

Degree of suppression. Without prior suppression the costs of SIT alone or ITC+SIT were, not surprisingly, grossly greater than for ITC alone (Fig. 5). With prior suppression, the costs of all measures were reduced but SIT alone still cost 39 times more than ITC alone (Fig. 5). Studies were made of the extent to which the costs of post-suppression measures were affected by using ITC alone to produce various suppressions down to 0.01% of the initial density (Fig. 5). Taking the range of suppression levels as a whole the costs for SIT declined more sharply than for ITC. However, when the suppression left populations small enough (<1%) to be tackled credibly by SIT the cost curves were of similar slope, *ie*, SIT did not then become cheaper relative to ITC as the population suppression increased. Moreover, although not shown on Fig. 5, the duration of post-suppression control was, as expected, always longer with SIT alone than with ITC alone, and sometimes shortest with SIT+ITC. For example, when suppression was to 10% the post-suppression eradication took 527 days with SIT alone, 141 days with ITC alone and 112 days with ITC+SIT. When suppression was to 0.03% the post-suppression eradication took 224 days for SIT alone and 41 days for either ITC alone or ITC+SIT, *ie*, the addition of SIT to ITC after suppression did not change the speed of eradication when the population remaining to be eradicated was very low. In such cases the ITC component completed the task before SIT became effective.

Mean age. Effects on the mean age of adults are illustrated by considering ITC and SIT applied separately without prior suppression. Since ITC killed flies the mean age declined to a third of its initial level, to be 14-17 days for females at 1-6 months after the start, according with field results of bait campaigns (Van Sickle & Phelps, 1988). By contrast, since SIT reduced breeding the mean age rose, increasing by ~50 days for females, to be 73-94 days at 6-20 months from the start.

Birth rate. This is defined as the daily number of larvae produced relative to the number of adult females, and was 0.082 initially. Not surprisingly, SIT produced a gradual reduction in the birth rate, to be 0.066, 0.044 and 0.023 in the originally un-suppressed population after one, two and four months, respectively. Perhaps more surprisingly, ITC reduced the birth rate rapidly, to be 0.031 at one month, *ie*, half the rate with SIT then. This was because with ITC an unusually high proportion of females were recently emerged from the initially large reservoir of pupae, and most were killed before breeding age. In the next few months the rate recovered slightly to an average of 0.047, due to a more stable balance between adults and emergence, but still reflecting many premature deaths.

Vectorial index. Changes in age structure, taken with the distinctive rates of population decline (Fig. 4), ensured that when ITC was used against the unsuppressed population the vectorial index declined by 99.9% in 99 days. With SIT this level of reduction took 555 days if the vectorial capacity of sterile males is included and 529 days if not. The distinction between SIT and ITC was particularly marked in post-suppression operations (Fig. 6). For ITC the index was soon negligible but for SIT the index *rose* when suppression stopped, and even when sterile males were regarded as non-vectors it still took 301 days to bring the index below the immediate post-suppression level. This is because the age structure changed markedly from the ITC to the SIT pattern, and because the female population was increased for five months after the start of SIT (Fig. 4, B2).

Different populations. To determine the robustness of the indications for the relative performance of SIT and ITC, each was applied alone with the following variations to the pre-treatment population.

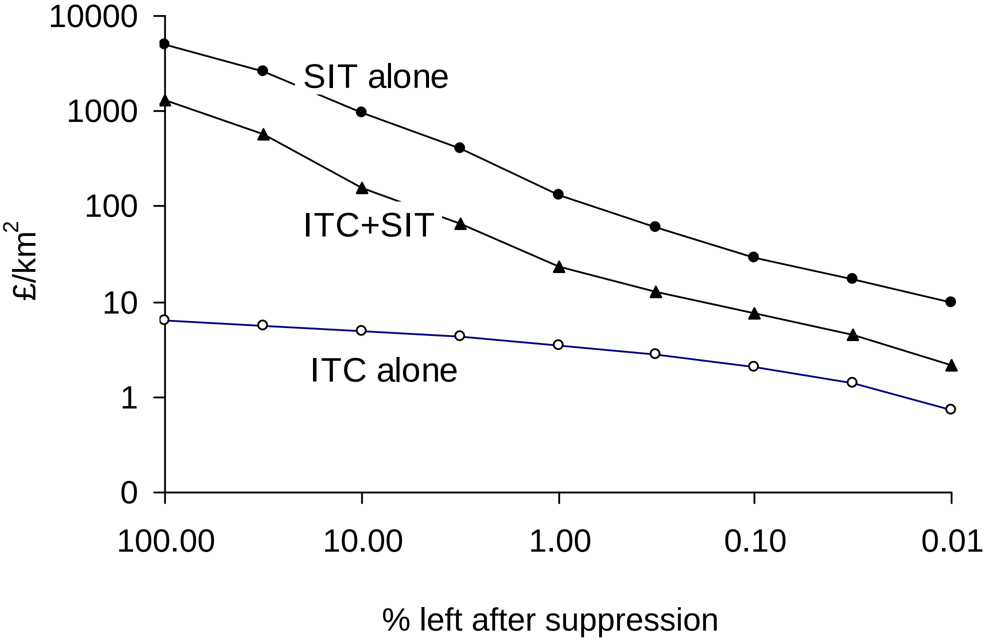


Fig. 5. Cost, in £/km2, of using ITC alone (open circles) SIT alone (solid circles) and SIT+ITC (triangles) for post suppression eradication following the use of ITC alone to suppress the population to various percentages of the pre-suppression density of males plus females of 7500/km2. Costs of suppression are not included.

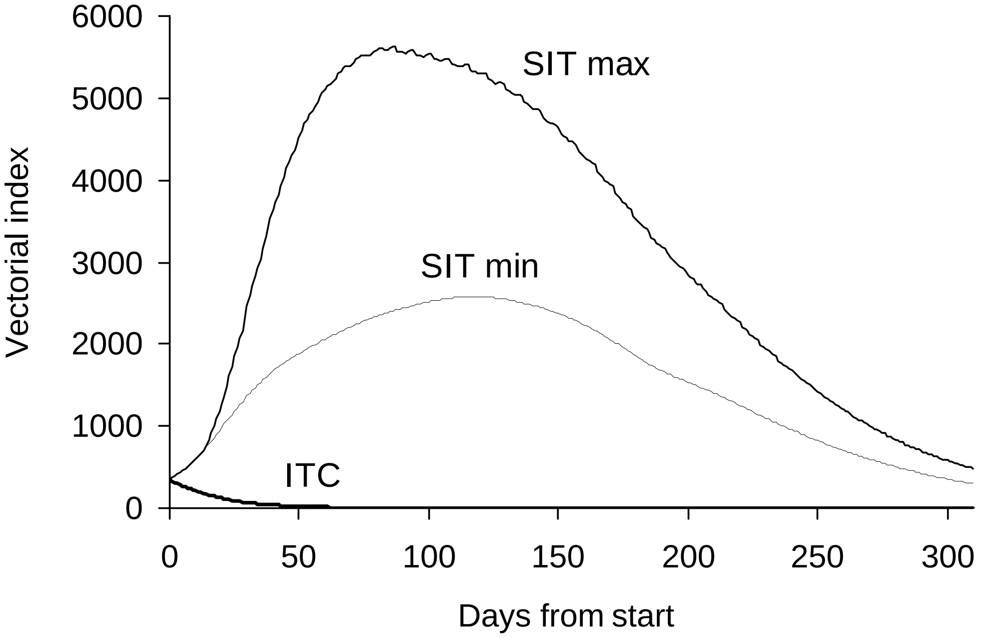


Fig. 6. Vectorial index in an isolated area at various days after the end of ITC suppression to 1% and the start of control by ITC (bold line), or SIT. With SIT the index is shown at its minimum, ie, not including sterile males (fine line), and maximum, ie, including sterile males (line of intermediate thickness).

Faster breeding. The cause of the poor performance of SIT is that tsetse breed slowly and, concomitantly, are long lived. Hence, it is pertinent to explore the effects of changes that enhance the breeding rate and reduce the longevity. This was done in part by allowing that the average temperature is raised by 5^{o}C, to become 30^{o}C. The pupal periods then reduce to 22 days for males and 20 days for females, and the time to the first larva and the interlarval period decline to 14 and 7 days, respectively. Mortalities of pupae and eggs/larvae were reduced to nil. Lifespan was reduced to 140 days for females and 70 days or males. Adult death rates required for stability then increased to 0.1012 for males and 0.0506 for females*, ie*, exceptionally high values (Hargrove, 2004). These changes meant that the costs and durations of both control measures declined, particularly for SIT (Table 2, rows 2 and 6). However, SIT still cost many hundred of times more than ITC, and still took much longer.

Sparse populations. The techniques were modelled against a population that was stable at a pre-treatment density of 25 males and 50 females/km^2*, ie*, 1% of the standard stable level, but with the standard age structure. With this sparse population the costs of SIT were much reduced (Table 2, rows 3 and 7). However, the costs of ITC also declined a little, ensuring that SIT was still 20 times more expensive than ITC. Moreover, SIT still took about three times as long as ITC. When the sparse population was also fast breeding the changes to the costs and durations of both control measures were inconsequential (Table 2, rows 4 and 8).

Table 2. Cost and duration of SIT alone, ITC alone and SIT relative to ITC, when the measures were applied without prior suppression to distinctive stable populations. Details of the densities and breeding are given in the text.

	Population				
	Density	Breeding	SIT	ITC	SIT/ITC
Costs, £/km^2					
	Standard	Standard	5,090.00	6.47	787
		Fast	4,450.00	6.16	722
	Sparse	Standard	74.20	3.67	20
		Fast	65.60	3.42	19
Duration, days					
	Standard	Standard	609	187	3.3
		Fast	555	178	3.1
	Sparse	Standard	371	106	3.5
		Fast	331	99	3.3

Control of non-isolated populations

Initial population. The simulated distribution of the standard, pre-intervention population in the non-isolated area (Fig. 7) shows that the abundance of tsetse started to decline rapidly at around 5 km into the operational area, *ie*, where the death rates began to increase in simulation of progressively poorer habitat. The population of males was <0.1/km^2 at distances greater than 33 km, so that the operational area was 0-33 km from the front.

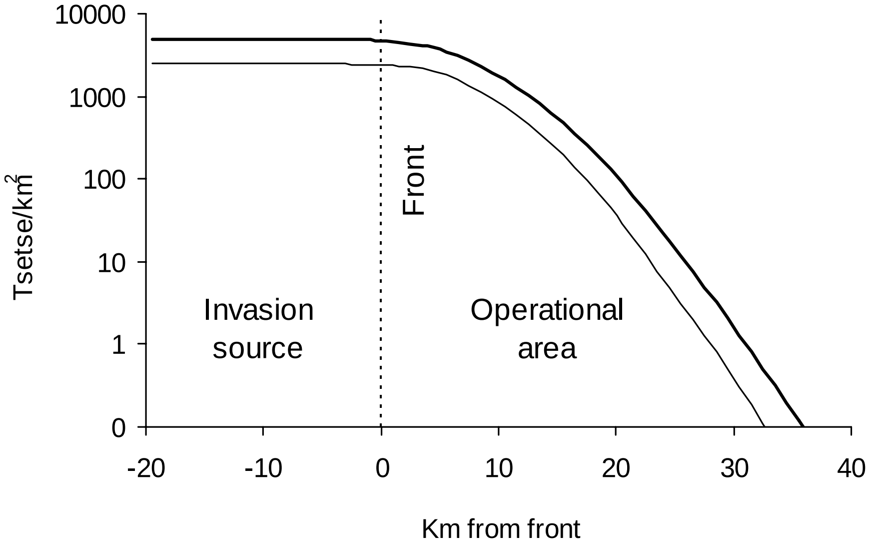


Fig. 7. Pre-intervention abundance of wild males (fine line) and females (bold line) at various distances from the invasion front (broken line), in and near the non-isolated operational area.

Without suppression. The tsetse distributions that stabilised after 1000 days of control (Fig. 8) show that with ITC alone the population declined rapidly on moving from the front and into the operational area. Taking fly densities <0.1 males/km^2 as representing local elimination, the population was eliminated from 8 km onwards, consistent with field results for bait operations giving approximately the present kill rate (Vale *et al.*, 1988). With SIT alone the population was eliminated only from 18 km onwards. This is because SIT did not kill the females that invaded. Moreover, if the invading females had been fertile-mated, as when at mating time they were in an area with few sterile males, then they could breed during invasion, and their offspring could invade yet further. The problem is compounded by the fact that the females are more mobile than males. This means that although the population was technically eliminated at 18-19 km from the front, there were still 0.93 females/km^2 there, *ie*, 16 times more than the 0.06 males/km^2, and they were mostly old, giving a mean age of 88 days, as expected from the fact that invading far takes a long time. Such old females are likely to be good vectors. Not surprisingly, the addition of SIT to ITC did not increase materially the area of elimination, since SIT killed no invaders.

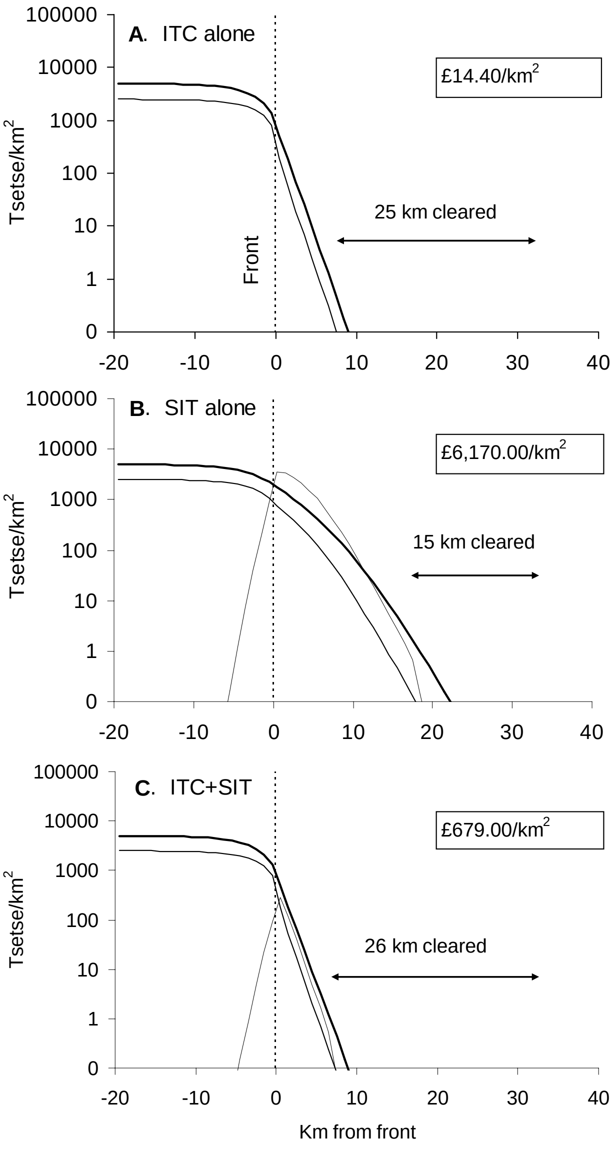


Fig. 8. Abundance of females (bold line), wild males (line of medium thickness) and sterile males (fine line) at various distances from the front, after 1000 days of applying ITC alone, SIT alone and ITC+SIT against a non-isolated population (Fig. 87), without prior suppression. Data in the boxes are the total 1000-day costs per square kilometre cleared to <0.1 wild males/km2 at 1000 days.

The poor showing of SIT as an invasion barrier could be improved a little by changes to the model. For example, if the invading females mated very frequently they would have a better chance of mating with a sterile male before moving far, and so would produce fewer offspring to invade yet further. As a rough “cover-all” for various modifications that might be proposed, let us make the drastic assumption that some imaginary variant of SIT stops absolutely all births in the operational area, so that the stabilised distribution of tsetse reflects only the distance the invaders travel before natural death. The stable distribution then results in male densities dropping to $<0.1/km^2$ at 7-8 km from the front. However, at that distance the female density is $56.8/km^2$, and does not drop to $<0.1/km^2$ until 17-18 km from the front, *ie*, 5 km less than with the normally modelled SIT alone (Fig. 9, B) but still 8 km more than with ITC alone (Fig. 9, A). The fact that females penetrate further than males is due to their longer life and greater daily displacement.

The massive invasion with the imaginary control measure indicates the rough magnitude of an inherent weakness in SIT or other techniques that operate primarily by reducing births. Unfortunately, although variations to the daily displacement or population density alter the absolute extent of invasion with each control measure, they do not change the relative extent. However, it might be supposed that SIT has a compensatory strength because some sterile males diffuse into the invasion source and prevent breeding there. This indeed occurred in the model, contributing to the fact that at 0-1 km inside the invasion source the pupal population was reduced to 37% of the pre-treatment level. On the other hand, ITC also reduced the pupal population there, to 28%. This is because diffusion of breeding females into the operational area from the invasion source was only partly offset by diffusion back, according with field data for adult distribution during bait campaigns (Vale *et al*., 1988). With ITC+SIT the reduction was to 27%. It appears that SIT, ITC and ITC+SIT are about equally effective in reducing populations at a distance.

With suppression. It is pointless to consider suppressing the population by ITC and then stopping the suppression to apply SIT. As soon as the suppression is withdrawn the population progresses towards the distribution shown by SIT alone (Fig. 8, B) and within a year most of the benefit of the suppression is lost. However, it is worth considering a type of suppression which is not aimed primarily at the resident population, but rather suppresses invasion. For example, when ITC alone formed an invasion barrier (Fig. 8, A) the population at 2-3 km from the front consisted of 19 males and 70 females/km^2, making 89/km^2 in all. This is 1.3% of the initial density there (Fig. 7). Hence, ITC was used at 0-3 km to suppress the large majority of invasion pressure; SIT from 3 km onwards dealt with the rest. The resulting stabilised distribution (Fig. 9) shows, as expected, a sharp decline in density in the ITC-treated area near the front. On going into the adjacent part of the SIT-treated area the decline was slower, because flies invading from or through the ITC area could survive unrestrictedly, and the fertile-mated females that arrived could breed. The fact that the wild males *increased* just inside the SIT-treated area is because many emerged there and did not disperse as quickly as females. The use of the partial barrier of ITC was little benefit to SIT (*cf* Figs. 9 and 8, B) and the use of SIT to reinforce the partial barrier was a poor substitute for a full barrier of ITC (*cf* Figs. 9 and 8, A).

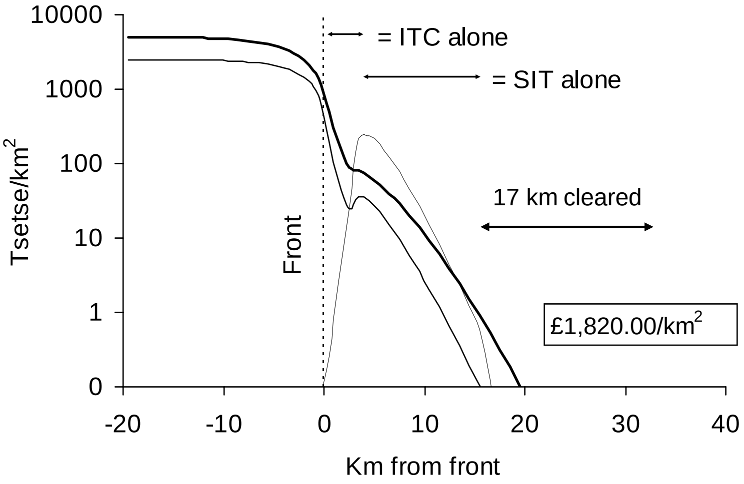


Fig. 9. Abundance of females (bold line), wild males (line of medium thickness) and sterile males (fine line) at various distances from the front, after 1000 days of applying ITC alone at 0-3 km into the operational area, and SIT alone applied initially at 3-33 km, against a non-isolated population (Fig. 7), Double-headed arrows indicate the extent of the control measures after 1000 days, and the length of transect cleared to <0.1 wild males/km2. Box shows the 1000 day cost per square kilometre cleared, to three significant figures.

2. The spatial distribution of baits

To explore how variation in the distribution of baits affected the outcome of tsetse control operations, it was assumed that the pre-treatment population comprised 2500 males and 5000 females/km^2, at an average temperature of 25^{o}C, with a mean daily displacement of 249m for males and 367m for females (Vale & Torr, 2005). The population was assumed to be evenly distributed in the operational area and the adjacent invasion source, rather than the uneven distribution assumed in the previous section and in Vale & Torr, (2005). As before, an imaginary line, called the invasion front, separated the invasion source and operational area. The population was considered to be eradicated where its density dropped to <0.1 females/km^2.

Invasion barriers. – The efficacy of baits in neutralising invasion of a treated area was one of the first matters considered by professional modellers (Hargrove, 1993). It is pertinent, therefore, to see that the present model can produce outputs of the same type. The specimen outputs now generated by Tsetse Muse (Fig. 10) refer to the stabilised distribution obtained after operating baits evenly within the operational area. Not surprisingly, the greater the daily kill rate imposed by baits the narrower the invaded area. A kill rate of 10% per day, produced by treating 3-4 large cattle/km^2 (Vale & Torr, 2005) meant that the invaded area was 9km wide.

While there is nothing new about these types of indications for barriers, it is novel that anybody can now produce the indications quickly, for whatever control technique and whatever input assumptions are selected.

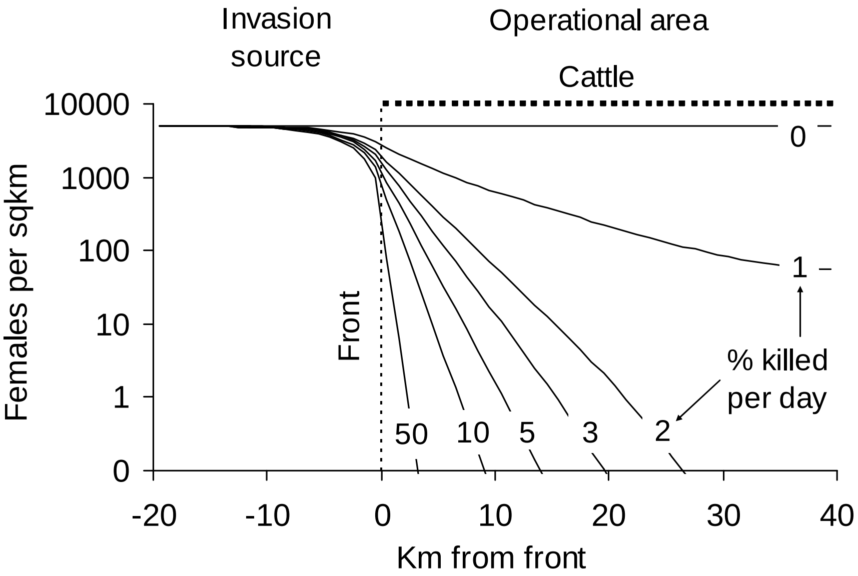


Fig. 10. Stabilised abundance of tsetse across the invasion front, when insecticide-treated cattle were evenly distributed cattle in the operational area and used to give various daily rates of kill of adult males and females

Residual pockets. -- Let us say that in most of the operational area there are enough cattle to allow a kill rate 10% per day. Let us also say that no cattle occur in a band, 5km wide, that runs parallel to the front at 17-22km inside the operational area. Hence, tsetse are not killed within this band. Despite this, the flies do disappear from the band (Fig. 2) since once the bait campaign begins the number of flies diffusing into the band from the treated area becomes less than the number diffusing out, and the population in the band cannot breed quickly enough to offset this net emigration. The population in the band is eliminated after 4.2 years, as against the 0.5 years it would have taken if the cattle treatments had been evenly applied throughout the whole operational area, ie, inside and outside the band.

The flies are eliminated from the untreated band in 0.7 years if it is only 1km wide, because the narrower the band the greater the proportion lost per day by outward diffusion. On the other hand, elimination takes 13 years if the band is 7km wide, and tsetse are never eliminated entirely from bands wider than this. All of the above bands were centred at 19-20 km from the front, but the programme allows untreated bands to be located anywhere. The programme also allows exploration of the most economical ways of avoiding or removing the residual infestations. An effective expedient is the deployment of artificial baits down the centre of the bands, it being unnecessary to treat the whole band.

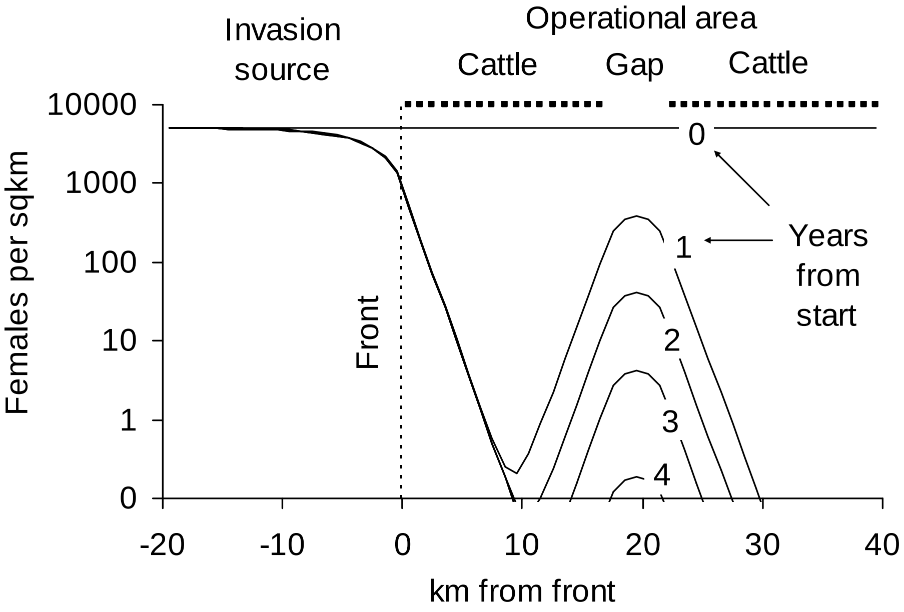


Fig. 11. Abundance of tsetse across the invasion front, at various times after the start of cattle treatments that killed 10% of the adult tsetse population per day, in all of the operational area except in a band 5km wide at 17-22km from the front.

Mosaic control. – Let us imagine that (i) insecticide-treated cattle are used in the first 10km from the front, and also at <30km from the front, and (ii) that the 20km-wide band in between is treated by four aerial applications of non-residual insecticide at 13-day intervals. The cattle treatments and the aerial spraying start at the same time. Each of these control techniques is, in itself, highly effective when applied singly and uniformly against an isolated population. However, when applied in the mosaic now envisaged, the results are disastrous (Fig. 3). Although the flies in the centre of the aerially sprayed block were eliminated after 40 days, when the spraying was complete, flies were still present in the cattle-treated areas then. Some of these flies invaded the aerially sprayed block and started breeding – indeed, some even invaded and deposited pupae during the 40 days. Hence, the population in the aerially-sprayed block increased rapidly to provide a stream of invaders into the cattle-treated areas, so preventing control reaching its full potential there. The upshot was that the flies were eliminated only at distances >36km from the front, not at the distances >9km if the cattle treatment had been used throughout (Fig.1, 10% kill).

The above types of problem threaten whenever the control measures to be combined operate at contrasting rates or at different times of year. The programme allows such problems and their solutions to be investigated. For example, it shows how the disasters can be avoided by: (i) overlapping the measures, (ii) starting the baits well in advance of the spraying and (iii) choosing where possible the measures that are the most compatible. For example, if each control measure is started at the same time, then insecticide-treated cattle and artificial baits are the most compatible pair; aerial spraying and SIT are the least compatible pair since they work at such different rates.

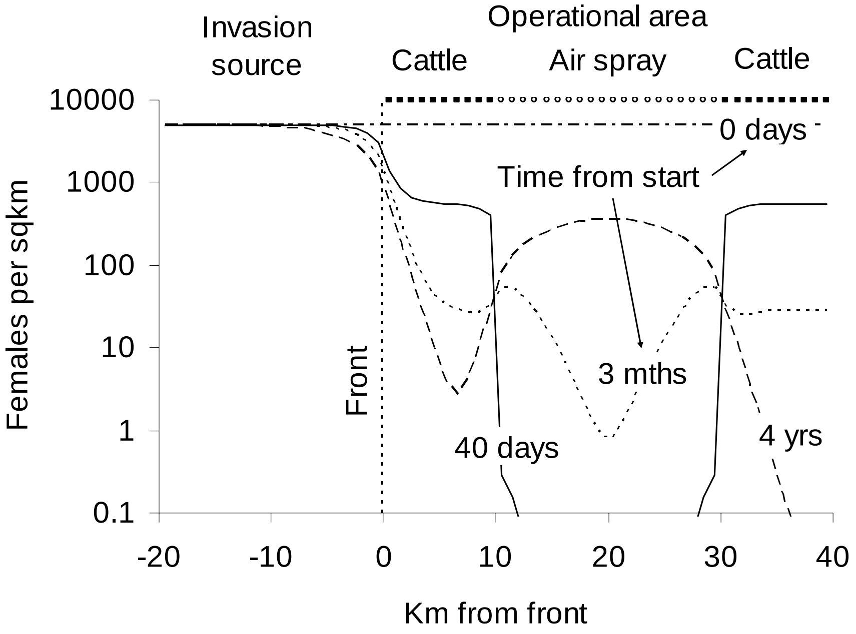


Fig. 12. Abundance of tsetse across the invasion front, at different times after the start of a campaign in which insecticide-treated cattle and aerial spraying were used to treat different parts of the operational area. Aerial spraying was completed at 40 days; cattle were used continuously.

Output 2. Dissemination and promotion.

The simulation model was incorporated into an interactive and user-friendly decision-support tool, 'Tsetse Muse' which was disseminated via www.tsetse.org and the distribution of >400 CD-ROMs at workshops and meetings conducted in Ethiopia, Uganda and Zimbabwe. To view Tsetse Muse, the reader is invited to visit www.tsetse.org or use the CD associated with this report. However, to provide a general flavour of the programme, a brief overview of 'Tsetse Muse', including examples of screenshots, follows.

Tsetse Muse – an overview

Tsetse Muse is readily installed onto the user's computer with an 'installation wizard' which automatically creates the appropriate directory structure for the programme and adds a short-cut icon for the programme to the Start Menu.

Upon launching the programme the user is presented with the screen shown in fig. 1. The user is provided with general information on the programme and its use, help with adjusting the view to suit the computer. The opening page also includes the smiling face of 'Helpful Harry' who appears throughout the programme. By clicking on 'Harry' the user is provided with tips, advice or shortcuts appropriate to the page.

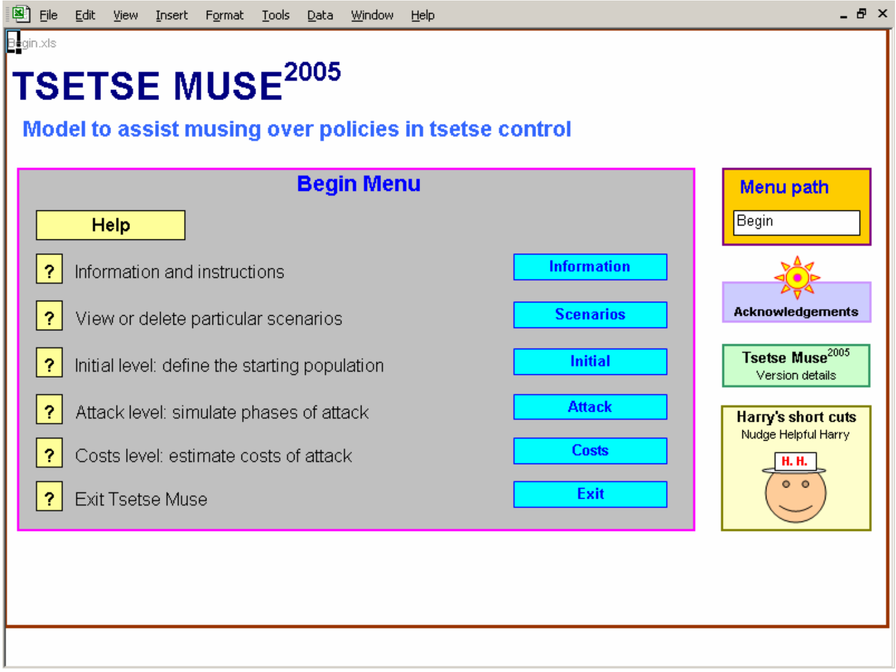
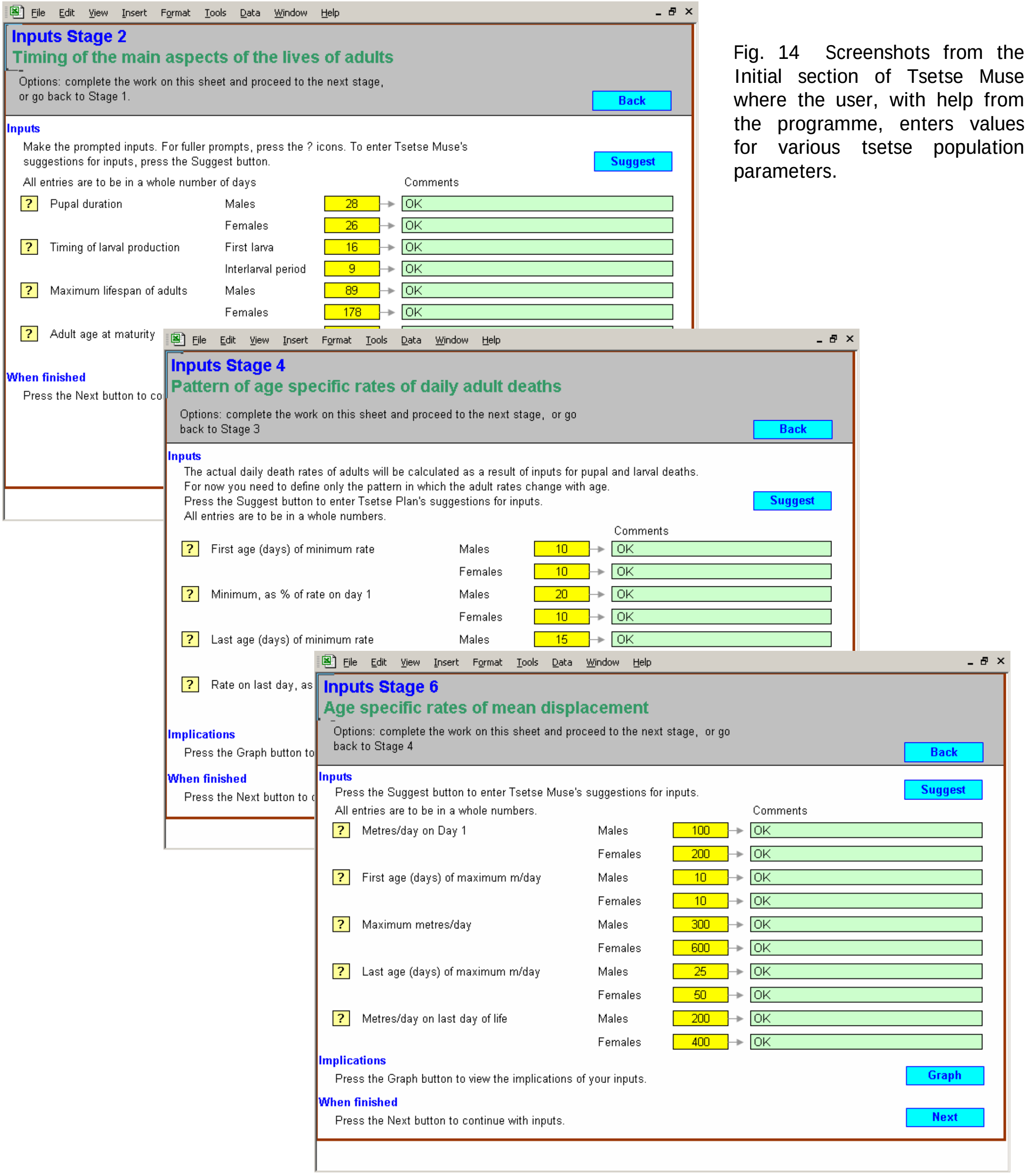


Fig. 13 A screenshot showing the starting view of Tsetse Muse, a user-friendly programme to assist in the rational development of strategies to control tsetse. The user specifies, with assistance from the programme, an 'initial' population of tsetse which can then be attacked using any combination of control methods chosen by the user. The programme simulates the impact of the intervention on the tsetse population and allows the user to compare the cost and efficacy of various strategies to control of eliminate tsetse.

Initial

Initially, the user has to define the conditions for the tsetse population by specifying rates of reproduction, mortality and movement and how these vary with population density. This process provides the values for the population model underpinning Tsetse Muse. The user is provided with a series of screens which ask for values relating to, say, the duration of the larval and pupal periods, density dependent changes in the mortality of various age and sex classes of tsetse and rates of movement (Fig. 2). For each question, the user can either enter a value of their choice or ask the programme to suggest one. Where appropriate, the programme also provides simple graphs to indicate the implications of values selected by the user. If the user enters a value that is clearly nonsense, such as, say, a pupal period of one day, then the programme alerts the user and asks for another value.



Inputs Stage 2
Timing of the main aspects of the lives of adults

Options: complete the work on this sheet and proceed to the next stage, or go back to Stage 1.

Inputs

Make the prompted inputs. For fuller prompts, press the ? icons. To enter Tsetse Muse's suggestions for inputs, press the Suggest button.

All entries are to be in a whole number of days

			Comments
Pupal duration	Males	28	OK
	Females	26	OK
Timing of larval production	First larva	16	OK
	Interlarval period	9	OK
Maximum lifespan of adults	Males	89	OK
	Females	178	OK
Adult age at maturity			

When finished

Press the Next button to co

Inputs Stage 4
Pattern of age specific rates of daily adult deaths

Options: complete the work on this sheet and proceed to the next stage, or go back to Stage 3

Inputs

The actual daily death rates of adults will be calculated as a result of inputs for pupal and larval deaths. For now you need to define only the pattern in which the adult rates change with age. Press the Suggest button to enter Tsetse Plan's suggestions for inputs. All entries are to be in a whole numbers.

			Comments
First age (days) of minimum rate	Males	10	OK
	Females	10	OK
Minimum, as % of rate on day 1	Males	20	OK
	Females	10	OK
Last age (days) of minimum rate	Males	15	OK
Rate on last day, as			

Implications

Press the Graph button to

When finished

Press the Next button to c

Inputs Stage 6
Age specific rates of mean displacement

Options: complete the work on this sheet and proceed to the next stage, or go back to Stage 4

Inputs

Press the Suggest button to enter Tsetse Muse's suggestions for inputs.

All entries are to be in a whole numbers.

			Comments
Metres/day on Day 1	Males	100	OK
	Females	200	OK
First age (days) of maximum m/day	Males	10	OK
	Females	10	OK
Maximum metres/day	Males	300	OK
	Females	600	OK
Last age (days) of maximum m/day	Males	25	OK
	Females	50	OK
Metres/day on last day of life	Males	200	OK
	Females	400	OK

Implications

Press the Graph button to view the implications of your inputs.

When finished

Press the Next button to continue with inputs.

Fig. 14 Screenshots from the Initial section of Tsetse Muse where the user, with help from the programme, enters values for various tsetse population parameters.

The user can choose to consider an isolated or non-solated population populations of density. If the latter is selected, then the user is asked to provide information on spatial variation in rates of birth and death. As before, the user can either enter a value that they think appropriate or ask the programme to suggest one. At the conclusion of the Initial phase, the user is provided with summary data on the various aspects of the tsetse population, such as the age structure and the critical density at which the population will collapse.

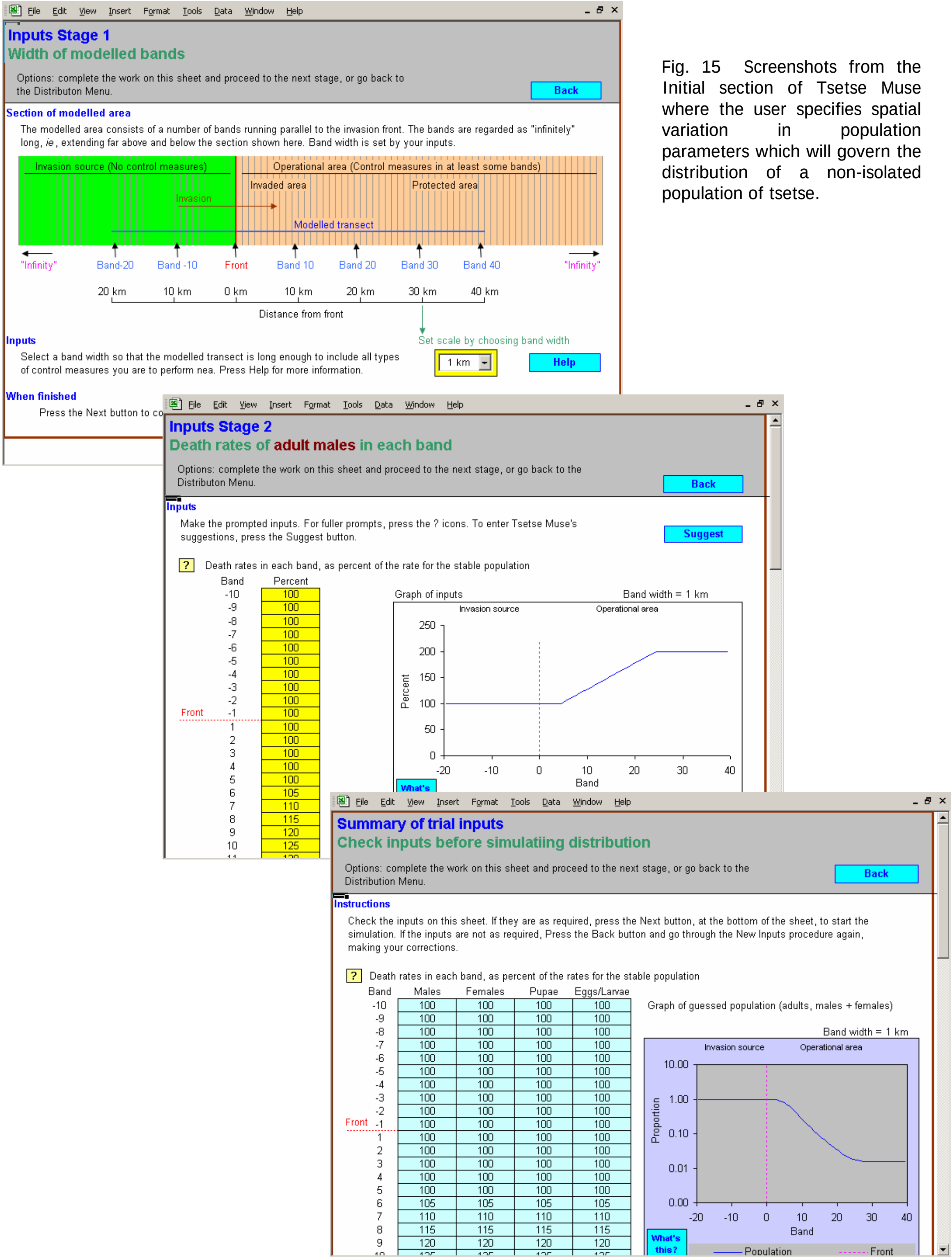


Fig. 15 Screenshots from the Initial section of Tsetse Muse where the user specifies spatial variation in population parameters which will govern the distribution of a non-isolated population of tsetse.

Inputs Stage 1

Width of modelled bands

Options: complete the work on this sheet and proceed to the next stage, or go back to the Distributon Menu.

Section of modelled area

The modelled area consists of a number of bands running parallel to the invasion front. The bands are regarded as "infinitely" long, *ie*, extending far above and below the section shown here. Band width is set by your inputs.

Inputs

Select a band width so that the modelled transect is long enough to include all types of control measures you are to perform nea. Press Help for more information.

When finished

Press the Next button to co

Inputs Stage 2

Death rates of adult males in each band

Options: complete the work on this sheet and proceed to the next stage, or go back to the Distributon Menu.

Inputs

Make the prompted inputs. For fuller prompts, press the ? icons. To enter Tsetse Muse's suggestions, press the Suggest button.

Death rates in each band, as percent of the rate for the stable population

	Band	Percent
	-10	100
	-9	100
	-8	100
	-7	100
	-6	100
	-5	100
	-4	100
	-3	100
	-2	100
Front	-1	100
	1	100
	2	100
	3	100
	4	100
	5	100
	6	105
	7	110
	8	115
	9	120
	10	125

Summary of trial inputs

Check inputs before simulatiing distribution

Options: complete the work on this sheet and proceed to the next stage, or go back to the Distribution Menu.

Instructions

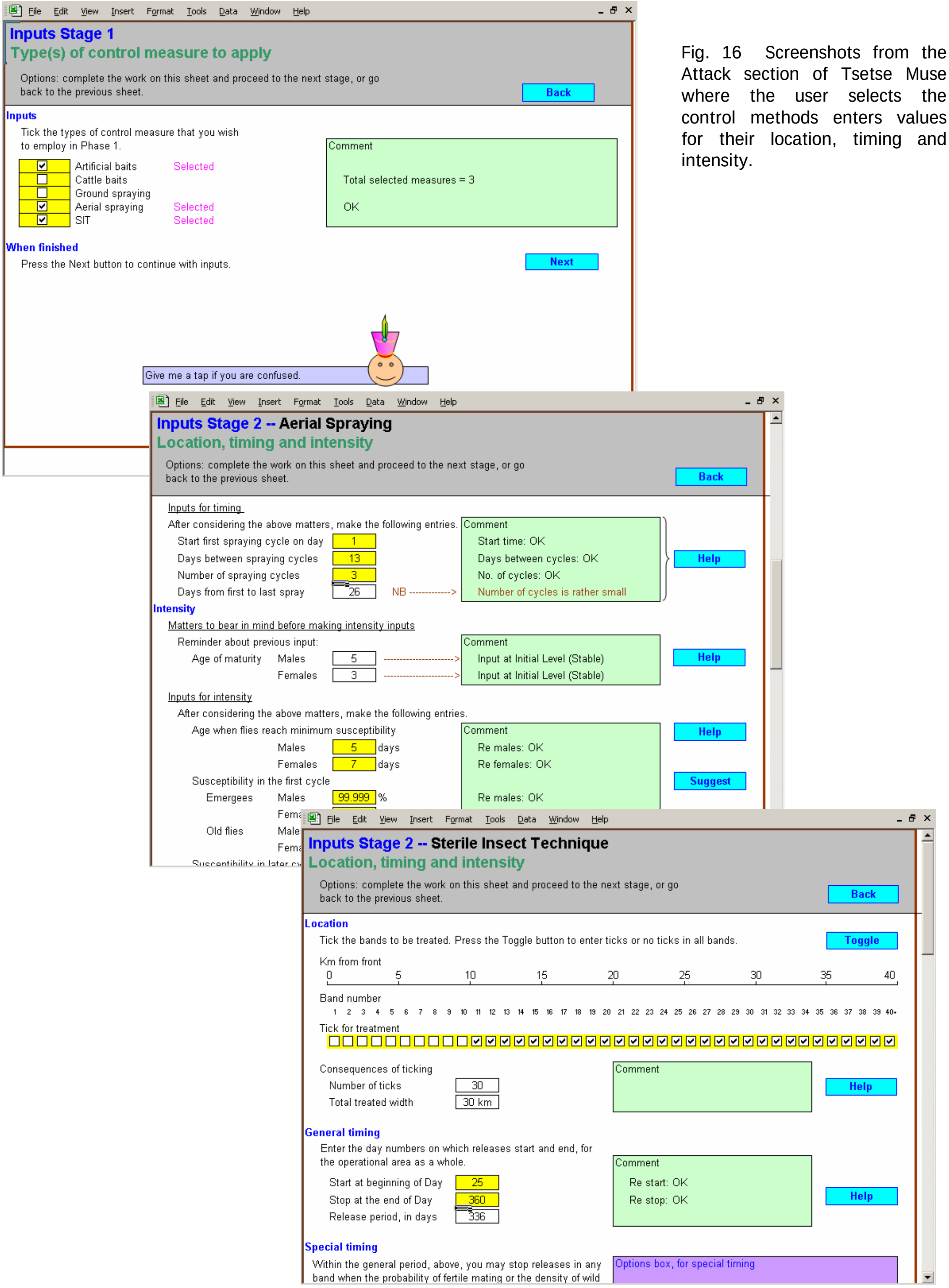
Check the inputs on this sheet. If they are as required, press the Next button, at the bottom of the sheet, to start the simulation. If the inputs are not as required, Press the Back button and go through the New Inputs procedure again, making your corrections.

Death rates in each band, as percent of the rates for the stable population

	Band	Males	Females	Pupae	Eggs/Larvae
	-10	100	100	100	100
	-9	100	100	100	100
	-8	100	100	100	100
	-7	100	100	100	100
	-6	100	100	100	100
	-5	100	100	100	100
	-4	100	100	100	100
	-3	100	100	100	100
	-2	100	100	100	100
Front	-1	100	100	100	100
	1	100	100	100	100
	2	100	100	100	100
	3	100	100	100	100
	4	100	100	100	100
	5	100	100	100	100
	6	105	105	105	105
	7	110	110	110	110
	8	115	115	115	115
	9	120	120	120	120

Attack

Having defined the population, the user can then attack it using various control techniques applied singly or in any spatial or temporal combination selected by the user. For each technique the user is asked to enter appropriate values relating to the timing and efficacy of the method. For example, for aerial spraying the user must enter the number of spraying cycles, the interval between cycles and the mortality produced by the insecticide. For the sterile insect technique, the user must enter values for the density and frequency with which sterile males are released and their competiveness. For all techniques, the timing of the operations must be specified and for non-solated populations, the user must also specify where the operation is applied.



Inputs Stage 1
Type(s) of control measure to apply

Options: complete the work on this sheet and proceed to the next stage, or go back to the previous sheet.

Inputs

Tick the types of control measure that you wish to employ in Phase 1.

- ☑ Artificial baits — Selected
- ☐ Cattle baits
- ☐ Ground spraying
- ☑ Aerial spraying — Selected
- ☑ SIT — Selected

Comment
Total selected measures = 3
OK

When finished

Press the Next button to continue with inputs.

Give me a tap if you are confused.

Inputs Stage 2 -- Aerial Spraying
Location, timing and intensity

Options: complete the work on this sheet and proceed to the next stage, or go back to the previous sheet.

Inputs for timing

After considering the above matters, make the following entries.

Start first spraying cycle on day: 1
Days between spraying cycles: 13
Number of spraying cycles: 3
Days from first to last spray: 26   NB ------------>

Comment
Start time: OK
Days between cycles: OK
No. of cycles: OK
Number of cycles is rather small

Intensity

Matters to bear in mind before making intensity inputs

Reminder about previous input:
Age of maturity   Males 5 ------------------->
Females 3 ------------------->

Comment
Input at Initial Level (Stable)
Input at Initial Level (Stable)

Inputs for intensity

After considering the above matters, make the following entries.

Age when flies reach minimum susceptibility
Males 5 days
Females 7 days

Susceptibility in the first cycle
Emergees   Males 99.999 %
Fema
Old flies   Male
Fema
Susceptibility in later cy

Comment
Re males: OK
Re females: OK
Re males: OK

Inputs Stage 2 -- Sterile Insect Technique
Location, timing and intensity

Options: complete the work on this sheet and proceed to the next stage, or go back to the previous sheet.

Location

Tick the bands to be treated. Press the Toggle button to enter ticks or no ticks in all bands.

Km from front: 0 5 10 15 20 25 30 35 40

Band number: 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40+

Tick for treatment: ☐ ☐ ☐ ☐ ☐ ☐ ☐ ☐ ☐ ☐ ☑

Consequences of ticking
Number of ticks: 30
Total treated width: 30 km

Comment

General timing

Enter the day numbers on which releases start and end, for the operational area as a whole.

Start at beginning of Day: 25
Stop at the end of Day: 360
Release period, in days: 336

Comment
Re start: OK
Re stop: OK

Special timing

Within the general period, above, you may stop releases in any band when the probability of fertile mating or the density of wild

Options box, for special timing

Fig. 16 Screenshots from the Attack section of Tsetse Muse where the user selects the control methods enters values for their location, timing and intensity.

Once all the conditions for the control interventions have been specified, the user can then run the simulation and watch the distribution of the population change as the methods are applied. At the conclusion of a particular simulation, the user can view a large number of graphs and tables summarising the operation and its impact on the tsetse population. These data can be saved as a scenario which can then be inspected at the user's convenience. Moreover, a tsetse population resulting from one phase of simulation can be selected as the starting population for a second phase, for up to five phases. This flexibility allows simulation of complex temporal and spatial combinations of techniques.

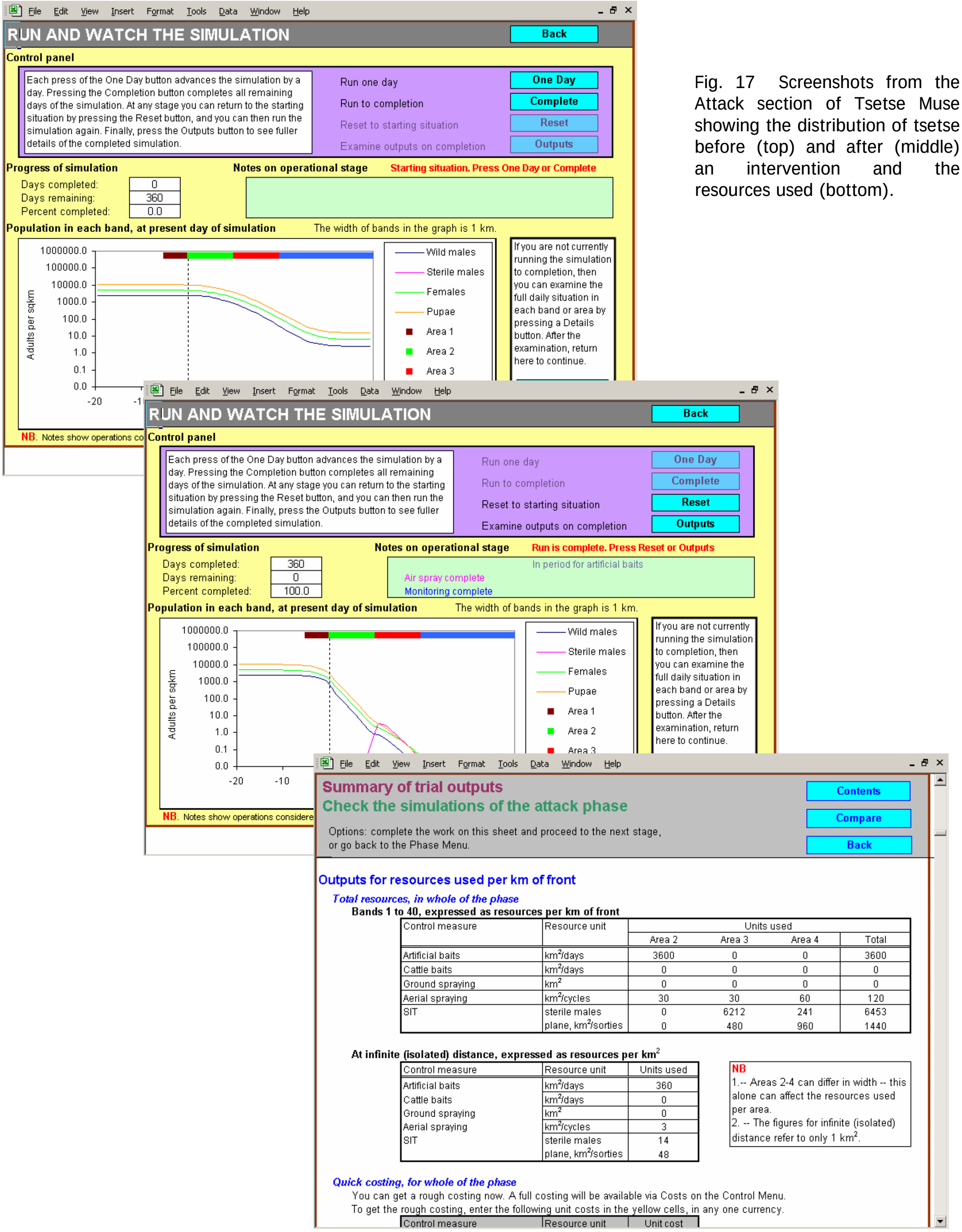


Fig. 17 Screenshots from the Attack section of Tsetse Muse showing the distribution of tsetse before (top) and after (middle) an intervention and the resources used (bottom).

RUN AND WATCH THE SIMULATION

Control panel

Each press of the One Day button advances the simulation by a day. Pressing the Completion button completes all remaining days of the simulation. At any stage you can return to the starting situation by pressing the Reset button, and you can then run the simulation again. Finally, press the Outputs button to see fuller details of the completed simulation.

Run one day
Run to completion
Reset to starting situation
Examine outputs on completion

Progress of simulation

Days completed: 0
Days remaining: 360
Percent completed: 0.0

Notes on operational stage Starting situation. Press One Day or Complete

Population in each band, at present day of simulation The width of bands in the graph is 1 km.

If you are not currently running the simulation to completion, then you can examine the full daily situation in each band or area by pressing a Details button. After the examination, return here to continue.

RUN AND WATCH THE SIMULATION

Control panel

Each press of the One Day button advances the simulation by a day. Pressing the Completion button completes all remaining days of the simulation. At any stage you can return to the starting situation by pressing the Reset button, and you can then run the simulation again. Finally, press the Outputs button to see fuller details of the completed simulation.

Run one day
Run to completion
Reset to starting situation
Examine outputs on completion

Progress of simulation

Days completed: 360
Days remaining: 0
Percent completed: 100.0

Notes on operational stage Run is complete. Press Reset or Outputs

In period for artificial baits
Air spray complete
Monitoring complete

Population in each band, at present day of simulation The width of bands in the graph is 1 km.

If you are not currently running the simulation to completion, then you can examine the full daily situation in each band or area by pressing a Details button. After the examination, return here to continue.

NB. Notes show operations considere

Summary of trial outputs

Check the simulations of the attack phase

Options: complete the work on this sheet and proceed to the next stage, or go back to the Phase Menu.

Outputs for resources used per km of front

Total resources, in whole of the phase

Bands 1 to 40, expressed as resources per km of front

Control measure	Resource unit	Units used			
		Area 2	Area 3	Area 4	Total
Artificial baits	km^2/days	3600	0	0	3600
Cattle baits	km^2/days	0	0	0	0
Ground spraying	km^2	0	0	0	0
Aerial spraying	km^2/cycles	30	30	60	120
SIT	sterile males	0	6212	241	6453
	plane, km^2/sorties	0	480	960	1440

At infinite (isolated) distance, expressed as resources per km^2

Control measure	Resource unit	Units used
Artificial baits	km^2/days	360
Cattle baits	km^2/days	0
Ground spraying	km^2	0
Aerial spraying	km^2/cycles	3
SIT	sterile males	14
	plane, km^2/sorties	48

NB
1.-- Areas 2-4 can differ in width -- this alone can affect the resources used per area.
2. -- The figures for infinite (isolated) distance refer to only 1 km^2.

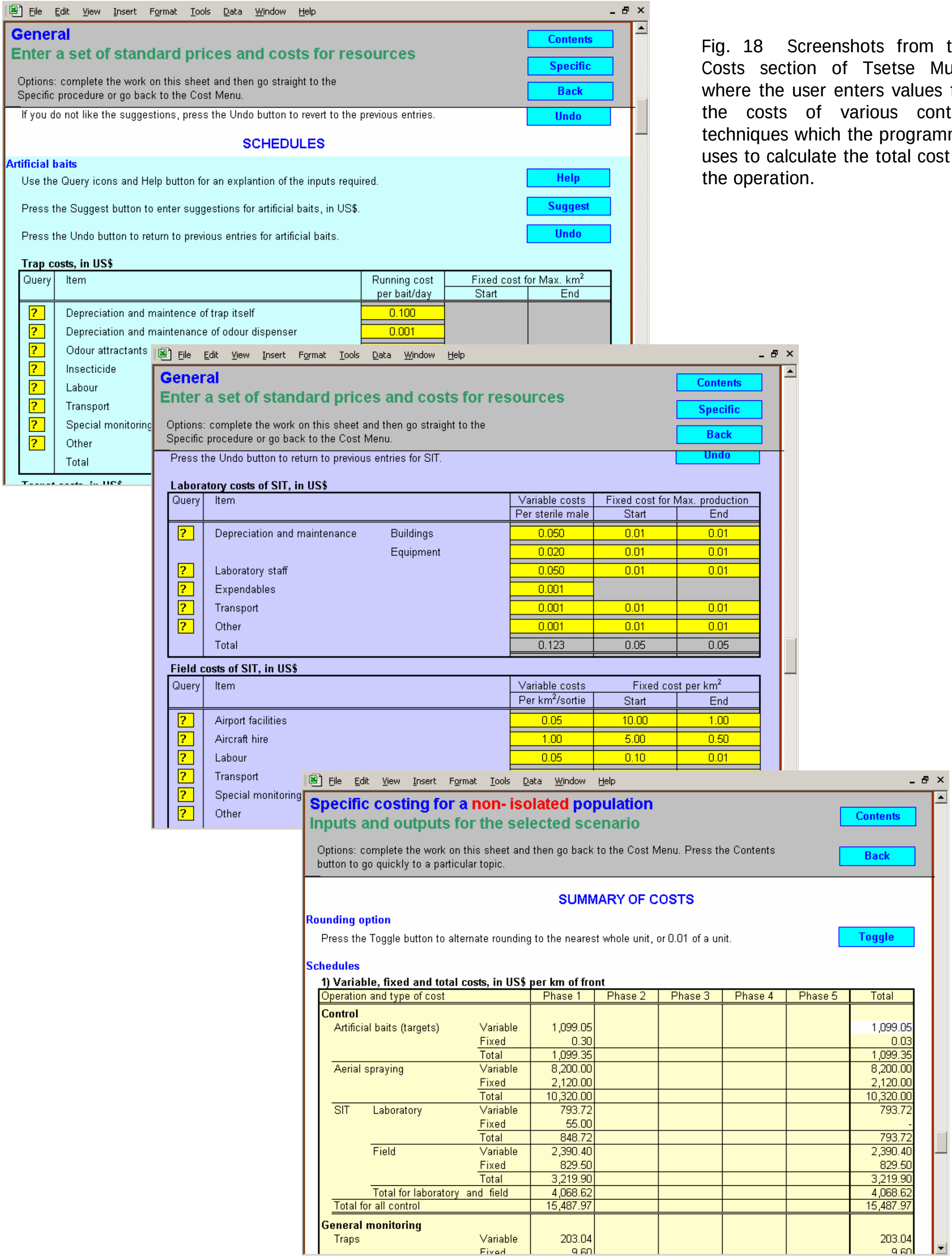
Quick costing, for whole of the phase

You can get a rough costing now. A full costing will be available via Costs on the Control Menu.
To get the rough costing, enter the following unit costs in the yellow cells, in any one currency.

Control measure	Resource unit	Unit cost

Costs

Finally, Tsetse Muse estimates the cost of the entire operation. As before, the user is asked to enter values for the direct and indirect costs of each control method and then the programme combines these values with data on the resources used (eg, numbers of baits deployed or sterile flies released) to estimates the total cost of the operation.



General

Enter a set of standard prices and costs for resources

Options: complete the work on this sheet and then go straight to the Specific procedure or go back to the Cost Menu.

If you do not like the suggestions, press the Undo button to revert to the previous entries.

SCHEDULES

Artificial baits

Use the Query icons and Help button for an explantion of the inputs required.

Press the Suggest button to enter suggestions for artificial baits, in US$.

Press the Undo button to return to previous entries for artificial baits.

Trap costs, in US$

Query	Item	Running cost per bait/day	Fixed cost for Max. km^2 Start	End
?	Depreciation and maintence of trap itself	0.100		
?	Depreciation and maintenance of odour dispenser	0.001		
?	Odour attractants			
?	Insecticide			
?	Labour			
?	Transport			
?	Special monitoring			
?	Other			
	Total			

General

Enter a set of standard prices and costs for resources

Options: complete the work on this sheet and then go straight to the Specific procedure or go back to the Cost Menu.

Press the Undo button to return to previous entries for SIT.

Laboratory costs of SIT, in US$

Query	Item		Variable costs Per sterile male	Fixed cost for Max. production Start	End
?	Depreciation and maintenance	Buildings	0.050	0.01	0.01
		Equipment	0.020	0.01	0.01
?	Laboratory staff		0.050	0.01	0.01
?	Expendables		0.001		
?	Transport		0.001	0.01	0.01
?	Other		0.001	0.01	0.01
	Total		0.123	0.05	0.05

Field costs of SIT, in US$

Query	Item	Variable costs Per km^2/sortie	Fixed cost per km^2 Start	End
?	Airport facilities	0.05	10.00	1.00
?	Aircraft hire	1.00	5.00	0.50
?	Labour	0.05	0.10	0.01
?	Transport			
?	Special monitoring			
?	Other			

Specific costing for a non- isolated population

Inputs and outputs for the selected scenario

Options: complete the work on this sheet and then go back to the Cost Menu. Press the Contents button to go quickly to a particular topic.

SUMMARY OF COSTS

Rounding option

Press the Toggle button to alternate rounding to the nearest whole unit, or 0.01 of a unit.

Schedules

1) Variable, fixed and total costs, in US$ per km of front

Operation and type of cost			Phase 1	Phase 2	Phase 3	Phase 4	Phase 5	Total
Control								
Artificial baits (targets)		Variable	1,099.05					1,099.05
		Fixed	0.30					0.03
		Total	1,099.35					1,099.35
Aerial spraying		Variable	8,200.00					8,200.00
		Fixed	2,120.00					2,120.00
		Total	10,320.00					10,320.00
SIT	Laboratory	Variable	793.72					793.72
		Fixed	55.00					-
		Total	848.72					793.72
	Field	Variable	2,390.40					2,390.40
		Fixed	829.50					829.50
		Total	3,219.90					3,219.90
	Total for laboratory and field		4,068.62					4,068.62
Total for all control			15,487.97					15,487.97
General monitoring								
Traps		Variable	203.04					203.04
		Fixed	9.60					9.60

Fig. 18 Screenshots from the Costs section of Tsetse Muse where the user enters values for the costs of various control techniques which the programme uses to calculate the total cost of the operation.

Dissemination workshops

Zimbabwe.

The Zimbabwe National Committee for Tsetse and Trypanosomiasis Control met at the Holiday Inn, Harare, on July 21st, from 1030-1630h, to draft a 5-year plan for the strategy of tsetse and trypanosomiasis control in Zimbabwe. The meeting was attended by 45 persons from Government departments, NGOs and the Zimbabwe Farmer's Unions. Professor Vale attended the meeting as an advisor and provided an update on the development of the Tsetse Muse programme. Professor Vale dealt with several aspects of the technology of tsetse control but his main contribution was to describe what Tsetse Muse indicated about the costs and effectiveness of the sterile insect technique. In particular, he warned that this technique is inappropriate for tsetse – an important matter since there were tentative plans to employ it in Western Zimbabwe. This warning seemed to be well received.

A course on the use of Tsetse Muse was held at the Headquarters of the Tsetse and Trypanosomiasis Control Branch, on Aug 2nd – 3rd. It was attended by eight research officers of the Branch and also by an officer, Mr J. Esterhuizen, from the Onderstepoort Veterinary Institute, Pretoria. The first day of the course was concerned with modelling tsetse populations in general and showing how simple models can be written in Excel. The second day was devoted to demonstrating the use of Tsetse Muse, allowing the trainees to model the cost and efficacy of the various control measures that the Branch is considering for inclusion in its 5-year plan. These techniques included ground spraying, aerial spraying, the sterile insect technique and various bait methods. Tsetse Muse worked well and the trainees were able to cope with it satisfactorily. The programme was left on their computers to allow them to explore it further on their own.

Ethiopia

Vale and Torr attended the ISCTRC meeting in Addis Ababa where they made a formal presentation of Tsetse Muse, displayed a poster of the tsetse.org website/CD-ROM and had several informal opportunities to discuss and/or demonstrate the use of Tsetse Muse with some of the ~300 scientists attending the meeting.

The technological priorities of the meeting can be gauged by the number of times differents method of tsetse control were mentioned in the opening speeches. Insecticide-treated cattle, traps and targets were each mentioned twice and aerial spraying was mentioned three times. The sterile insect technique however was mentioned 18 times.

The oral presentation was made by Vale using a novel and custom-made system based on Excel, with animations produced via Visual Basic for Applications. The introduction to the presentation suggested that past experience alone could be a misleading guide to present planning since history is capable of many interpretations. Models offering facilities for what-if analyses could assist provided the models were suitably comprehensive, ie, not the simple growth equations that were intended to model insects with non-overlapping generations. It was indicated that the comprehensive modelling available via Tsetse Muse could help PATTEC in the following topics.

- Identification of the strengths and weaknesses of SIT. The outputs suggest that SIT will be a serious hindrance to the cost-effectiveness and image of PATTEC-related operations. Delegates were challenged to dispel these anxieties.

- Optimising the barriers that can be produced by various control measures.

- Identifying the causes of residual pockets of infestation and designing methods of avoiding or removing the pockets.

- Warning of the dangers of mosaic-type integration of contrasting control measures, and identifying means of overcoming these dangers.

- Assessing the benefits that could arise from constructive tinkering with the weapons in the tsetse control armoury. Sterile insects, rather than SIT per se, could be helpful here.

- Offering a novel teaching aid.

- Help with interpretation of bygone operations.

Immediately following the presentation, the following comments were made.

- Udo Feldman (IAEA Vienna) made a statement that: 1) the model was faulty because it did not allow for the uneven distribution of tsetse and control measures, and 2) the alternatives to SIT had proved technically inadequate during the history of the RTTCP. Vale indicated that the model did indeed allow for the uneven distribution of tsetse (as in the MVE article) and cattle (as in the talk). Vale also noted that the statement exemplified one of my main points of the presentation: that history is indeed subject to contrasting interpretations.

- A francophone delegate expressed disappointment that the talk did not go into much scientific detail. Vale responded that the time allowed for the talk (15 mins) prevented entering into such detail – the intention had been merely to stimulate interest in Tsetse Muse by exemplifying the range of things it could address.

- John Kabayo (PATTEC) was worried that Tsetse Muse could be seen as deliberately biased against SIT. Vale indicated that the model had made special attempts to avoid any inbuilt bias since the user was able to make or avoid assumptions to suit his own inclinations. The model was intended merely to expose the arithmetical implications of user-specified inputs, not support any preconceptions of the authors.

As a global response to all “questioners”, Vale stressed that the creation of Tsetse Muse was motivated only by the wish to be of maximum possible help to the technical aspects of PATTEC.

The talk had a substantial impact, as evidenced by the demand to obtain copies of the tsetse.org CD and reprints of the Vale & Torr article recently published in *Medical and Veterinary Entomology*. Nearly 300 copies of the tsetse.org CD and ~50 copies of the article were distributed during the meeting.

At the conclusion of the entomological session, the Chairman, Dr Francis Oloo, allowed three persons to speak from the floor. Two of these persons indicated that they objected to, what they saw as, the aspersions cast on SIT but did not say anything about why these aspersions were deemed to be invalid. The third speaker, from West

Africa, was more specific: he said that the success of SIT against *G. austeni* on Zanzibar, and against screw-worms and fruit flies elsewhere, was clear proof that SIT should be an important tool for PATTEC. The Chairman did not permit Vale to respond to these comments and re-iterate the points made previously (Vale & Torr, 2005) that the experiences with a small pocket of tsetse infestion on Zanzibar, and the results with faster breeding insects, cannot be extrapolated to prompt and cost-effective success of SIT with tsetse on the mainland. In considering the final report of the meeting, the Chairman indicated that the model was to be characterised as biased against SIT. However, at no point in the meeting had anybody indicated a cause or effect of bias.

Uganda

Torr was invited to a workshop an IFAD-supported meeting on 'Decision support for trypanosomiasis control in Uganda'. The workshop formed part of a collaborative project between ILRI, FAO and the Coordinating Office for the Control of Trypanosomiasis in Uganda (COCTU). Amongst other things, the project aims to improve decision making and the use of decisions tool for trypanosomiasis control in Uganda.

Uganda is currently planning an 'Integrated area-wide programme for creation of tsetse and trypanosomiasis free-zones in Uganda' as part of the PATTEC initiative. The Ugandan programme development document indicates that the programme will aim to eliminate tsetse (*G. fuscipes fuscipes* and *G. pallidipes*) from 40,000 km^2 of Uganda using the sterile insect technique following suppression of the tsetse population using baits and aerial spraying. The programme is estimated to cost US$53 million over ten years, of which US$17 million is required to establish tsetse rearing facilities.

At the meeting, Torr gave a presentation on the use of Tsetse Muse to assess the impact and cost of various methods to control tsetse. The presentation not only gave a brief summary of the mechanics of using the programme but also used some of the outputs from Tsetse Muse to illustrate features of particular techniques. These included the importance of using a barrier to protect areas controlled with aerial spraying, the relative speed of different techniques and the rebound of a population that occurs if suppression is relaxed as sterile flies are released. Copies of the tsetse.org CD were distributed to all participants.

Following the presentation by Torr, Tim Robinson (FAO) made a presentation entitled "Dealing with tsetse: looking for a cost-effective approach to poverty alleviation'. The presentation combined (i) GIS-based data on the distribution of livestock, vectors and disease in Uganda, (ii) entomological outputs from Tsetse Muse, (iii) financial data on the costs of control from Uganda's programme development document and (iv) estimates of the likely benefits of tsetse control from herd models developed by Dr Alex Shaw. The main purpose of the presentation was to illustrate a rational framework for developing strategies to control trypanosomiasis. However, some preliminary conclusions arising from the work were that for Uganda, the cost of different control methods increased in the order insecticide-treated cattle, traps, aerial spraying, sterile insect technique. Moreover, apart from the islands in Lake Victora, there do not appear to be any truly isolated tsetse populations in Uganda and in these circumstances, SIT is very difficult to justify.

Output 3. Lessons learned

This report show only a little of what can be modelled using Tsetse Muse. Moreover, Tsetse Muse can assess sensitivity to operational imperfections and the likely benefits of improved control methods; it can also distinguish technical problems that are potentially superable, and fundamental biological limits that are not. However, work to date exemplifies what can be provided. The merits of putting the programme in easy reach of non-specialist modellers depends on two matters: the validity of the model, and the importance of its outputs.

Validity

Biology. The present type of model that tracks each component of the population is more realistic than the growth equations commonly used to predict the effects of control measures (reviewed by Barclay, 2005). Such equations do not allow for population structure and the long time needed for its adjustment when SIT is applied to long-lived insects – an important matter since the demand for sterile males is greatest in the adjustment period. Admittedly, however, the present simulations of biological matters are imperfect. For example, the vectorial index is only a rough guide to epidemiological impact. The natural death rates and their change with age and population density are approximate. Nevertheless, any input changes would produce only slight variations in output flavour since one cannot escape the fly's slow breeding, long life, and its way of transmitting disease. Moreover, the outputs accord with data for field operations and show more fully why the few SIT campaigns carried out on the mainland were disappointing (Feldmann, 2004).

Costs. – The model confirms the generally accepted view that ITC is much cheaper than SIT, but the extent to which ITC appears cheaper may seem incompatible with data commonly used to compare costs (*eg*, Allsopp & Hursey, 2004; Leak, 1999). However, such data must be interpreted cautiously since they do not always refer to the various techniques being operated under identical conditions to tackle the same type of problem and with uniform standards of planning, supervision and accounting. Moreover, the data assume that all cattle present are treated with insecticide, and do not allow for recent reductions in insecticide prices. However, in some respects the present costs put SIT in too harsh a light. For example, where no cattle occur it is necessary to consider insecticidal techniques other than ITC, and some of these are not so grossly cheaper than SIT (Leak, 1999). Against this, present studies made optimistic assumptions about the costs and competitiveness of sterile males and ignored the problem that SIT costs increase relative to insecticides when multi-species infestations are tackled (Molyneux, 2001).

Case studies. – The distinctive efficacy of ITC in relation to SIT is due to the fact that ITC immediately increases deaths, so that the results with ITC apply to most insecticidal techniques. Moreover, the results also apply to removal trapping, a killing system that covers the threat of insecticide resistance. The poor indications for the performance of SIT that releases sterile males as adults are not entirely applicable to the introduction of sterile male pupae. For example, the survival of the sterile males might be improved by pupal releases but there would be no opportunity to feed trypanocides; pupae cannot be introduced satisfactorily by plane, so requiring the inconvenience and cost of frequent ground access. Other techniques that directly reduce births may be a little better than SIT. For example, auto-sterilisation of wild males and females (Vale *et al.*, 1986) ensures that fertile-mated females do not reproduce, even if they do live long.

Implications for the use of SIT

Currently, several African governments are considering investing in expensive SIT facilities and in the case of Ethiopia they are already doing so. Is this investment justified? Tsetse Muse allows the politico-economic wrangles that surround this question to be settled largely by biological outputs. First, SIT lacks particular strengths, *eg*, it reduces tsetse abundance at a distance and diminishes birth rates, but so do insecticides. Second, SIT for tsetse has severe and inescapable weaknesses that have had little or no consideration to date: the technique is slow to have an effect, gives no direct protection against invasion, and increases the mean age of the population. Hence, several tenets of SIT, as stated or implied by Feldmann (2004), need reappraisal.

1) The achievements of SIT with screw-worms do not prove the applicability of SIT against tsetse. Screw-worms can breed quickly, and it is their breeding, not feeding, that is the immediate problem. Whereas SIT does reduce breeding , it does not affect directly the number of feeding males and females.

2) Success on islands should not be extrapolated to mainland success. All control methods become more problematical when invasion threatens, but this is particularly severe with SIT.

3) Although the high costs of SIT drop rapidly when the starting density of tsetse is lowered, the costs of ITC decline at about the same proportional rate when the population is suppressed enough for SIT to approach cost-competitiveness. It is difficult to view SIT as preferable to briefly continuing the suppression technique.

4) Present work does not simply confirm that SIT is best used with prior suppression, it emphasises how crucial the suppression is. Hence, it is inappropriate to make theoretical comparisons between SIT and insecticides as if SIT stands alone. It matters little that SIT itself is insecticide-free and can need less ground access than some insecticidal techniques.

5) If it *is* decided to use SIT, it would be cheaper, faster and less of a disease risk to employ it with continued insecticidal suppression. Stochastic modelling confirms this (Hargrove, 2005). Admittedly, continued suppression can appear sacrilegious since it will kill many of the costly sterile males. However, wild males are killed also, so the sterile:wild ratio is unaffected.

6) Since SIT takes several seasons to become effective, there is reduced scope for improving its cost-effectiveness by applying it in a season that is naturally unfavourable to tsetse.

7) It could be disastrous if SIT were used in a mosaic with other control measures. Breeding females could spread from the SIT-treated area into any adjacent insecticide-treated area for many months, so preventing quick eradication there. Females that emerge and are fertile-mated in the insecticide-treated area could diffuse to the SIT-treated area to breed safely.

Furthermore, it is incorrect that SIT “takes care of the last fly” and “also deals with newcomers” (U. Feldmann & R. Mattioli quoted in Ahmed, 2003). SIT does nothing significant to the last fly – it merely waits for that fly to die naturally. Moreover, SIT does not kill the newcomers and so hardly deals with the problem that most will be fertile-mated females and potentially infectious.

To assess fairly the performances of SIT and insecticides it has been taken that each method is used properly. It is difficult to see how insecticides or traps could produce the marked suppression required for SIT without also being able to achieve eradication if used correctly. However, insecticides are not always used correctly, as when they fail to neutralise invasion pressure or are applied patchily, so leaving residual *foci* (Hargrove, 2003). The spread of tsetse from the invasion source or *foci* then creates the false impression that insecticides cannot clear tsetse from all or much of the operational area. In these circumstances it would be simpler and quicker to rectify the use of insecticides, rather than switching to SIT. Indeed, the switch could allow the *foci* of breeding, infective tsetse to expand unrestrictedly for ~6 months, perhaps increasing by many square kilometres the area to be covered by SIT.

Contribution of Outputs

All the project outputs were achieved. These included:

- A general simulation model of the impact of any tsetse control technique on tsetse populations
- A user-friendly and interactive utility to enable non-specialists to use the simulation model
- Decision support system disseminated to target institutions

The project's duration was only 10 months and thus it is too early to assess the final impact of the research on the project's goal. Nonetheless, the project already shows signs of having an impact on national policies and decision-making in relation to the control of tsetse-borne trypanosomiasis.

Promoting rational interventions against tsetse

On a continental scale, the extent and impact of trypanosomiasis is probably worse than it was 50 years ago. Alleviating the extent of tsetse would have an enormous impact on the livelihoods of the poor in sub-Saharan Africa. This lack of progress is because, at least in part, most recent interventions against tsetse have been applied on too small a scale. To achieve greater impact, existing methods of tsetse control need to be applied on a larger scale.

Currently, large-scale programmes to control tsetse are being developed by national, regional and donor agencies in ten countries as part of the PATTEC initiative. These programmes aim to eliminate trypanosomiasis over large areas (eg, >25,000 km^2 per country) using a range of control methods that include not only bait techniques but also aerial spraying, ground spraying and the sterile insect technique (SIT). The scale, complexity and cost of these operations mean that effective planning is not only crucial but more difficult. Consequently, there is a pressing need for more specialised decision support tools to assist donor and government agencies in this planning process. Tsetse Muse will assist these countries to develop cost-effective strategies. The most important contribution, we believe, in this regard is the warning (Vale & Torr, 2005; Torr *et al.,* 2005) against the proposed use of SIT in integrated management of tsetse populations. However, present outputs from Tsetse Muse show that even with various insecticidal techniques the planning of integrated campaigns, such as those envisaged by PATTEC, can be difficult. On the other hand, Tsetse Muse can help to identify the best integration systems, and to find appropriate methods of avoiding or removing residual pockets of infestation.

Use of decision support tools
During the course of the project, scientists and institutions concerned with formulating national policies for controlling trypanosomiasis in several tsetse-affected countries were provided the Tsetse Muse programme and examples of its application to their particular countries. In the case of Uganda for instance, senior staff involved with developing and implementing the ADB-supported initiative were provided with specific examples of how Tsetse Muse and other decision support tools can help them develop a cost-effective strategy for controlling tsetse. For Botswana, Tsetse Muse has helped the Tsetse Control Division assess how the use of aerial spraying and artificial baits might be combined to eliminate tsetse from the country cost-effectively.

Capacity building
Tsetse Muse provides a novel means of training scientists and policy makers in the best use of techniques to control tsetse. During the course of this project, *Tsetse Muse* and the associated information on tsetse biology and control available at www.tsetse.org, were used in the training of veterinary students and junior scientists from national veterinary insitutions in Ethiopia, Tanzania and Zimbabwe.

Further development of decision support tools for trypanosomiasis
Tsetse Muse is far from complete but it is anticipated that it will evolve with contributions from a range of scientists, so enhancing the services offered, improving its authority and broadening its ownership. For example, it would be useful to expand the model's treatments of costs and trypanosomiasis risk, and to enhance the section on economic analysis. The collaboration between economists, GIS specialists and entomologists contributing towards Uganda's plans for controlling trypanosomiasis exemplify this multidisciplinary approach.

References

Ahmed, K. (2003) Tsetse eradication programme under fire. *The Lancet Infectious Diseases* **3**, 4.

Brightwell, B., Dransfield, B., Maudlin, I., Stevenson, P., and Shaw, A. (2001). Reality v. Rhetoric – a Survey and Evaluation of Tsetse Control in East Africa. *Agriculture and Human Values* **18**, 219-233.

Budd, L.T. (1999) DFID-funded tsetse fly and trypanosomiasis research and development since 1980 – an economic analysis. DFID LPP/AHP. pp. 123.

Hargrove, J.W. (1994) Reproductive rates of tsetse flies in the field in Zimbabwe. *Physiological Entomology* **19**, 307-318.

Hargrove, J.W. (1995) Towards a general rule for estimating the day of pregnancy of field-caught tsetse flies. *Physiological Entomology* **20**, 213-223.

Hargrove, J.W. (1999) Reproductive abnormalities in field tsetse flies in Zimbabwe. *Entomologia Experimentalis et Applicata* **92**, 89-99.

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. (2003) Optimized simulation of the control of tsetse flies (Glossina pappidipes) and G.m. morsitans using odour-baited targets in Zimbabwe. *Bulletin of Entomological Research* **93**, 19-29.

Hargrove, J. W., Omolo, S., Msalilwa, J.S.I. & Fox, B. (2000) Insecticide-treated cattle for tsetse control: the power and the problems. *Medical and Veterinary Entomology*, **14**, 123-130.

Hargrove, J.W., Torr, S.J. & Kindness, H.M. (2003). Insecticide-treated cattle against tsetse (Diptera: Glossinidae): what governs success? *Bulletin of Entomological Research*, **93**, 203-217.

Kabayo, J.P. (2004) The Pan African Tsetse and Trypanosomiasis Eradication Campaign. Paper presented at the AfriCANDO Conference 2004, Miami, Florida 16-18 September 2004.

Maudlin, I., Holmes, P.H. & Miles, M.A. (2004) The Trypanosomiasies. 614 *pp*. CABI International, Wallingford, UK.

Molyneux, D.H (2001) Sterile insect release and trypanosomiasis control: a plea for realism. *Trends in Parasitology* **17**, 413-414.

Rogers, D.J. & Randolph, S.E. (1990) Estimation of rates of predation on tsetse. *Medical & Veterinary Entomology* **4**, 195-204.

Rogers, D.J. & Randolph, S.E. (2002) A response to the aim of eradicating tsetse from Africa. *Trends in Parasitology* **18**, 534-536.

Taverne, J. (2001) Trypanosomes on the Web. *Trends in Parasitology* **17**, 49.

Vreysen, M.J.N., Saleh, K.M., Ali, M.Y., Abdulla, A.M., Zhu, Z-R., Juma, K.G., Dyck., V.A., Msangi, A.R., Mkonyi, P.M. & Feldmann, H.U. (2000). The use of the sterile insect technique (SIT) for the eradication of the tsetse fly *Glossina austeni* (Diptera: Glossinidae) on the Island of Unguja (Zanzibar). *Journal of Economic Entomology* **93**, 123-135.