

User-friendly models of the costs and efficacy of tsetse control: application to sterilizing and insecticidal techniques

G. A. VALE and S. J. TORR

Natural Resources Institute, University of Greenwich, Chatham, U.K.

Abstract. An interactive programme, incorporating a deterministic model of tsetse (Diptera: Glossinidae) populations, was developed to predict the cost and effect of different control techniques applied singly or together. Its value was exemplified by using it to compare: (i) the sterile insect technique (SIT), involving weekly releases optimized at three sterile males for each wild male, and (ii) insecticide-treated cattle (ITC) at 3.5/km². The isolated pre-treatment population of adults was 2500 males and 5000 females/km²; if the population was reduced by 90%, its growth potential was 8.4 times per year. However, the population expired naturally when it was reduced to 0.1 wild males/km², due to difficulties in finding mates, so that control measures then stopped. This took 187 days with ITC and 609 days with 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, tsetse control by increasing deaths is more appropriate than reducing births, and SIT is particularly inappropriate. User-friendly models can assist the understanding and planning of tsetse control. The model, freely available via <http://www.tsetse.org>, allows further exploration of control strategies with user-specified assumptions.

Key words. *Glossina*, insecticide-treated cattle, mathematical model, population dynamics, sterile insect technique, tsetse, tsetse control, Africa.

Introduction

Strategies for controlling several insects of medical and veterinary importance are based on mathematical models.

Correspondence: G. Vale, 93, The Chase, Mount Pleasant, Harare, Zimbabwe. Tel: 263 4304902; E-mail: gvale@healthnet.zw

The Ross–Macdonald model (Ross, 1911; Macdonald, 1957) and its elaborations (e.g. Anderson & May, 1991; Smith & Ellis McKenzie, 2004) rationalized strategies to control malaria for more than 50 years. More recently, population models of *Aedes aegypti* L. (Focks *et al.*, 1993a, b; Maguire *et al.*, 1999) and *Lucilia sericata* Meigen (Fenton *et al.*, 1999; Wall *et al.*, 2000) have helped to design strategies for controlling dengue and sheep strike. Paradoxically, however, the control of tsetse-borne trypanosomiasis has not been generally guided by models, even

though we know more about the bionomics of tsetse (*Glossina* spp.) than the mosquito vectors of malaria and dengue and hence have reliable models for tsetse and trypanosomiasis (e.g. Rogers, 1988; Hargrove, 2003). Should models play a bigger part in tsetse control?

Although tsetse can be controlled by several methods (Hargrove, 2003), the flies are still widely distributed (Rogers & Robinson, 2004). Part of the problem is that donors and many African governments have reduced their commitment to tsetse control, leaving operations to local communities and other inexperienced agencies. These agencies often need help to select the appropriate method and its best use – matters in which models could assist. However, existing models are inaccessible to the general user (Hargrove, 2003). To improve accessibility, a user-friendly programme called 'Tsetse Plan' has been developed and is freely available via the world-wide web at <http://www.tsetse.org>. This helps non-specialists to develop a fully costed plan of control in relatively small areas (~1000 km²) using bait techniques such as odour-baited targets and insecticide-treated cattle (ITC).

The need for a more sophisticated programme is suggested by the recent inception of the Pan-African Tsetse and Trypanosomiasis Eradication Campaign (Feldmann, 2004). This initiative encourages consideration of baits, spraying measures and the sterile insect technique (SIT) to control tsetse over large areas (i.e. >10 000 km²). In particular, SIT is promoted (Feldmann, 2004) following its use to eradicate *Glossina austeni* Newst. on Unguja Island, after initial suppression by baits (Vreysen *et al.*, 2000). The increased scale and complexity of operations make planning more difficult. For example, where and when should invasion barriers be formed and what techniques should they employ? If baits are to be used to suppress a population prior to SIT, should they be removed when SIT begins, as occurred when tackling the worst infestation on Unguja Island (Vreysen *et al.*, 2000)?

The choice of control technique is sometimes limited absolutely. Aerial spraying is dangerous among mountains; ground spraying with residual insecticide can be banned in nature reserves; ITC is impossible where cattle are absent. However, much of the remaining choice involves highly debatable opinion. For example, it is sometimes implied that the effectiveness of SIT for screw-worms, *Cochliomyia hominivorax* Coquerel, shows that SIT will be satisfactory for tsetse (Feldmann, 2004). Against this, tsetse and screw-worms are different insects and cause trouble in distinctive ways. Not surprising, therefore, there are polarized assessments of SIT for tsetse. Some say 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). Others regard SIT as 'inappropriate, unaffordable, unsustainable and irrelevant' (Molyneux, 2001) and question its efficacy (Rogers & Randolph, 2002; Hargrove, 2003). In this and other

disputes, models would help if all sides could enter the inputs they consider appropriate and it became possible to identify conclusions that are materially the same whatever the inputs.

There is therefore a need for a model-based programme somewhat similar to Tsetse Plan, but allowing comparisons between a wider variety of control techniques. Such a programme, called Tsetse Muse, is being developed and can be accessed from www.tsetse.org. Ideally it will evolve with extensions and updates suggested by many persons. However, the programme is already usable. This study exemplifies the value of Tsetse Muse by using it to compare two control strategies: reducing the births and increasing the deaths, taking SIT and ITC as case studies. As the strategies are biologically distinct, it is appropriate to focus primarily on their biological powers, but cost must be considered to see whether the stronger strategy is economically acceptable.

Materials and methods

Model

The tsetse population comprised: (i) pupae, (ii) wild adult males, (iii) sterile adult males, (iv) virgin females, (v) breeding females, i.e. fertile-mated in time to produce the next larva, (vi) sterile-mated females, and (vii) 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, i.e. 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 1 day. After each wave the displayed data were summarized and plotted against time.

Values for the parameters controlling all calculations can be specified by the user. For present purposes the values were based on the following assumptions.

Standard population

The baseline tsetse population, pre-intervention, was stable at an average daily temperature of 25°C (Table 1). Females mated only once and lived for up to 178 days, i.e. 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

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

	Males	Females	Source§
Adult flies per km ²	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*	0.0614	0.0307	M, H
First day	0.1421	0.1362	M, H
Young adult†	0.0284	0.0136	M, H
Last full day‡	0.0852	0.0409	M, H
Daily displacement, m, average*	249	367	M, V, L

*Rates vary with age, as discussed in the text.

†Days 10–15 for males, 10–50 for females.

‡All remaining flies died at the start of the next day.

§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.

probability of 0.10 if there was only one mature male per square kilometre. Females mated less than 5 days, i.e. 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, i.e. 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.

Density dependence

It was assumed that field populations stabilize 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, i.e. females plus wild and sterile males. For pupal mortality the reference was the daily rate of larval deposition, i.e. 409/km²/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

Two types of area were considered. 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, i.e. 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.

Control measures and costs

SIT. Sterile males, 3 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 sterilizing 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, Zimbabwe), so that the release cost is £0.45/km²/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/km².

Although 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 $1 - 0.97^n$ (Vale & Torr, 2004), which indicates a rate of 0.1 when 3.5 cattle/km² are treated. To check this, let us say that there are a total of 40 cattle/km². 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, because 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

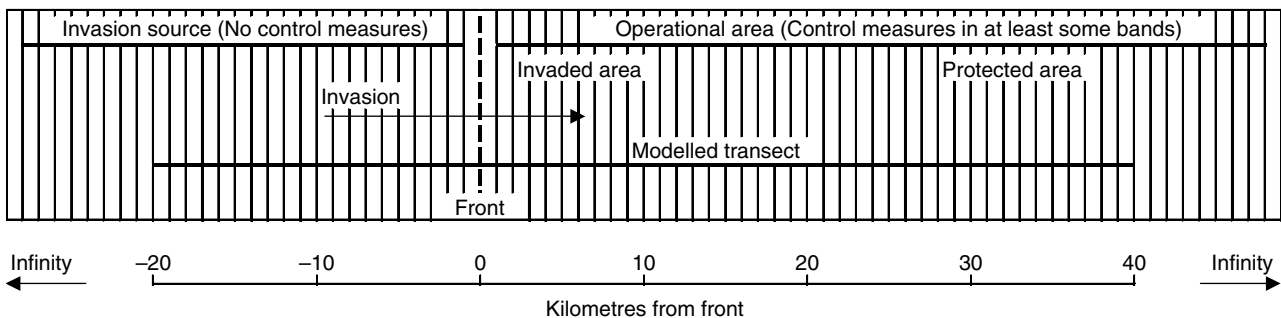


Fig. 1. Modelled transect through the non-isolated operational area and its invasion source. The whole of the mapped area consists of imaginary bands, 1-km wide, extending for many kilometres up and down the page. Other bands were present to an effectively infinite distance to the left and right, but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

(personal communication, F. O'Shea, Appropriate Applications Ltd, Berkhamstead, U.K.). With dilution at 2000:1 and spraying at 2 L per animal per fortnight, the cost becomes £0.001/animal/day. This was multiplied by 10 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/km² 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 because 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, i.e. 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, i.e. 17 days.

Results

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

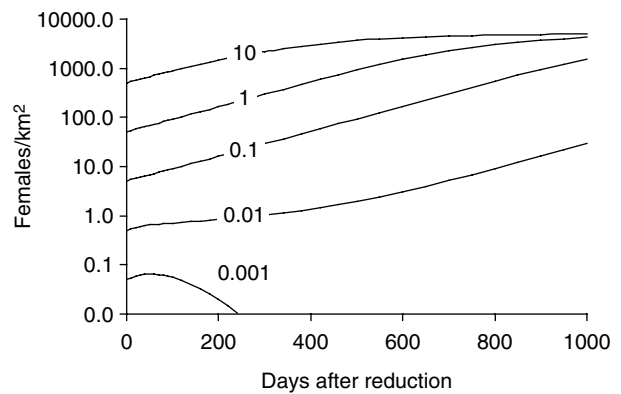


Fig. 2. Numbers of adult females per square kilometre in days following various instant reductions in population density, to levels of 10%, 1%, 0.1% and 0.001% of stable density. The reductions applied equally to pupae and adults of each age and sex, so that the sex ratio and age structure of the population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

only 0.01%, growth was rapid initially because 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/km² accord with field observations of mating difficulties at or near such densities (Glasgow, 1963).

As the modelled population eventually expires naturally when the density of wild adult males drops below 0.2/km², 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/km². 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/km².

Control of isolated populations

Optimization 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. Although 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

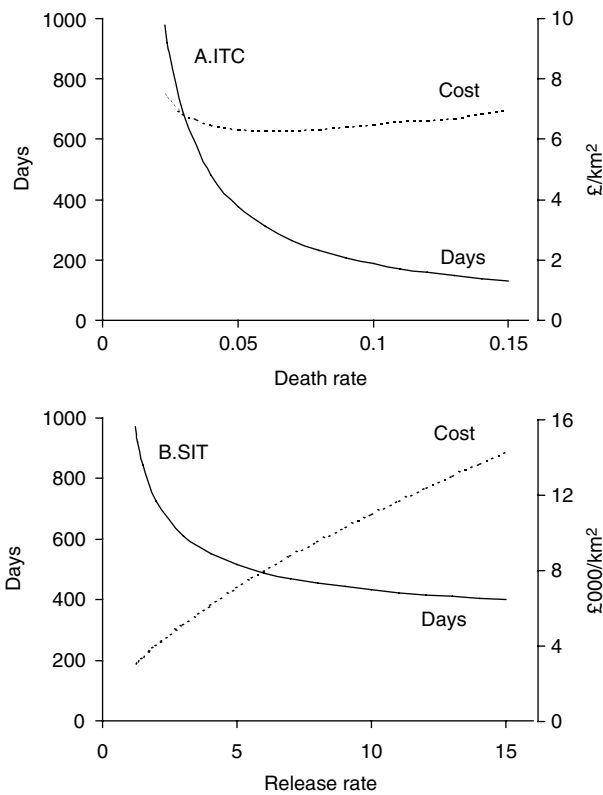


Fig. 3. Days required for eradication (solid line) and costs (broken line), at various daily death rates imposed by insecticide-treated cattle (ITC) or various release rates with sterile insect technique (SIT). Each technique was used alone against an isolated population, without prior suppression. Cost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

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. 3B). 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, i.e. 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).

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, i.e. around 5:1 initially, rising to about 400:1 after 2 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 £4420. This cost is 22% lower than the cost of £5640 when the release rate was steady at 3.55, i.e. 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.

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. 4A1), 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

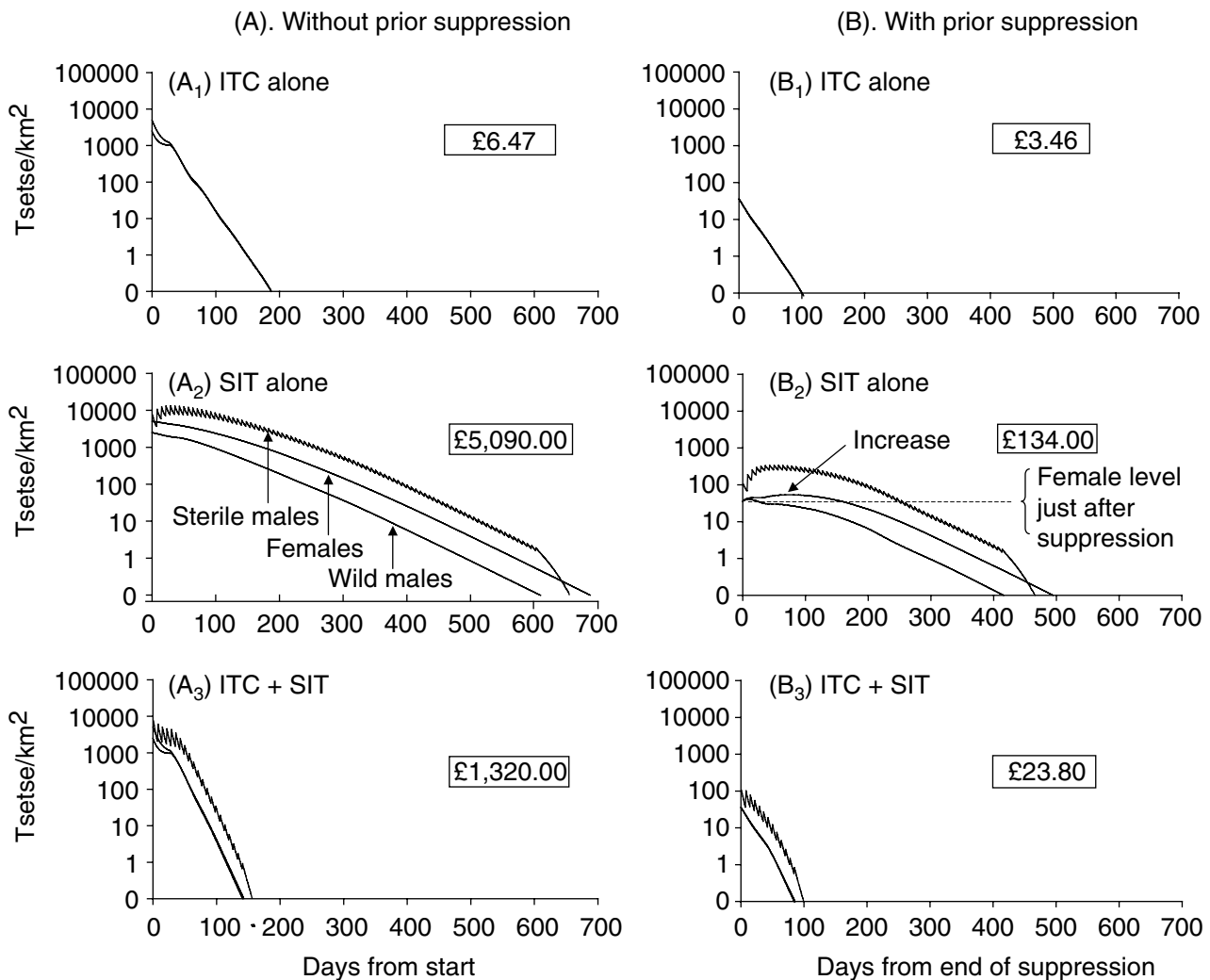


Fig. 4. Abundance of females, wild males and sterile males in an isolated population at various times after the start of insecticide-treated cattle (ITC) alone, sterile insect technique (SIT) alone and ITC + SIT, applied without (A) and with (B) the prior use of ITC to produce population suppression to 1% of the pre-treatment level of adult males plus females. Eradication costs per square kilometre are shown to three significant figures, exclusive of any suppression costs.

logged catches of actual bait campaigns in effectively isolated areas (Hargrove *et al.*, 2000; Hargrove, 2003).

With SIT alone (Fig. 4A2), 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 because 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 $<0.1/\text{km}^2$, i.e. when releases stopped. With the simultaneous combination of ITC and SIT (ITC + SIT) (Fig. 4A3), 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, i.e. from day 88 onwards (Fig. 4B). If SIT was *not* introduced to replace ITC at this stage (Fig. 4B1), the population decline was merely a continuation of that during the suppression. If ITC was halted and SIT now used alone (Fig. 4B2), 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. 4). With prior suppression, the costs of all measures were reduced but SIT alone still cost 39 times more than ITC alone (Fig. 4). 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, i.e. 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, i.e. 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. Because 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,

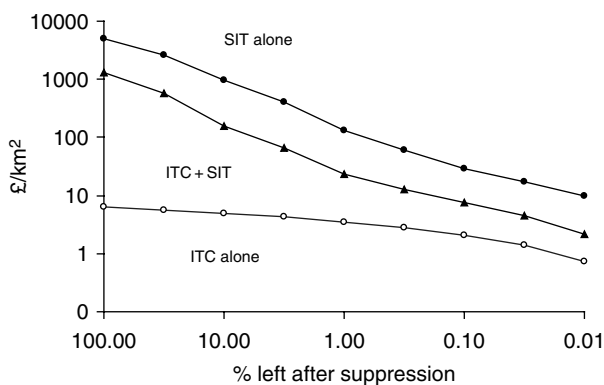


Fig. 5. Cost, in £/km², of using insecticide-treated cattle (ITC) alone (open circles), sterile insect technique (SIT) alone (solid circles) and ITC + SIT (triangles) for post-suppression eradication following the use of ITC alone to suppress the population to various percentages of the pre-suppression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

according with field results of bait campaigns (Van Sickle & Phelps, 1988). By contrast, because 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 unsuppressed population after 1, 2 and 4 months, respectively. Perhaps more surprisingly, ITC reduced the birth rate rapidly, to be 0.031 at 1 month, i.e. 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 5 months after the start of SIT (Fig. 4B2).

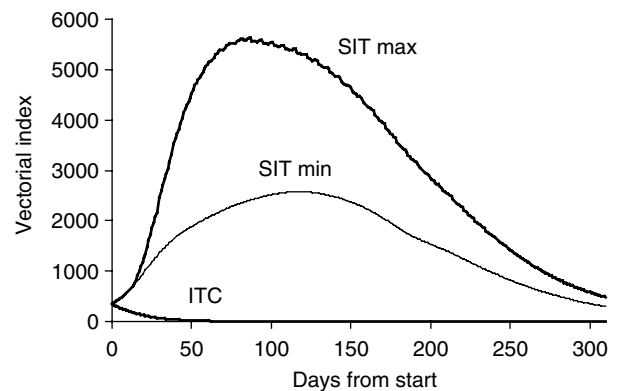


Fig. 6. Vectorial index in an isolated area at various days after the end of insecticide-treated cattle (ITC) suppression to 1% and the start of control by ITC, or sterile insect technique (SIT). With SIT, the index is shown at its minimum, i.e. not including sterile males, and maximum, i.e. including sterile males.

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.

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°C, to become 30°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 for males. Adult death rates required for stability then increased to 0.1012 for males and 0.0506 for females, i.e. 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/km², i.e. 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 sterile insect technique (SIT) alone, insecticide-treated cattle (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, £/km²				
Standard	Standard	5090.00	6.47	787
	Fast	4450.00	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, i.e. where the death rates began to increase in simulation of progressively poorer habitat. The population of males was <0.1/km² at distances greater than 33 km, so that the operational area was 0–33 km from the front.

Without suppression. The tsetse distributions that stabilized 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/km² 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/km² there, i.e. 16 times more than the 0.06 males/km², 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, because SIT killed no invaders.

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,

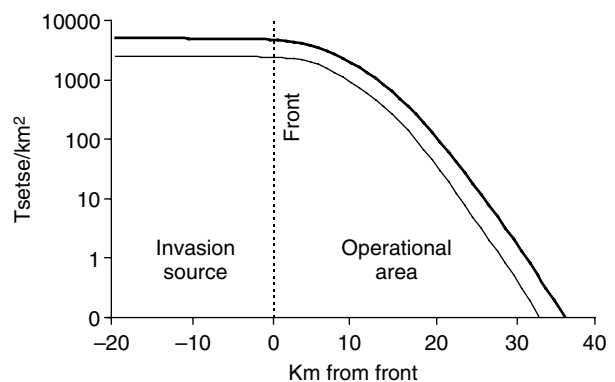


Fig. 7. Pre-intervention abundance of wild males (fine line) and females (bold line) at various distances from the invasion front (broken line), in and near the non-isolated operational area.

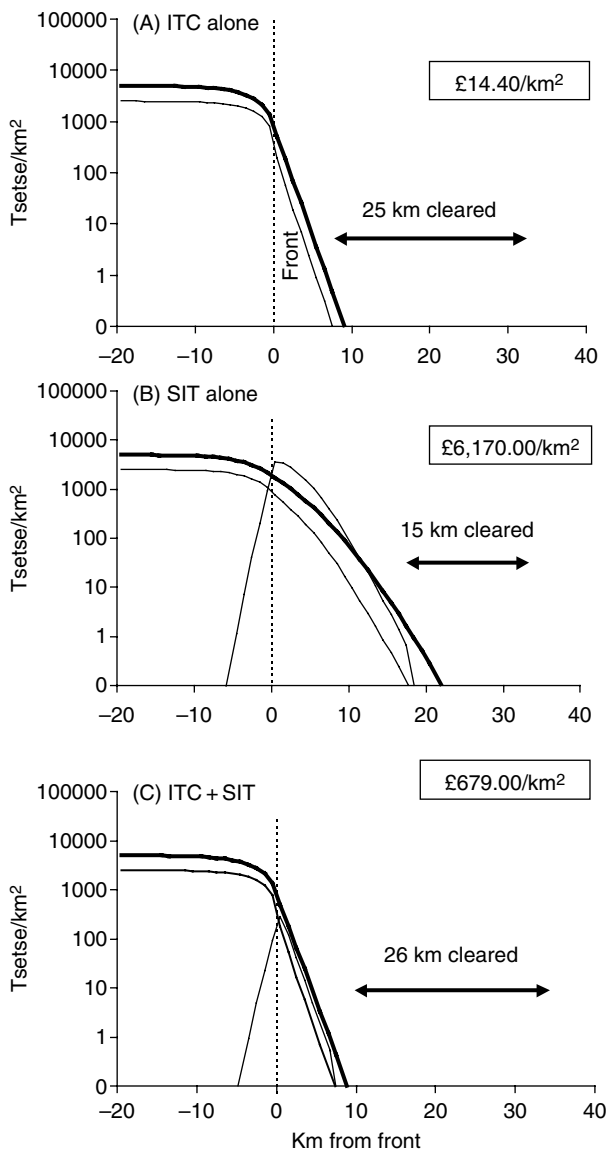


Fig. 8. Abundance of females (bold line), wild males (line of medium thickness) and sterile males (fine line) at various distances from the front, after 1000 days of applying insecticide-treated cattle (ITC) alone, sterile insect technique (SIT) alone and ITC + SIT against a non-isolated population (Fig. 7), without prior suppression. Data in the boxes are the total 1000-day costs per square kilometre cleared to <0.1 wild males/ km^2 at 1000 days.

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 stabilized distribution of tsetse reflects only the distance the invaders travel before natural death. The stable distribution then results in male densities dropping to $<0.1/\text{km}^2$ at 7–8 km from the front. However, at that distance the female density is $56.8/\text{km}^2$, and does not drop to $<0.1/\text{km}^2$ until 17–18 km from the front, i.e. 5 km

less than with the normally modelled SIT alone (Fig. 8B) but still 8 km more than with ITC alone (Fig. 8A). 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. 8B), and within a year most of the benefit of the suppression is lost. However, it is worth considering a type of suppression that is not aimed primarily at the resident population, but rather suppresses invasion. For example, when ITC alone formed an invasion barrier (Fig. 8A), the population at 2–3 km from the front consisted of 19 males and 70 females/ km^2 , making $89/\text{km}^2$ 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 stabilized 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 8B) and the use of SIT to reinforce the partial barrier was a poor substitute for a full barrier of ITC (*cf.* Figs 9 and 8A).

Discussion

Present results show only a little of what can be modelled using Tsetse Muse. For instance, the present study

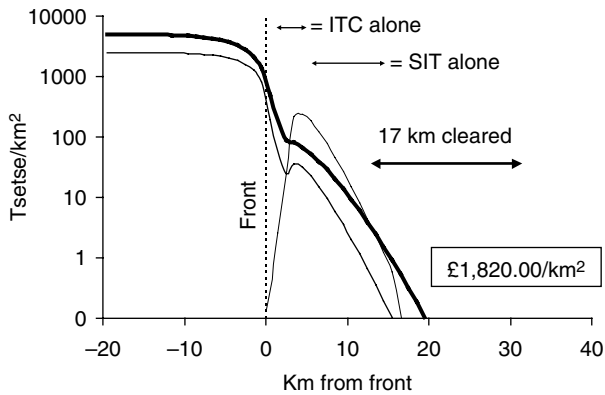


Fig. 9. Abundance of females (bold line), wild males (line of medium thickness) and sterile males (fine line) at various distances from the front, after 1000 days of applying insecticide-treated cattle (ITC) alone at 0–3 km into the operational area, and sterile insect technique (SIT) alone applied initially 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/ km^2 . Box shows the 1000 day cost per square kilometre cleared, to three significant figures.

examines how outputs change with assumptions about tsetse abundance and breeding rates, whereas other analyses could have studied the sensitivity to variations in age-dependent patterns of tsetse mobility and death, the fitness of sterile males or the distribution of insecticide-treated cattle. Instead of examining the relative merits of SIT and ITC, the programme could have elucidated the efficacy of various insecticidal barriers, the desirability of establishing barriers well before the main control campaign, or the dangers of combining widely different control measures in a mosaic. 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, present work 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, because 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 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 (e.g. Leak, 1999; Allsopp & Hursey, 2004). However, such data must be interpreted cautiously, as 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 multispecies 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-sterilization of wild males and females (Vale *et al.*, 1986) ensures that fertile-mated females do not reproduce, even if they do live long.

Importance

Should poor African governments be encouraged to invest in expensive SIT facilities (Feldmann, 2004)? Fortunately, the model allows politico-economic wrangles of this type to be settled largely by biological outputs. First, SIT lacks particular strengths, e.g. 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 long-winded, 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 emphasizes 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, as it will kill many of the costly sterile males. However, wild males are killed also, so the sterile:wild ratio is unaffected.
- 6 Because 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 neutralize invasion pressure or are applied patchily, so leaving residual *foci* (Hargrove *et al.*, 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.

In conclusion, present work suggests two things. First, the strategy of increasing the deaths of tsetse is likely to be more beneficial than reducing their births; in particular, tsetse appear to be text-book examples of insects for which SIT is contra-indicated. Second, and more to present purpose, a readily available model that helps the user to explore the cost and effectiveness of different control strategies could improve substantially the understanding and planning of tsetse control.

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