

A theoretical study of the invasion of cleared areas by tsetse flies (Diptera: Glossinidae)

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Abstract

Large-scale eradication campaigns against tsetse flies *Glossina* spp. are giving way to smaller operations aimed at disease and vector containment. There has been little discussion of the effects of these changes in policy. This study estimates the rate at which tsetse re-infect treated areas after the termination of control efforts. Movement is modelled as a diffusion process with a daily root mean square displacement (λ) of 0.2–1 km^{-1/2} and population growth as logistic with a growth rate (r) $\leq 1.5\%$ day⁻¹. Invasion fronts move as the product of λ and \sqrt{r} . For $r = 0.75\%$ day⁻¹ a front advances at 2.5 km year⁻¹ for each 100 m increment in λ . If there are 0.001% survivors in 10% of the treated area, the population recovers to within 1% of the carrying capacity (K) within three years. If the control area is subject to invasion from all sides, a treated block of 10,000 km² is effectively lost within two years – except at the lowest values of λ and r . Cleared areas of 100 km² are lost in a year, as observed in a community-based suppression programme in Kenya. If the treated area is closed to re-invasion, but if there is a block where tsetse survive at 0.0001–0.1% of K , the population recovers within 3–4 years for up to 20 km outside the surviving block. If the surviving flies are more widely spread, re-infection is even more rapid. The deterministic approach used here over-estimates re-invasion rates at low density, but comparisons between control scenarios are still valid. Stochastic modelling would estimate more exactly rates of re-infection at near-zero population densities.

Introduction

Over the past 30 years there has been a progressive decline in the amount of money spent by African governments on the control of tsetse and trypanosomiasis, and on associated research. Moreover, the proportion of budgets spent on operations has steadily declined in favour of salaries. There have been consequent reductions in the scale of tsetse control campaigns in almost all affected countries. The tendency has been accelerated recently by a decline in donor support accompanied, and partly caused, by growing concerns about the wisdom of removing tsetse from large tracts of land. In particular, there are concerns in the donor community and elsewhere that environmental

considerations are given insufficient weight and that agreed land-use plans are not enforced.

Donors have increasingly moved towards a position where they are not willing to fund the eradication of tsetse from land which is not currently farmed. Thus, the EC-funded East African regional programme entitled 'Farming in Tsetse Controlled Areas' is funded with the clear understanding that donor money will be used to alleviate problems for people who are already farming in tsetse areas. It is furthermore understood that control operations are to be carried out, and ultimately paid for, by the livestock owner.

The overall impact of all these changes is that the scale of tsetse and trypanosomiasis control operations is decreasing and that there will be a shift from campaigns which achieve eradication to those which simply contain the disease within acceptable limits. This trend is likely to continue for the foreseeable future. There appears to have been little thought,

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and even less discussion in the literature, given to the effects of these changes in policy.

In this study quantitative estimates are made of the rate at which tsetse re-invade areas from which they have been suppressed but not necessarily eradicated. The effect of the size of the control area is of special interest. The simulation study is limited to the case where tsetse populations have been suppressed or eradicated, but where there is no longer any residual effect of the treatment preventing the recovery of a surviving population, or re-invasion from surrounding untreated areas. In particular, there is no consideration of the case where there is an ongoing maintenance of insecticide-treated baits (traps, targets or livestock) in the control area, or on its boundaries acting as a barrier. Further work is planned to study these scenarios.

Methods

Models for dispersal and growth

The rates at which cleared areas are lost to tsetse depend on the rates, and patterns, of population movement and growth. Estimated loss rates thus depend on the choice of models for these two components. Modern authors generally agree that tsetse dispersal can be adequately modelled as a random movement or, equivalently, diffusion process (Bursell, 1970; Rogers, 1977; Hargrove, 1981; Hargrove & Lange, 1989; Williams *et al.*, 1992).

The pattern of growth has not been as extensively studied. Populations must be regulated by some manner of density-dependent mechanism (Rogers, 1979, 1990) but it is not clear at what stage such a process operates. Following a control programme in the Lambwe Valley of Kenya, Turner & Brightwell (1986) found that the growth of the surviving population of *Glossina pallidipes* Austen (Diptera: Glossinidae) was well fitted by a logistic model. In the absence of evidence for any better model, we follow Williams *et al.* (1992) in assuming that tsetse populations grow logistically at rate r towards carrying capacity K . The above models for movement and growth then lead to the following differential equation (Williams *et al.*, 1992):

$$\frac{\partial \rho(\mathbf{d}, t)}{\partial t} = \alpha \nabla^2 \rho(\mathbf{d}, t) + r \rho(\mathbf{d}, t) [1 - \rho(\mathbf{d}, t) / K] \quad (1)$$

where the operator $\nabla^2 \equiv \delta^2 / \delta x^2 + \delta^2 / \delta y^2$, $\rho(\mathbf{d}, t)$ is the population density at time t , at position \mathbf{d} in the x, y plane, and α is the diffusion coefficient. It can then be shown that 4α is the mean square displacement per unit time in any direction from the origin (Williams *et al.*, 1992). In this model, known as the Fisher equation (Murray, 1989), density-dependence acts only via birth and death processes. No allowance is made for density dependence in the diffusion rate. This factor could exist but there appears to be no evidence for its action, much less any estimate of its quantitative importance. There is no general analytical solution to the Fisher equation. It is possible, however, to approximate the changes occurring over small finite time steps in a grid whose mesh can be defined as required. This is conveniently done using a spreadsheet taking the cells to represent blocks of land.

Using a spreadsheet to simulate growth and diffusion processes in tsetse populations

Let a block X of country be defined by an $n \times n$ lattice, where cell $X(i, j)$ ($i = 1, n; j = 1, n$) is equivalent to a 1×1 km

square. For any cell $X(i, j)$ in the interior of the square let the population at time t be $N_t(i, j)$. One unit of time later this population will have grown, due to birth and death only, according to the logistic equation, such that:

$$N_{t+1}(i, j) = N_t(i, j) r \left(1 - \left(N_t(i, j) / K \right) \right) \quad (2)$$

In the finite approximation, the change in $X(i, j)$ due to movement into and out of the cell is:

$$N_{t+1}(i, j) = N_t(i, j) + \alpha \left((N_t(i, j-1) + N_t(i-1, j) + N_t(i, j+1) + N_t(i+1, j)) - 4N_t(i, j) \right) \quad (3)$$

The total change is obtained simply by adding the components in equations (2) and (3).

Practical aspects of the simulation

All simulations were carried out in EXCEL using macros written in Visual BASIC. EXCEL provides a spreadsheet consisting of a lattice of cells. The unit length of the side of each cell is defined equivalent to some length on the ground. This length is referred to below as the grid. The choice of the grid depends in the first place on the total area over which the simulation is being carried out. Thereafter it depends on a balance between the requirements of speed and definition. For each time step, EXCEL must carry out the required calculations on each individual cell. Thus the finer the grid the greater will be the detail, but also the longer will be the time required to complete the calculation.

Where the scale is changed between two simulations, the two can be made equivalent by dividing the diffusion coefficient (α) by the square of the ratio of the grid sizes. Thus, if we change from a grid size of 1 km to a size of 3 km, we must divide α by nine.

The value of the carrying capacity (K) was always set arbitrarily to 100 for each cell. All quoted population levels are thus percentages of K , not absolute population densities (see Discussion). This choice also makes the simulations independent of the chosen scale.

Conformation of cleared areas and re-invasion fronts

The study aims to estimate re-invasion rates into areas, of different conformations and sizes, where tsetse have been subjected to varying levels of control. Situations were studied where flies were controlled or eradicated from areas subject to re-invasion from: (i) one direction only, termed the invasion 'front' (fig. 1A); (ii) inward from all sides of a square (fig. 1B; situation 1); (iii) outward from all sides of a single square (fig. 1B; situation 2); (iv) outward from all sides of a large number of squares (fig. 1C).

Estimates of rates of movement and of population growth

A major aim of the study was to estimate the effects of varying dispersal and population growth rates on re-invasion. It was therefore necessary only to produce rough estimates of the bounds of the dispersal and population growth rates of tsetse. Moreover, since zero is the limiting minimum value, only the maximum values need to be

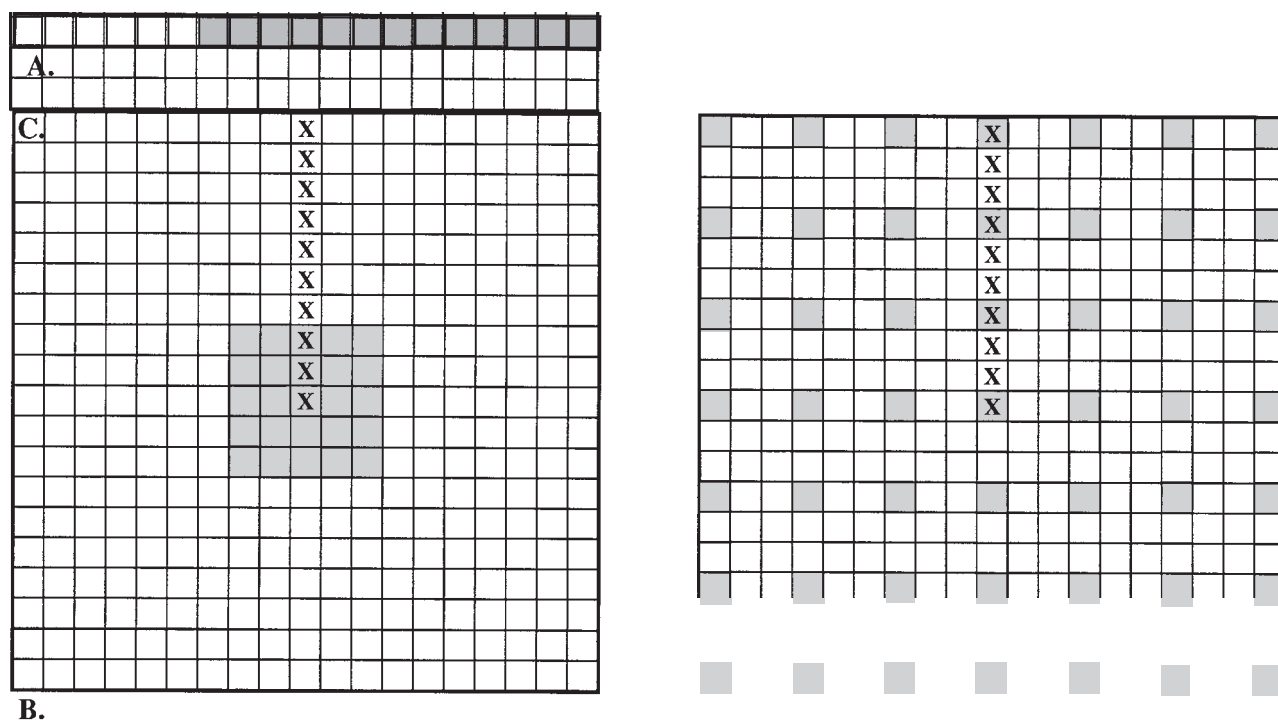


Fig. 1. Conformation of spreadsheet cells for simulation of the situation where tsetse have been controlled or eradicated from part of a region. A. Re-invasion on a one-dimensional front. It is assumed that tsetse have been eradicated from the un-shaded areas but not from the shaded. In this case it is assumed, at the boundary, that the input from the cell beyond the range is the same as the input from the cell immediately to the interior. B. Re-invasion in a two-dimensional field from a single source. Situation 1: Flies have been eradicated in the shaded areas, but not from the un-shaded. Situation 2: Flies have been eradicated in the un-shaded areas, but not in the shaded. During the simulation, population levels were monitored in the strip of cells marked with X's. C. As for B (Situation 2) but flies now survive in scattered locations. Special provision must be made for flies at the edges of the area since, for a finite spreadsheet, there is no possibility of movement past the endpoints. In B and C circular boundary conditions were assumed (Williams *et al.*, 1992), i.e. flies leaving an edge or corner cell immediately enter the opposite site of the square.

estimated. Glasgow (1963), Rogers (1977) and Williams *et al.* (1992) have collated estimates of the advance rates for tsetse fronts and of movement rates in experimental situations (table 1). The latter estimates depend both on the rate of fly movement and on the population growth rate. The highest estimates of diffusion rates were obtained by Vale *et al.* (1984) when the rate of re-invasion was monitored following the killing of tsetse by aerial spraying in a small block of woodland (c. 2×2 km). For *G. pallidipes* there was, surprisingly, no discernible drop in trap catches even one day after spraying. A preliminary analysis suggested that this result could only be explained if, in this experiment, $\lambda \oplus 1$ km day^{-1/2} or, equivalently, $\alpha = 0.25$ km² day⁻¹. This might over-estimate the true value for λ since the flies were caught in traps, which attracted and intercepted flies during their day's flight. In the absence of further evidence the figure of 1 km is taken as an upper bound, but it is acknowledged that daily displacements may seldom approach this limit.

Turner & Brightwell's (1986) estimate of a growth rate of 0.15% per day appears to be the highest recorded for a natural tsetse population. Similar values were seen in island populations of *G. m. morsitans* Westwood and *G. pallidipes* in Zimbabwe (Vale *et al.*, 1986) and a figure of 0.15% per day is accordingly taken as the upper bound for the present study.

Results and Discussion

Invasion on a single front

No survivors in treated area

The easiest re-invasion pressure to contain is one coming from a single direction. It is also the easiest to model since the simulation is reduced to a one-dimensional problem and the operator reduces to:

$$N_{t+1}(i) = N_t(i) + \alpha((N_t(i-1) + N_t(i+1)) - (2N_t(i))) \quad (4)$$

The situation simulated was one where tsetse were eradicated up to a sharp edge, but began to re-invade the cleared area immediately after the end of the control programme. As expected, the rate at which an invasion moves is strongly influenced by the rate of diffusion (fig. 2). It is also a function of the growth rate, but even when this value was halved from its maximum value of 1.5% day⁻¹ the rate of invasion was still substantial.

It is possible to produce a single function which relates the rate of movement of the front to both r and α (or λ) simultaneously. As a preliminary step in this exercise it was necessary to define a standard measure of the position of the

Table 1. Estimates of the rates of dispersal of tsetse.

A. Rates of advance of invasion fronts

Species	Distance moved (km)	Time (years)	Rate km year ⁻¹	Author(s)
<i>G. m. morsitans</i>	3-5	1	3-5	Jackson (1933)
	59	17	3.5	Jackson (1950)
	10-11	1	10-11	Ford (1971)
	72	17	4.2	Jack (1914)
<i>G. m. morsitans</i> and				
<i>G. pallidipes</i>	11	1	11	Ford (1960)
<i>G. m. submorsitans</i>	3.2	0.16	20	Davies & Blasdale (1960)

B. Experimental estimates of daily displacement rates.

Species	Displacement (km)	Time (days)	Daily displacement (m)	Author(s)
<i>G. m. morsitans</i>	0.64	7	243	Jackson (1948a)
	1.6	42	249	Jackson (1948a)
	-	-	134	Jackson (1946)
	524-886	7-21	232	Jackson (1948b)
-	-	700	Vale <i>et al.</i> (1984)	
<i>G. pallidipes</i>	-	-	800	Vale <i>et al.</i> (1984)
<i>G. swynnertoni</i>	-	-	246	Jackson (1948b)
<i>G. longipennis</i>	-	1	397	Power (1964)

front. An arbitrary cut-off level of 30% of the holding capacity was selected and the measure (*D*) was the distance from the edge of the control area at which the population fell to this level.

For a given coefficient of diffusion (α), *D* increased approximately linearly with *t* over the tested values of α and of *t* (fig. 3A). Each graph must also, by assumption, pass through the origin since we assume that all flies were eradicated up to the boundary so that, at time *t* = 0, *D* must also be 0. The estimated intercepts of each graph did, however, differ consistently from zero, indicating that the function is not linear close to the origin. Over the time frame 0.5-3 years, however, the linear fits are good and may be used for all practical purposes to estimate rates of loss due to re-invasion.

The slopes of graphs of *D* against *t* increased, of course, with increasing α , and the rate of increase of this slope was also a linear function of λ (fig. 3B). Each of these graphs should also pass through the origin and, in this case, it was reasonable to use this approximation, since the non-linear departures from this expectation were small.

The slope of each of the resulting graphs (fig. 3B) depended, in turn, on the population growth rate (*r*) and, again, the slopes of these graphs were linearly related to \sqrt{r} (fig. 3C). What these results mean is that, given estimates of *r* and α , it is a simple matter to estimate the annual movement of a tsetse front. From fig. 3C the function relating slope (*S*) and growth rate is given by:

$$S = -4.6 + 33.9\sqrt{r} \tag{5}$$

This can be incorporated into the results in fig. 3B, where we have assumed that each of the lines, defining the rate (*L*, in linear km per year) at which country is lost, passes through the origin and has slope *S*. It then follows that:

$$L = (-4.6 + 33.9\sqrt{r})\lambda = (-9.2 + 67.8\sqrt{r})\sqrt{\alpha} \tag{6}$$

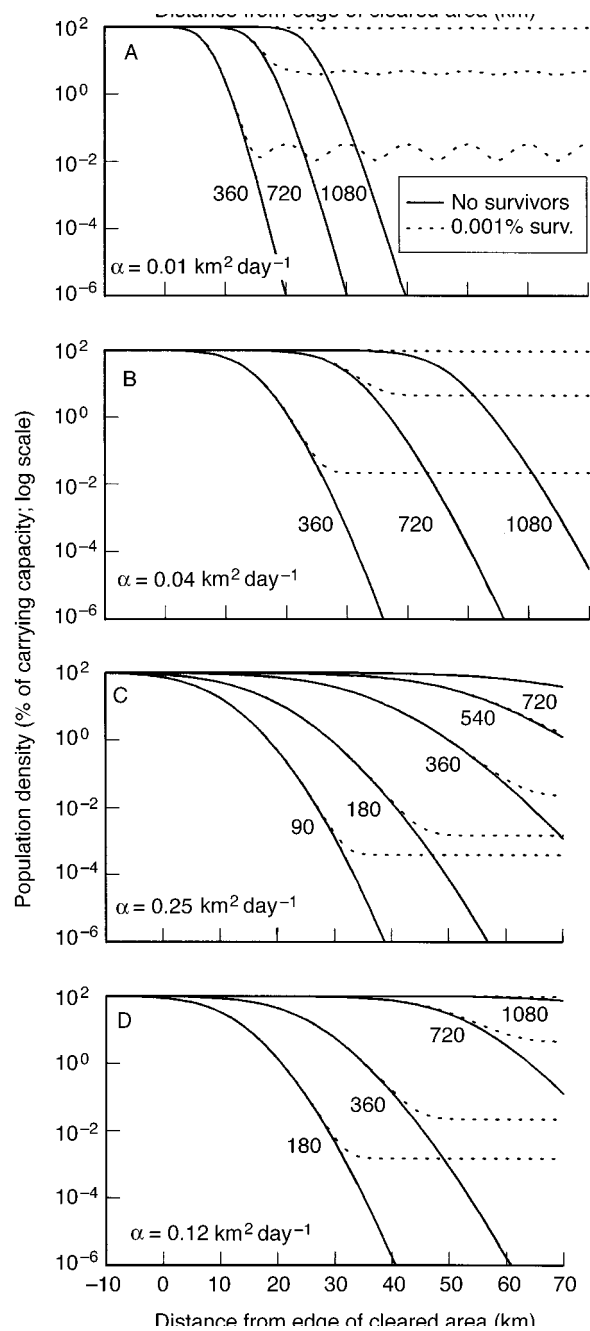


Fig. 2. The rate of advance of a tsetse front under different assumptions of diffusion rates in the cases where tsetse were either eradicated or radically reduced in the control area. Numbers in the body of the graph refer to the number of days since the end of the eradication campaign.

As an example of the use of this 'rule of thumb' formula, for a population with a growth rate of 1% day⁻¹ and a diffusion coefficient of 0.04 km² day⁻¹, the predicted annual loss is (-9.2 + 67.8) × 0.2 = 11.7 km. The predicted annual losses for populations with a range of values of *r* and α are shown in table 2. Careful checks against the values plotted in fig. 3 show that discrepancies between the results from the

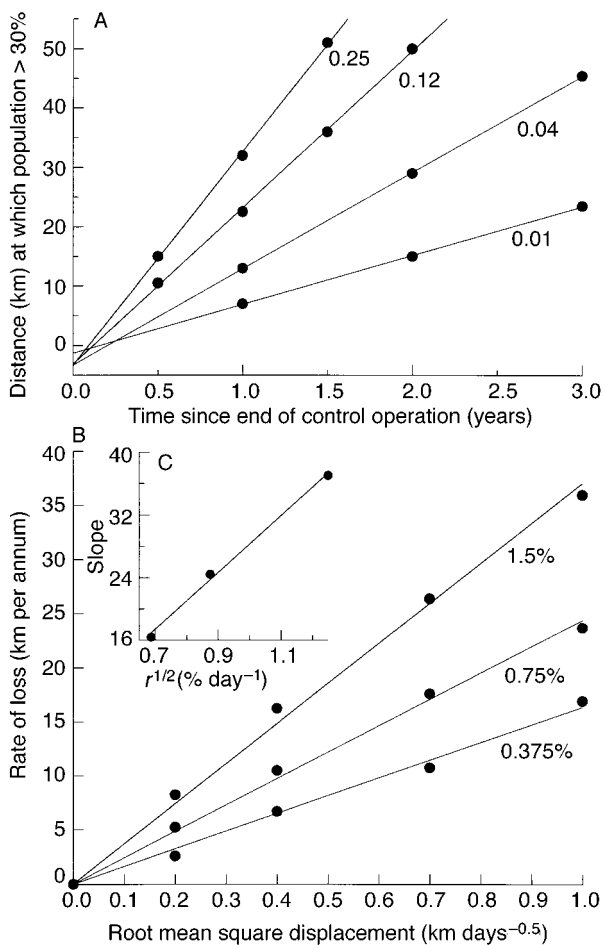


Fig. 3. A. The advance of a tsetse front as a function of the value of the diffusion coefficient (α ; values shown in the body of the graph). B. The slopes of graphs such as those shown in fig. 3A, for populations with different daily growth rates (r ; values shown in the body of the graph) plotted against the root mean square displacement (λ). C. The slopes of the graphs in fig. 3B plotted against the square root of the growth rate (r).

predictive equation and simulated values are small and unimportant in view of the approximate nature of the model itself.

It is useful to get a general feel of what the results in table 2 are predicting for likely values of growth and movement rates in tsetse populations. Populations which have been suppressed may be expected thereafter to grow exponentially, since density-dependent mortality should be at a minimum. If r takes a value of $0.75\% \text{ day}^{-1}$, only half of the maximum assumed growth rate, the appropriate column in table 2 indicates that the re-invasion front will advance annually at *c.* 2.5 km for every 100 m of daily displacement. Modest changes in the daily displacement (or errors in estimating its value) will thus not make a great deal of difference to the rate at which the front advances.

Williams *et al.* (1992) used dimensional analysis to show that the rate of advance of a front, for particles moving by diffusion, is proportional to $(\alpha r)^{0.5}$ or, equivalently to $\lambda \sqrt{r}$. Equation (6), which relates to the rate at which the 30% contour of population advances, includes this term, but also

Table 2. Predicted annual rates of advance (in km) of tsetse fronts using $L = (-9.2 + 67.8\sqrt{r})\sqrt{\alpha}$.

α ($\text{km}^2 \text{ day}^{-1}$)	λ ($\text{m day}^{-1/2}$)	r (%/day)					
		0.25	0.50	0.75	1.00	1.25	1.50
0.0025	100	1.2	1.9	2.5	2.9	3.3	3.7
0.0100	200	2.5	3.9	5.0	5.9	6.7	7.4
0.0225	300	4	6	7	9	10	11
0.0400	400	5	8	10	12	13	15
0.0625	500	6	10	12	15	17	18
0.0900	600	7	12	15	18	20	22
0.1225	700	9	14	17	21	23	26
0.1600	800	10	15	20	23	27	30
0.2025	900	11	17	22	26	30	33
0.2500	1000	12	19	25	29	33	37

has a term dependent only on λ . The difference is due to the fact that the contour defining the limit of points where the population falls to 30% of the carrying capacity does advance even when the population growth rate is zero, as is confirmed by simulation (table 3). Williams *et al.* (1992) predicted that the front will not advance at all when $r = 0$. This is true if the last point at which the population is at 100% of the carrying capacity defines the front. The cleared area is being re-invaded from adjacent populated areas but there is no growth by these invading flies and thus the population never reaches the carrying capacity. Moreover, the population in adjacent untreated areas is being depleted by emigration, and this deficit persists since the growth rate is zero by assumption. It follows that the front, as implicitly defined by Williams *et al.* (1992), actually retreats from the position it held immediately after the end of the control operation.

Given the difference in the two methods of estimating the advance of a tsetse front, the estimates of the velocity naturally differ, but the differences are not large. Thus for a population growth rate of $r = 1\% \text{ day}^{-1}$, and for $\lambda = 200 \text{ m day}^{-1/2}$, Williams *et al.* (1992) predict a front velocity of 7 km year^{-1} , while the estimate using Equation (6) is 6 km .

Small pockets of survivors in treated area

The presence of even very small numbers of survivors in the treated area markedly increases the rate of re-invasion. When it was assumed that every tenth cell had survivors to the level of 0.001% of the carrying capacity, the results showed that the tsetse population had recovered, over the entire area, to the carrying capacity within three years, regardless of the rate of movement (fig. 2). Of course the rate of re-infection was greater for populations where the flies dispersed most rapidly (cf. fig. 2A and D).

Williams *et al.* (1992) note that 'if a low density population

Table 3. Re-invasion of a cleared area by a population of tsetse with zero growth rate, estimated as a function of the diffusion coefficient (α) and the time (t) since the end of the control exercise.

α ($\text{km}^2 \text{ day}^{-1}$)	t (days)								Slope
	180	360	540	720	900	1080	1440	1800	
0.0100	2	3	5	6	8	10	12	13	2.60
0.0400	4	6	9	12	15	19	26	34	6.72
0.1225	6	10	15	20	26	31	43	-	10.74
0.2500	8	14	22	29	37	46	68	-	16.93

The figures in the body of the table give the distance in km from the edge of the cleared area to the point at which the population falls to 30% of the carrying capacity.

is present beyond the apparent front, this population will grow uniformly and the front will appear to advance very rapidly'. The present simulation results are entirely in accord with that prediction (fig. 2). They are also in accord with the earlier prediction that when λ is small relative to r 'the tail of the fly front is flat and the front advances mainly because of the logistic growth' (fig. 2A). When λ is large relative to r 'the tail is steep and the front advances mainly because of the diffusion'. The latter tendency is seen increasingly in fig. 2 going from B to D.

Problems resulting from the assumption of continuity when population levels are very low

The assumed levels of fly survival for the above simulation are very low. Thus if the original population density was 10,000 flies km^{-2} then over a (100×1) km strip there would have been an original population of 1000,000 flies. We assume that there are no flies left in 90 of the cells in this strip and $(0.001/100) \times 10^6 = 10$ flies in the other 10.

At these low levels of survival, the present simulations over-estimate the rates of re-infection. This problem arises because a deterministic growth model has been used and the population size (N) is being treated as a continuous function of time, whereas it is in reality a discrete function, since a fraction of a fly is not a viable unit. The assumption of continuity in N provides a reasonable approximation when numbers are large ($N > 10$) but becomes progressively worse as N decreases.

The problem can be overcome by using a stochastic simulation procedure in which the movement and growth of discrete cohorts are followed. This procedure is beyond the scope of the present study, but would provide a useful adjunct to it. Despite the problems with the present approach it is clear that the existence of even modest numbers of survivors in a treated block will greatly increase the rate at which treated territory is lost to re-invasion.

Re-invasion of square blocks surrounded by tsetse infested country

Consider first a situation where tsetse are eradicated from an area of 10,000 km^2 , about four times the size of the blocks treated in Zimbabwe using aerial spraying (Hursey & Allsopp, 1983, 1984). If the block is subject to re-invasion from all sides (fig. 1B, situation 1) the rate of loss of cleared areas is much higher than when there is a single re-invasion front (fig. 4). Even if there are no survivors in the treated block, it is effectively lost within two years, except at the lowest movement and population growth rates.

Not surprisingly, therefore, control campaigns, such as the large aerial spraying exercises described by Hursey & Allsopp (1983, 1984), are generally designed to attack the edge of an infested area for the specific purpose of reducing re-invasion problems. It is, nonetheless, important to look at the problems implied in fig. 4 because these are exactly the problems which will be faced by local communities farming in tsetse infested areas when they attempt to carry out their own tsetse control activities. Indeed, the problems will be very much worse than indicated in fig. 4 since it may be expected that control operations will be carried out on scales closer to 100 than to 10,000 km^2 .

This is, for example, the order of magnitude of the size of the community-based control operation against *G. pallidipes* in the Nguruman area of Kenya (Dransfield *et al.*, 1990) which appears to have served as an encouragement to donors to fund similar operations in other areas. The history of this operation shows that the area is very rapidly re-

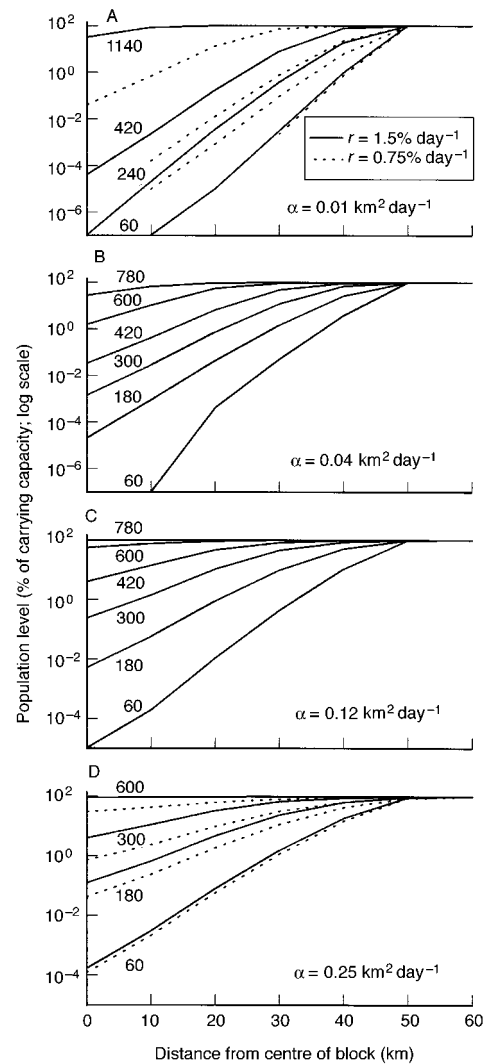


Fig. 4. Rates of re-invasion of a 10,000 km^2 square of country in which tsetse have been eradicated but which are subject to re-invasion from all sides. Numbers in the body of the graph refer to the number of days since the end of the eradication campaign. The simulations have been carried out for populations with two different growth rates. Graphs for the lower rate are shown only for the simulations at the lowest and highest diffusion rates.

invaded as soon as control operations are relaxed (Brightwell *et al.*, 1997). The current model predicts this situation. Thus, a 100 km^2 block (in the conformation of a square of side 10 km) will be re-infected within a year of the cessation of control operations (fig. 5) even at the lowest rates of growth and movement studied here.

Re-infection of square blocks from surviving pockets of tsetse within a block

A more favourable situation, from the point of view of tsetse control, is one where the fly is controlled over a large area immune to re-invasion from without. There is, of course, only a problem if pockets of flies survive within the treated area. Consider first the situation where flies were eradicated from an entire belt, except for a 10×10 km block within which tsetse survive at 0.1% of the holding capacity (fig. 6). This means that, if the original density over the whole belt was 10,000 flies km^{-2} , then the total number of

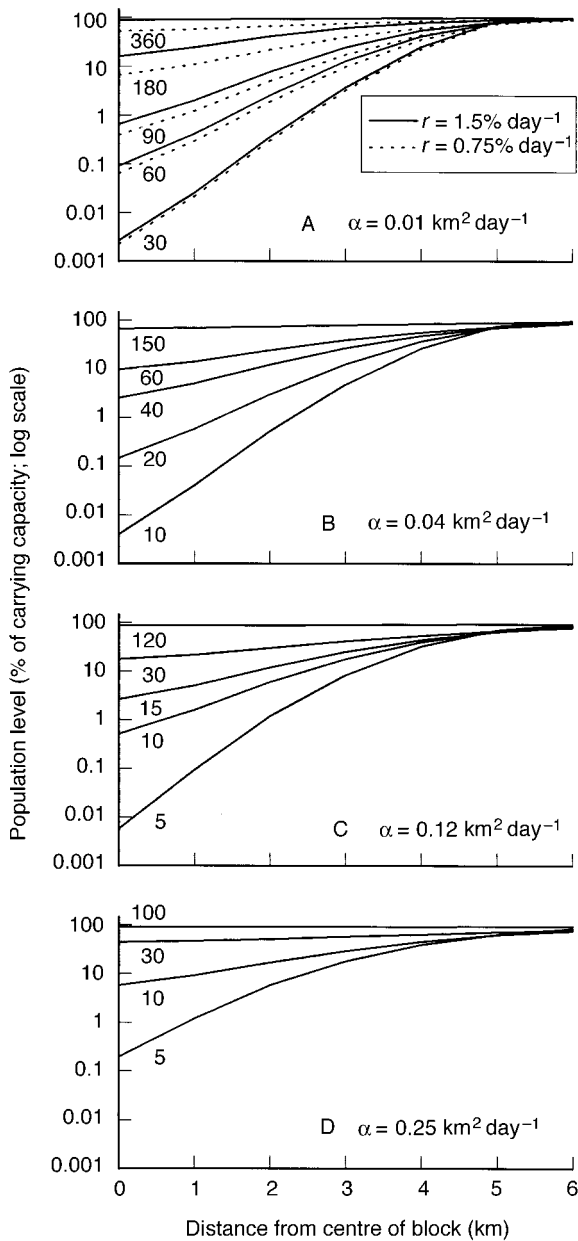


Fig. 5. Rates of re-invasion of a 100 km² square of country in which tsetse have been eradicated but which are subject to re-invasion from all sides. Numbers in the body of the graph refer to the number of days since the end of the eradication campaign. The simulations have been carried out for populations with two different growth rates. Graphs for the lower rate are shown only for the simulations at the lowest diffusion rates.

flies in a 100 × 100 = 10,000 km² block was 10⁸ flies. The number surviving in the central 100 km² is (0.1/100) × 10,000 × 100 = 1000 flies. The total percentage surviving is thus (10³/10⁸) × 100 = 0.001%.

The rate of re-invasion is judged from plots of the change in tsetse population along a transect from the edge of the belt to its centre (fig. 1B). The situation is not now as serious as it was when the treated area was subject to re-invasion from without. Nonetheless, even when the daily displacement is only 100 m

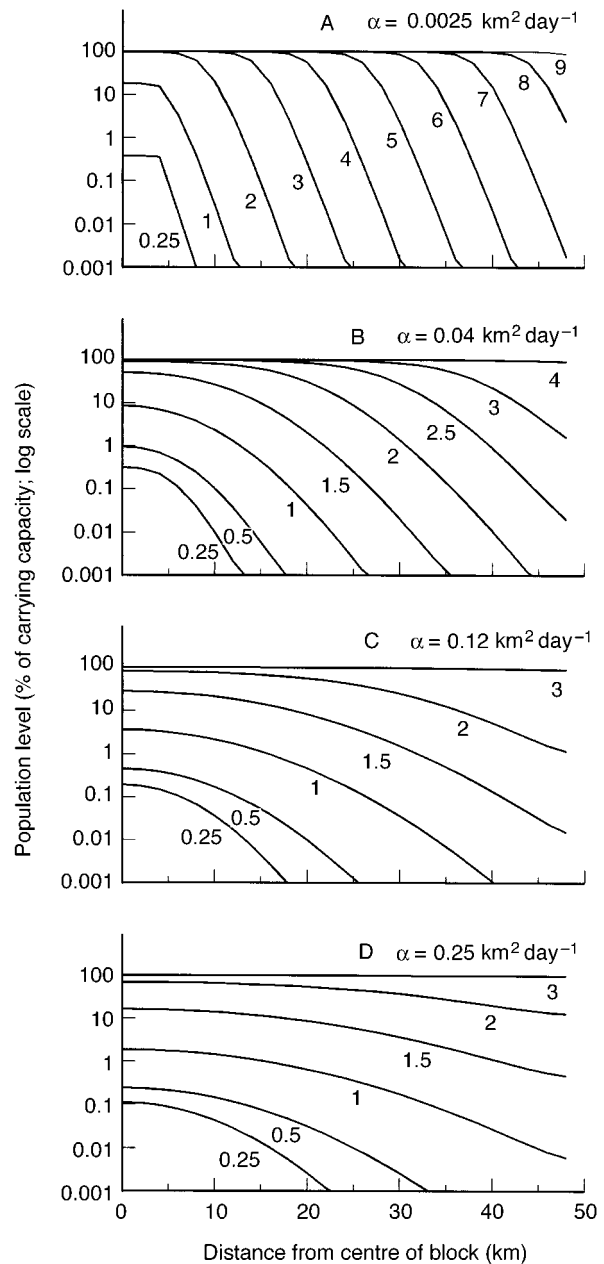


Fig. 6. Rates of re-invasion of an area where tsetse have been eradicated except in a 10 × 10 km block of country in which tsetse survive at 0.1% of the carrying capacity. Population growth rate 1.5% day⁻¹. Numbers in the body of the graph refer to the number of years since the end of the eradication campaign.

day⁻¹, after three years the tsetse population is >0.99 K for up to 20 km outside the surviving block.

If the control was such that the population density was only 0.001% of K in the central block, then only 10 flies would have survived in the entire 10,000 km² control block. The rate of re-invasion is then of course lower but there is surprisingly little increase in the extent of the relief provided. Even with the lowest rates of diffusion tested, the population is > 0.99 K up to 20 km from the edge of the block

within five years of the end of the control exercise. The whole 10,000 km² block is still essentially re-infected within 10 years, even with the lowest diffusion coefficient tested. At all higher rates the block is re-infected in 4–5 years. This is only one year longer than the time required for complete re-infection when there were 0.1% survivors in the central block.

It is stressed again that the same concerns arise as with the deterministic simulations of the rate of advance of an invasion front. Inaccuracies will arise as a consequence of treating the growth of very small populations as a continuous function. Stochastic simulations in which flies are treated as discrete units are required before we can be confident about the growth rate at population levels < 10 fly km⁻². Nonetheless, it is clear that even quite small numbers of survivors are likely to cause major problems in a short space of time.

Re-invasion from scattered sources

The most likely scenario for an operation which fails to achieve eradication is that there are survivors in isolated small pockets. These surviving pockets can be in any configuration, but the only situation considered here is where there are survivors in a regular lattice (fig. 1C). To study other configurations it is only necessary to define a map in the EXCEL worksheet in which the distribution of the surviving flies are defined accordingly.

In order to compare the rate of re-infection with the situation where the surviving flies were all in a central block, the number of cells with survivors was kept the same. Only the distribution of the cells was changed. Re-infection rates are now more-or-less uniform throughout the block. Significant departures from this general picture only appear when the diffusion coefficient is low, until the flies in adjacent surviving cells have merged (fig. 7A). For all but the slowest moving flies, the pattern of re-infection is largely independent of the coefficient of diffusion. Both effects result from the assumption that the small number of survivors are widely spread. The assumption of a much lower percentage survival again slows the rate of re-infection but only makes about one year's difference to the time at which the entire block is re-infected (fig. 7B–D).

Conclusions

Growth rates of very small populations are over-estimated by the present deterministic model (which assumes that population growth is a continuous function) and this leads in turn to over-estimates of the rate of re-infection. The inaccuracies should, however, apply in a similar fashion to all of the above simulations and it is therefore possible to draw several conclusions from comparisons between the runs:

1. Failure to achieve eradication markedly increases rates of re-infection.
2. Widely spread survivors pose a greater threat than a concentration of the same number.
3. Attacking the edge of a fly belt minimizes the rate of re-invasion.
4. Problems are most severe where the cleared area is surrounded by untreated tsetse infested country, particularly where the treated area is small (order 100 km²).

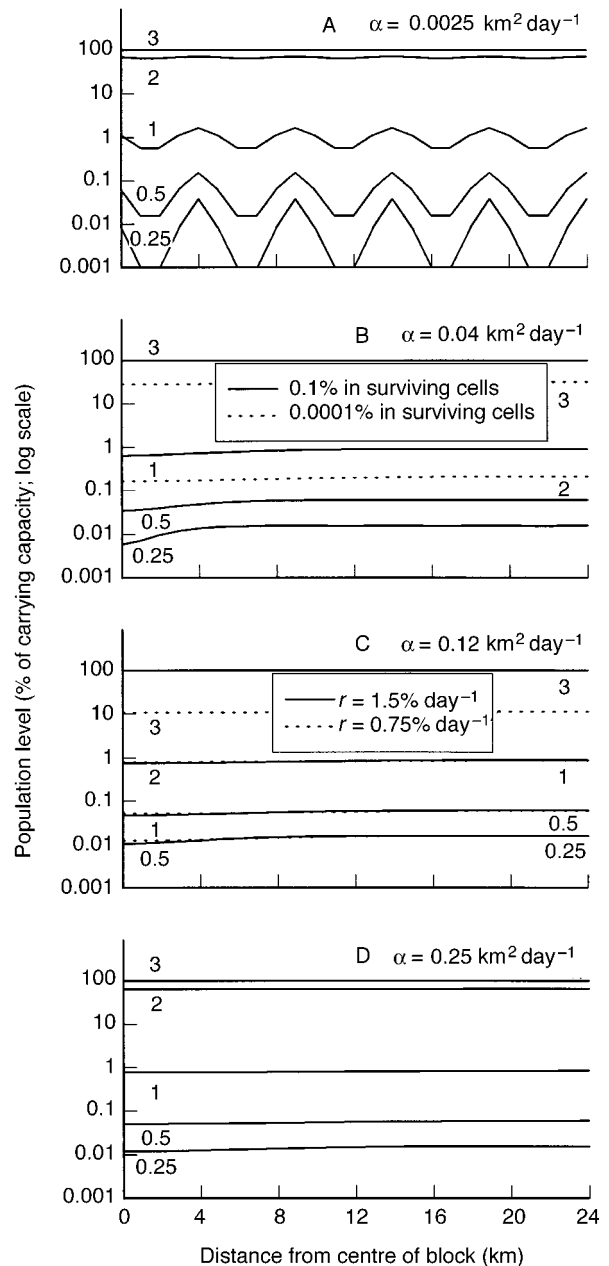


Fig. 7. Rates of re-invasion of an area where tsetse have been eradicated except in a lattice of 1×1 km blocks of country in which tsetse survive at either 0.1% or 0.0001% of the carrying capacity. Population growth rate $1.5\% \text{ day}^{-1}$. Numbers in the body of the graph denote years since the end of the eradication campaign.

The present study deals only with the case where control measures are not sustained and where there is no bar to re-infection once the initial control operation has been completed. It is implicitly assumed here that there is no residual insecticidal effect of the control operation. This scenario is exemplified by aerial spraying operations of the type studied by Turner & Brightwell (1986) and carried out in the Lambwe Valley of Kenya. The simulations also cover the case (e.g. Brightwell *et al.*, 1997) where baits deployed to

kill tsetse are either removed or fall into disrepair. The situation is quite different if insecticide treated baits (traps, targets or livestock) are continuously maintained in the control area. Comparative studies are being carried out to model the expected population changes under this alternative system of tsetse control.

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