Tsetse eradication: sufficiency, necessity and desirability

J.W. Hargrove

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The question, however, which still confronts us is: What is the most scientific and economical means by which to overcome the pest?

(Harris, 1932)

It is important…to ask whether…the control and eradication of tsetse is really relevant to the present situation, whether it is now a marginal activity which could be dispensed with, or whether it is actually harmful.

(Ormerod, 1986)

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Preface

This review was commissioned by the DFID Animal Health Programme to lay the foundation for a meeting held in Edinburgh in September 2002, *Tsetse control: the next 100 years*. An excellent presentation based on the review was made to participants on the eve of the Edinburgh meeting and it very effectively served the intended purpose of focusing minds and stimulating rational discussion and debate.

Before looking to the future, which was the objective of the Edinburgh meeting, I thought it would be a good idea to look into the past and learn from past attempts at tsetse control. In this review, John Hargrove considers, in turn, the different approaches to tsetse control that have been utilised over the past century. His aim was to revisit a question asked more than 70 years ago by R.H.T.P. Harris: 'What is the most scientific and economical means by which to overcome the pest?' and also to consider a second question posed by W.E. Ormerod five decades later: '…whether the control and eradication of tsetse is really relevant…or whether it is actually harmful.' Both questions are still very pertinent in the context of the recently launched Pan-African Tsetse and Trypanosomiasis Eradication Campaign (PATTEC).

For those who were unable to be at the Edinburgh meeting, the DFID Animal Health Programme has now published two companion volumes: the report of the meeting *Tsetse control: the next 100 years*[1] and this review. I believe that each makes a useful and timely contribution to the ongoing debate about how best to tackle the problem of tsetse and trypanosomiasis. And, not before time, both provide some answers to the questions posed by Harris and Ormerod.

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Edinburgh, May 2003

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[1] Tsetse control: the next 100 years. Report of a meeting organised by DFID–AHP, 9–10 September 2002, Edinburgh, Scotland. Department for International Development Animal Health Programme.

Acknowledgements

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Summary

A declaration by African Heads of State, calling for the eradication of tsetse from Africa, motivated this review of the available means of tsetse control and eradication and the necessity and desirability of carrying out such campaigns. For each control method, field data were used to develop quantitative models of the time course of past tsetse control operations. The aim was to use these models to forecast the results of using one or a combination of control techniques. This modelling approach is crucial for predicting the impact of a planned campaign on the incidence of tsetse-borne disease, which can, in turn, help to anticipate the consequent social and economic costs and benefits. It is particularly important to identify methods that can be used for tsetse *control*, and which are also necessary, sufficient and desirable for the *eradication* of tsetse populations.

Bush clearing and game destruction have been used successfully in the past to eradicate tsetse populations. The efficacy of the former may well be due to the destruction of the essential habitat of the tsetse hosts. Tsetse populations can, nonetheless, exist in areas with remarkably low game densities. While these methods of destruction are now viewed as deeply repugnant from an ecological standpoint, it is recognised that they are often a natural consequence of tsetse eradication by other means and, conversely, are a natural part of agricultural development which leads to tsetse eradication.

Ground spraying has been used to eradicate tsetse in large areas, particularly in Zimbabwe and Nigeria. This method is seldom used because of concerns over residual insecticides, because it makes operational demands that are beyond most tsetse control departments in Africa, and because there are alternatives that are often simpler, cheaper or more effective.

Odour-baited targets, alone or in conjunction with other methods, have similarly been used to good effect to eradicate tsetse in large areas of Zimbabwe and Zambia. They have also been used successfully as a barrier to invasion on Zimbabwe's northeast border with Mozambique. The method is as cheap as ground spraying and cheaper than aerial spraying, although when applied on a large scale, it makes operational and logistical demands that often cannot be met by African governments. Moreover, operations using targets have sometimes failed due to widespread theft of the targets. The simplicity of the system lends itself to being used at a local level but, unfortunately,

is sometimes applied on a scale so small that control efforts are bound to be frustrated by re-invasion.

Insecticide-treated cattle provide a more attractive form of bait system where cattle and tsetse coexist. This is currently the cheapest, simplest and most effective means of tsetse control. Recent work in Zimbabwe has shown that it is possible to kill tsetse effectively by spraying only the legs of cattle, rather than the whole animal. This not only reduces the cost but also lowers the risk of killing dung beetles and destroying the stable relationship between cattle and ticks. Moreover, since different sizes and ages of cattle in a herd are fed on at quite different rates, it is not even necessary to treat every animal. As with the use of targets, the risk of re-invasion puts limits on the minimum scale required and on the shape of the area treated. Where cattle populations are low and/or fragmented, it may be necessary to provide additional protection for them using odour-baited targets; however, these may be neither affordable nor manageable for local communities. Such problems are often not appreciated early enough in a control campaign, and highlight the benefit of using evidence-based models to predict the likely outcome of any proposed campaign that relies on bait methods.

Aerial spraying is relatively expensive and requires substantial economic and infrastructural support at the national and even international level. When this support is available, aerial spraying can effectively clear large areas of tsetse in a relatively short time, as demonstrated by the first major eradication campaign against *Glossina pallidipes* Austen in South Africa. Recent advances in aircraft guidance systems have considerably increased the accuracy and hence the efficiency of insecticide delivery, as shown in a recent control operation in the Okavango Delta. The main limitation of aerial spraying, and other large-scale methods such as ground spraying and the sterile insect technique, is that there is little or no protection from re-invasion once the initial control operation is completed and the gains achieved in reducing tsetse densities can be rapidly lost.

By contrast, odour-baited targets and insecticide-treated cattle provide an ongoing level of suppression, and the former, in particular, can provide effective barriers to invasion. The combined use of aerial spraying and odour-baited targets in Zimbabwe saw the eradication of tsetse from a large proportion of the northwest of the country in the 1980s and 1990s. The combination makes good sense, particularly if due attention is given to regular sampling to monitor the progress of the campaign. Aerial spraying provides a quick kill of a vast majority of the tsetse present, over relatively large blocks of land, while targets protect against re-invasion and eradicate surviving foci within treatment blocks – particularly in rough terrain where aerial spraying may be less effective.

The sterile insect technique (SIT) is intended for use when conventional techniques succeed in reducing populations to extremely low levels, but fail to achieve eradication. The most notable success of SIT against tsetse was in eradicating *G. austeni* Newstead on Unguja Island,

Zanzibar. An analysis of this project reveals, however, that there was a significant discrepancy between the apparent ratio of sterile to wild males and the effective ratio, as evidenced by the slow rate of decline of the wild population. The results of the Unguja campaign do not show conclusively that SIT will be a sufficient means of eradicating larger tsetse populations, particularly those open to re-invasion on the African mainland. An estimate of the true cost of future campaigns will require further independent economic analysis.

1. Introduction

The questions of whether tsetse should be controlled or eradicated and, if so, how this should be achieved, have been debated with varying intensities during the last 100 years. No universally accepted answers have been found, largely because the perceived benefit of eradicating tsetse depends on the extent to which the flies either upset, or appear to protect, the distinctive type of land use beloved by each lobby, and because the people and institutions that do recommend attacking the fly often prefer the particular control technique that they themselves have developed or refined, or are best able to afford.

The closing decade of the last century saw a reduction in the intensity of debate due to a decline in opportunities for the sort of extensive control campaigns run by governments and aid donors. International donors tired of funding large control operations whose gains required further heavy donations to maintain. Broad considerations of sustainable rural development became more appealing than focusing on a single insect pest. Moreover, the development of improved methods of bait control had suggested to many socio-economists that such methods could be used on a relatively small scale by local communities, in self-help policies of 'living with tsetse'.

Unfortunately, but quite predictably, the reduced emphasis given to tsetse control did not make the problem disappear. This was recognised in July 2000 when the Lomé meeting of the Organization of African Unity (OAU) Heads of State declared that renewed efforts against tsetse should start in 2001 (Appendix 1) and requested the Secretary General of the OAU to set up a Pan-African Tsetse and Trypanosomiasis Eradication Campaign (PATTEC). The Heads of State also called upon the Secretary General to support the recently established Sterile Insect Technique (SIT) Forum – the only technical organisation that was then giving serious consideration to large-scale eradication. This forum had been instituted with encouragement from the International Atomic Energy Agency (IAEA) and was largely concerned with the SIT promoted by the IAEA. SIT was not, however, the only concern of the SIT Forum, all of whose members recognised that any campaign would require substantial use of other control methods to suppress the tsetse population prior to releasing sterile males. Moreover, many members were not convinced that SIT should be an

obligate part of the campaigns and believed that the 'suppression' techniques alone might be effective and economical means of eradication in most, perhaps even all, circumstances.

The upshot of the above developments was that in the latter half of 2000 the sort of questions raised by Harris and Ormerod were moving centre-stage once more. The questions came to the fore when, as a result of the Lomé declaration, the IAEA asked the British Government for UK£25 million to start the eradication work. This request prompted the Animal Health Programme (AHP) of the Department for International Development (DFID) to organise a workshop entitled 'Tsetse control: the next 100 years', held in Edinburgh, Scotland in September 2002. The workshop was run as an informal debate to discuss campaigns of various scale and employing different techniques.

One of the most encouraging aspects of the renewed debate before, during and after the Edinburgh meeting was that the polarity of opinion seems to be more apparent than actual. For example, at Edinburgh the speakers recommending small-scale operations also volunteered the view that large campaigns could be justified under some circumstances. The 'opposing' speakers freely conceded that for the foreseeable future the idea of Africa-wide eradication is unrealistic, and that they would have to be content with much smaller campaigns in many situations. The latter point was emphasised by the Advisory Group of the Programme Against African Trypanosomiasis (PAAT), at a meeting held in Nairobi, Kenya two weeks after the Edinburgh debate, attended by representatives of PATTEC and the SIT Forum. While welcoming the PATTEC aim of Africa-wide eradication, the meeting recognised that, for the time being, progress towards this ultimate objective will vary from country to country and that a member state should not be expected to eradicate tsetse if less ambitious control would be cost-effective in that state's particular circumstances (Appendix 2).

The debate is thus less polarised and heated than it has been in preceding decades. Regardless of the scale of operations planned for the near future, however, and whether or not these are part of a grand design of continent-wide eradication, the problem of deciding which techniques should be used under various circumstances remains. In this regard, we must recognise that we are currently unable to predict quantitatively the outcome of various interventions. We do not know exactly what impact on the tsetse population would occur, over how great an area and how soon, if different types of control methods were applied with various intensities and durations against each species of tsetse in different environmental and social situations.

The OAU declaration called for a massive increase in tsetse control efforts, with concomitant increases in spending, and clearly underlines the need to provide answers to the above questions. Failure to do so will very likely lead to the use of inappropriate methods, consequent wastage of time and public money, and further disenchantment among donors supporting PATTEC and funding the newly expanded initiatives.

We therefore need to identify and explain the successes and failures of past tsetse control operations. Such a review formed the basis of a commission given by the AHP and is the primary subject of the present report.

The aim in carrying out this task was to use field data to develop quantitative models of the time course of past tsetse control operations and to use these models to forecast the basic entomological eventualities of using one or a combination of control techniques. These eventualities are crucial for further predicting the impact on the incidence of tsetse-borne disease in relation to socio-economic costs and benefits. Objective modelling should allow us to determine the efficacy and desirability of various technical options in reply to Harris's challenge of 70 years ago. The aim of this review is not only to identify methods that can be used for tsetse *control*, but also to assess which are necessary, sufficient and desirable for the *eradication* of tsetse populations. In so doing, it is hoped that we may begin to address Ormerod's philosophical queries, and to assess how we might find answers that suit all lobbies in the debates about the ultimate implications for land use.

While the modelling deals with a variety of control methods, time has not allowed consideration of more than one or a few examples of each method. The examples chosen tend to reflect the extent to which suitable data were available to the author. As a consequence, all the examples developed in this review of the use of bait systems for tsetse control come from the eastern and southern regions of Africa and apply only to the savannah species of tsetse.

The limited availability of time and data has resulted in the omission of many successful and interesting examples of tsetse control and eradication. For example, I have not included campaigns using bait systems carried out in West Africa against isolated populations, particularly of the forest species of tsetse. This report should not be regarded as in anyway definitive; rather it is a first salvo in the extended campaign required to put the planning and implementation of tsetse control and eradication on a more rational and scientific footing.

2. Results of tsetse control and eradication campaigns

2.1 Game destruction

Tsetse flies (*Glossina* spp., Diptera: Glossinidae) are unusual among insects in that both sexes feed exclusively on vertebrate blood. Moreover, since the flies show no diapause, they can occur only where the vertebrate hosts are more or less continuously present. The effect of this simple requirement was illustrated most vividly during and following the rinderpest panzootic of the 1890s. In Zimbabwe (then Southern Rhodesia), the death of wild and domestic stock on a massive scale led to the northern fly-belt being reduced to a few residual foci. As the game recovered, so did the tsetse population. This association was not lost on tsetse control authorities; when cases of trypanosomiasis began to occur in cattle in the west of Zimbabwe in 1919, the government instituted a policy of game eradication in the area and cases of trypanosomiasis disappeared by 1921 (Lovemore, 1994).

2.1.1 The Shinyanga experiment

Success in the early Zimbabwe operations – and in similar campaigns elsewhere – led Potts and Jackson (1952) to carry out a game destruction exercise in an area of around 1000 km^2 of uninhabited bush immediately west of Shinyanga, Tanzania. The experiment is important because, for the first time, data were produced for the numbers and types of animals shot and the simultaneous decline in catches of tsetse.

The study area was isolated from invading tsetse by the surrounding treeless grassy plains. Invasion of game was prevented on the northern border by an 80 km game fence and game did not occur in the settlements forming the other borders.

Originally, the intention was to shoot only the larger animals, but this 'objective was unfortunately defeated completely, because it proved impossible to prevent the shooters from killing the smaller species' (Potts and Jackson, 1952). Between 1945 and 1951, more than 8000 animals were killed (Table 1). During this period, the mean numbers of non-teneral male *G. swynnertoni* Austen caught on fly-rounds declined from around 180 to zero, whereas the numbers caught in the control area close to Shinyanga showed little variation (Fig. 1).

Table 1. **The Shinyanga game destruction experiment**

Total animals shot:					
Zebra	339	Topi	654	Bushbuck	60
Rhino	15	Hartebeest	36	Impala	1217
Hippo	1	Wildebeest	218	Gazelle	2038
Giraffe	641	Reedbuck	1484	Ostrich	469
Buffalo	3	Eland	891	Warthog	???
Roan	393	Kudu	91	Bushpig	???
Sable	3	Sitatunga	1	Others	???

Question marks indicate that unknown (presumed large) numbers of animals not on the hunters' lists were shot, but not recorded. Source: Potts and Jackson (1952)

Two other species, *G. morsitans morsitans* Westwood and *G. pallidipes* Austen, which had occurred in smaller numbers in the experimental area, likewise disappeared from fly-round catches. From November 1950 to October 1951, eleven cattle were stationed at five widely spaced sites in the experimental area. They remained free of trypanosomiasis, suggesting that tsetse had probably been eradicated from the area.

Shortly after the publication of the results of the Shinyanga experiment, Weitz (1956, 1963) developed an antibody method for identifying the species of animal on which a tsetse fly had last fed. When this technique was applied in Zimbabwe in the early 1960s it became apparent that, in many areas, *G. m. morsitans* and *G. pallidipes* took over 75% of their meals from just four mammals – warthog, bushpig, bushbuck and kudu (Robertson, 1983). It then became apparent that much of the slaughter of game of earlier days was neither necessary nor desirable since many of the animals destroyed hardly, if ever, provided a meal for tsetse.

Accordingly, an experiment was carried out in Zimbabwe in the 1960s in an area of 541 km^2 on the headwaters of the Nagupande River, to see whether tsetse could be successfully controlled, and perhaps even eradicated, by removing just the four favoured host species. The study was unique among game destruction exercises in that detailed monthly records were kept of the numbers of tsetse caught and animals shot. The data therefore provide a sound platform for quantitative modelling of the control process. Such an analysis is presented below. Descriptions of experimental details are taken from synopses of the work provided by Ford (1970, 1971), Cockbill (1971) and Robertson (1983).

Figure 1. **Shinyanga game destruction experiment**
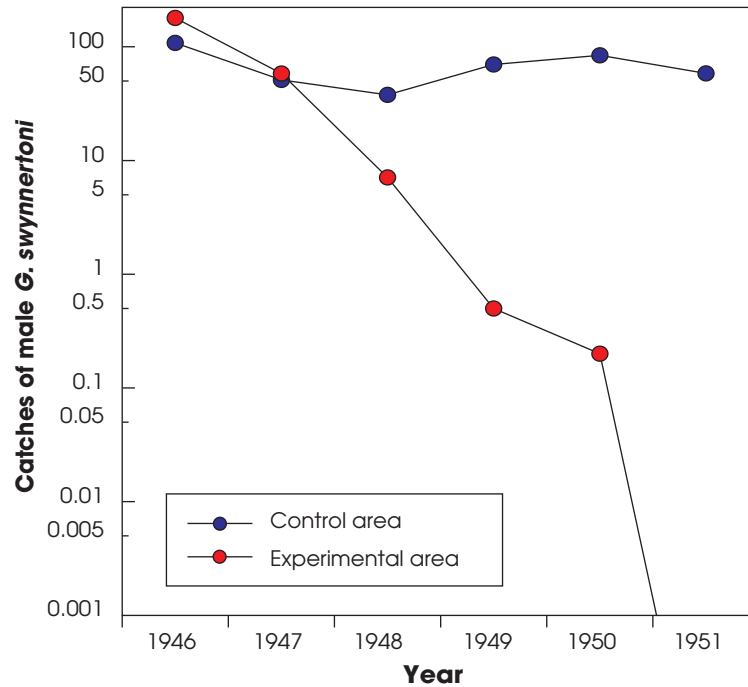
Mean catches of non-teneral male *G. swynnertoni* on fly-rounds in the experimental and control areas. For the experimental area there were zero catches of *G. swynnertoni* in 1951.

Source: Potts and Jackson (1952)

2.1.2   The Nagupande experiment
Study area and selective game elimination

Preliminary hunting was carried out in the Nagupande area between June 1958 and October 1960 (Lovemore, 1963). In this operation a game fence was erected, running east–west on the edge of the dense tsetse infestations on the headwaters of the Nagupande, Busi, Sengwa and Lutope Rivers. A further east–west fence was erected to the south, on the edge of the settled areas around the Kana and Shangani Rivers, to prevent cattle moving into the hunting area from the south. The distance between the fences varied between 16 and 30 km and the area between them was around 3100 km². All mammals in the area, with the exception of lion, leopard, cheetah, vervet monkey and small nocturnal mammals, were shot.

When the Nagupande experiment started, the northern fence of the preliminary operation was used as the southern fence of the selective hunting area (Fig. 2: the line between the Nagupande

Figure 2. **Nagupande selective hunting experiment**
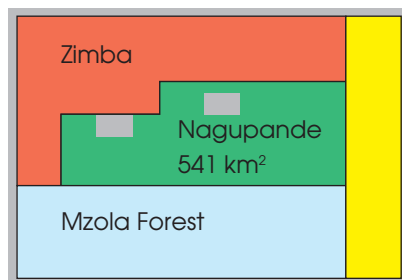
60 hunters employed over a 5-year period.

Warthog, bushpig, bushbuck and kudu shot; plus buffalo and elephant to protect fences.

Tsetse and game populations modelled assuming logistic growth and diffusive movement (see Appendix 3 for details).

Schematic map of the Nagupande and surrounding country showing the area over which simulation was carried out. Hunting was carried out in the green-shaded area, which was surrounded by a game fence. The purple rectangles within this area indicate the positions of the fly-round sampling teams.

area and the Mzola Forest). As a consequence of the earlier operation, there was a much-reduced game population, and virtually no tsetse, south of this fence (Lovemore, personal communication). Further fences were erected as indicated in Fig. 2 so that by October 1962, a 12-strand game fence enclosed the entire area, apart from a gap left for some months in the northeast at Chebira Springs. Hunting then started and, 'as anticipated, [the gap] enabled considerable numbers of elephant and buffalo to evade destruction by moving out of the area' (Robertson, 1983).

Between October 1962 and September 1964, 60 hunters, working from 20 camps distributed throughout the study area, hunted the four favoured tsetse hosts. To protect the game fence, elephant, buffalo and other animals found in the neighbourhood of the fence were also shot. This 'other animals' category accounted for only 2% (40/1950) of the animals shot by January 1964. All species were included in the analysis since those less favoured by the tsetse fly tend to be fed on when the favoured hosts are removed or depleted. Vale and Cumming (1976), in a later experiment, showed that when warthog alone were removed from an area at Sengwa tsetse then took 20–50% of their blood-meals from elephant and a large proportion of the remainder from bovids, including buffalo.

In February 1965, 90 cattle were introduced into the Nagupande area, in nine separate herds. The intention was to treat these cattle with insecticide but no suitable chemical was available. The cattle were gradually withdrawn after June 1966, but for at least 16 months they provided an additional food source for the tsetse population.

After the early success of the Nagupande trial, selective hunting was extended (from October to November 1964) to all sections of the Sebungwe Operations Area adjoining the Nagupande area in Kamezu and Kariangwe to the north and west and Tivuli to the east. However, in the Nagupande area itself, hunting intensity, as measured by hunter-days, was reduced to only one third of its

former level, and in November 1965, following political upheavals, it was suspended entirely. Hunting was resumed in February 1966, but instead of a large number of hunters based at static camps, a single mobile team of 25 hunters covered only selected parts of the area each month. This procedure was continued until the end of 1967, although there was no hunting in November and December 1966 or September 1967.

Tsetse population monitoring

No estimates of the absolute tsetse population are available from this study. The only data available are catches of male and female *G. m. morsitans* from ox fly-rounds. Six 3000-yard (2743 m) fly-rounds were operated in the Nagupande area and two in the control area, at Lusulu Research Station, 30 km to the northeast of the study area. The catches, corrected to the catch per 10,000 yards (*c.* 9144 m), are referred to as 'apparent densities'. They provide a rough measure of relative population changes subject to the error that capture probability will undoubtedly vary with time and, particularly, wild host density (see below).

Modelling methods

All modelling of tsetse populations in this study follows the pattern outlined in Appendix 3 and described in detail by Hargrove and Williams (1998) and Hargrove (2000, 2003).

Theoretical development

In order to carry out the modelling it was necessary to develop ways of estimating the relationship between host density and the mortality and abortion rates of tsetse. It was also necessary to estimate the host population in the Nagupande area from the numbers of animals shot monthly. The theoretical development is shown in Appendix 4.

Results: host population estimates

Warthogs comprised by far the largest proportions (75%) of the animals shot during the Nagupande operation (Table 2). The total numbers shot, for all six species, declined approximately exponentially during the experiment (Fig. 3).

The theoretical development (Appendix 4) shows that the predicted number of hosts ($N_K(i)$) remaining in the Nagupande area on day *i*, given a kill rate *K* and a population growth rate of *r,* is given by:

$$N_K(i) = \int_{i-1}^{i} KN(0)\exp((r-K)t)dt$$

$$= k_1[\exp(k_2(i-1) - \exp(k_2 i)] \qquad (1)$$

$$\text{where } k_1 = \frac{-KN(0)}{k_2} \text{ and } k_2 = r - K$$

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Table 2. **Total kills of selected game species**

		Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
1962	Elephant	35	9	0	0	0	0	0	0	0	0	1	0
to	Buffalo	0	2	1	1	6	5	1	2	3	0	0	0
1963	Kudu	20	29	16	16	10	6	6	16	13	16	6	5
	Bushbuck	9	6	4	0	0	0	1	1	2	1	0	3
	Warthog	218	302	90	123	89	52	78	102	85	81	41	28
	Bushpig	18	13	1	7	5	7	1	9	10	3	2	3
	Totals	300	361	112	147	110	70	87	130	113	101	50	39
	Cumulative	300	661	773	920	1030	1100	1187	1317	1430	1531	1581	1620
1963	Elephant	0	0	0	0	1	0	0	1	0	0	0	0
to	Buffalo	1	0	0	1	0	1	0	0	0	0	0	0
1964	Kudu	10	12	8	9	4	4	8	5	9	9	7	6
	Bushbuck	6	5	1	2	0	1	3	0	3	2	4	4
	Warthog	59	54	39	60	22	22	23	31	28	24	14	23
	Bushpig	6	10	4	3	7	4	2	1	5	2	5	0
	Totals	82	81	52	75	34	32	36	38	45	37	30	33
	Cumulative	1702	1783	1835	1910	1944	1976	2012	2050	2095	2132	2162	2195
1964	Elephant	0	1	0	0	3	0	2	0	0	0	1	0
to	Buffalo	0	0	9	2	6	6	0	2	0	0	5	0
1965	Kudu	3	2	0	3	2	0	0	0	0	1	1	1
	Bushbuck	3	3	0	0	1	3	0	1	0	2	1	1
	Warthog	7	19	12	8	10	10	4	7	5	6	13	13
	Bushpig	3	4	4	0	4	2	1	1	1	0	2	1
	Totals	16	29	25	13	26	21	7	11	6	9	23	16
	Cumulative	2211	2240	2265	2278	2304	2325	2332	2343	2349	2358	2381	2397
1965	Elephant	0	0	–	–	0	5	–	–	–	–	–	0
to	Buffalo	0	1	–	–	0	0	–	–	–	–	–	0
1966	Kudu	0	0	–	–	0	3	–	–	–	–	–	4
	Bushbuck	1	0	–	–	0	1	–	–	–	–	–	0
	Warthog	11	0	–	–	0	22	–	–	–	–	–	5
	Bushpig	1	0	–	–	0	5	–	–	–	–	–	0
	Totals	13	1	–	–	0	36	–	–	–	–	–	9
	Cumulative	2410	2411	2411	2411	2411	2447	2447	2447	2447	2447	2447	2456
1966	Elephant	0	–	–	0	0	0	0	0	0	0	0	–
to	Buffalo	0	–	–	0	0	0	0	0	0	0	0	–
1967	Kudu	3	–	–	0	8	4	0	2	2	0	0	–
	Bushbuck	0	–	–	0	0	0	0	0	1	0	4	–
	Warthog	4	–	–	16	12	7	7	3	10	12	11	–
	Bushpig	1	–	–	8	4	0	3	1	1	0	1	–
	Totals	8	–	–	24	24	11	10	6	14	12	16	–
	Cumulative	2464	2464	2464	2488	2512	2523	2533	2539	2553	2565	2581	2581

Kills in the Nagupande area (1962–67) including kills on the Nagupande game fence. Dashes indicate there was no hunting during that month.   Source: Robertson (1968)

Preliminary efforts to fit equation (1) to the data in Table 2 showed that a markedly higher proportion of the population was shot in the first two months than in subsequent months (Fig. 3). Potts and Jackson (1952), in a similar experiment in Tanzania, noted that 'the game early became very wary and retiring and difficult to approach' and this unsurprising effect probably accounts for the early rapid decline in the numbers shot in the Nagupande area.

When the first two data points were excluded from the fit, the r^2 increased from 0.78 to 0.82 and there was a marked reduction in the estimate of the parameter k_2 and in its estimated standard error (Table 3). The parameter estimates from the latter fit were used for all subsequent calculations.

Figure 3. **The numbers of host animals shot each month during the Nagupande selective hunting experiment**
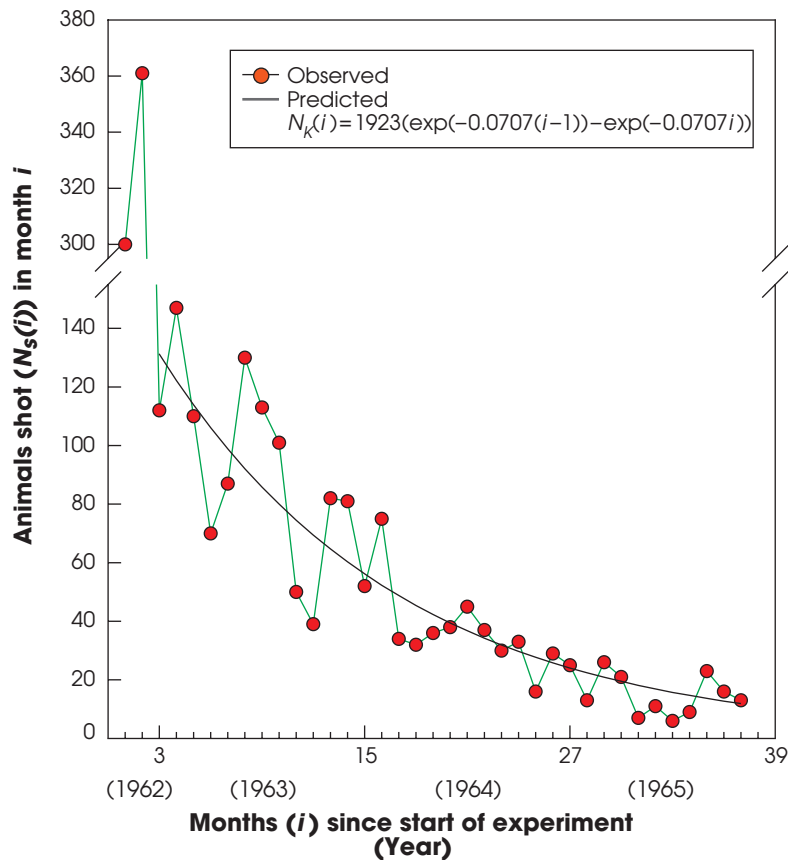

$$N_K(i) = 1923(\exp(-0.0707(i-1)) - \exp(-0.0707i))$$

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Table 3. **Parameter estimates**

First month	k_1	k_2	r^2	n
Oct 1962	2205.6 ± 119.5	−0.129 ± 0.017	0.78	37
Dec 1962	2214.4 ± 131.9	−0.0707 ± 0.0069	0.82	35

Parameter estimates (± standard errors) resulting from fitting the equation: $N_K(i) = k_1(\exp(k_2(i-1) - \exp(k_2 i))$ to data on the total number ($N_K(i)$) of animals shot at Nagupande in each month (i) between October 1962 and September 1965 (see Fig. 3).

In order to use k_1 and k_2 to estimate the remaining population of game at any time, we need first an estimate for the growth rate, r (see Appendix 4). Cumming (1975) found a maximum rate of increase of 19% per annum (~1.5% per month) in a population of warthog at Sengwa Research Station, 50 km east of Nagupande. Warthog accounted for the majority of animals killed at Nagupande (Table 2) and their birth rate is at least as high as any of the species hunted. Dr D.H. Cumming (personal communication) considers, moreover, that Sengwa was a more favourable habitat for warthog than Nagupande. It therefore seems reasonable to assume that 1.5%/month provides a conservative estimate of the upper limit for the natural rate of increase at Nagupande.

The total host population at the beginning of December 1962 was estimated using Equations (3) and (4) of Appendix 4, for values of r varying between 0 and 1.5% per month. Population levels for the first two months were then estimated by controlling for the growth rate and then adding in the actual numbers of animals shot in each of these months. Population estimates decreased as the assumed growth rate increased (Fig. 4) but were rather insensitive to small changes in this parameter. Thus by September 1965, the estimated populations for $r = 0$ and 1.5%/month were 162 and 134 respectively. The estimated value for K was, similarly, little affected by the assumed growth rate, varying only between 7.1 and 8.6% (Table 4).

The theoretical development in Appendix 4 shows that the probability of starvation in the tsetse population changes rather slowly with changes in the host population (Fig. 5). Moderate errors in estimates of the host population do not therefore have a serious effect on the outcome of the study.

Tsetse catches

In the three months after the start of hunting in October 1962, catches of male and female *G. m. morsitans* in the Nagupande area actually increased (Fig. 6). Robertson (1968) attributed

Figure 4. **Number of host animals remaining**
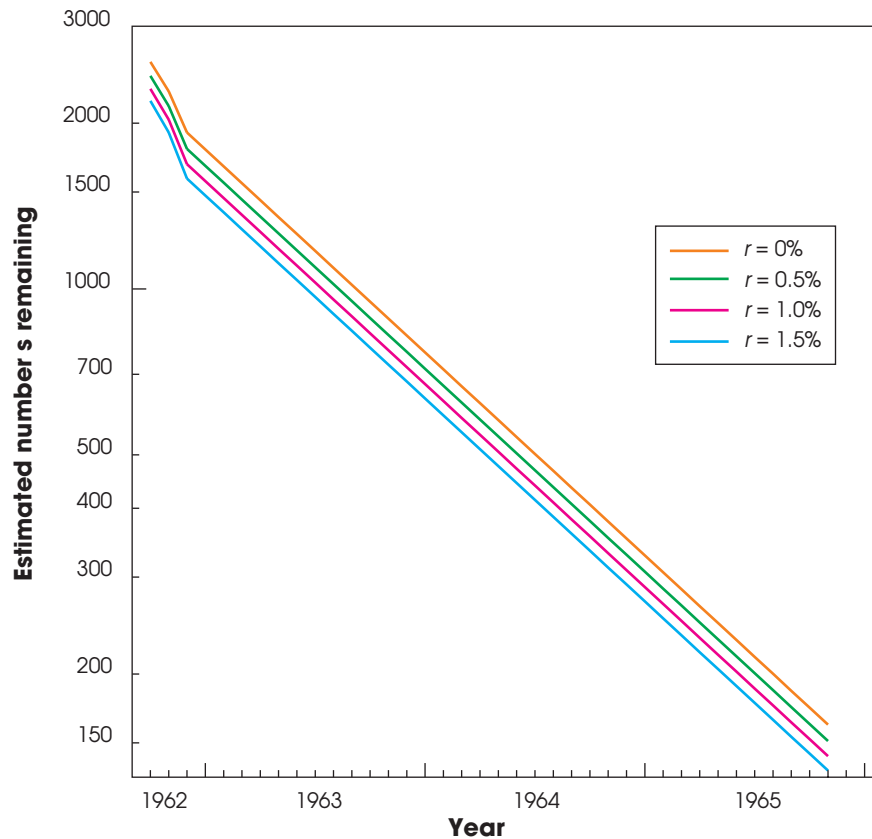
Number of host animals remaining in the Nagupande area at various times during the hunting campaign, estimated under varying assumptions of the monthly growth rate (r).

this to the disturbance of the game population and the greater likelihood of being caught by men as a consequence of the reduced availability of wild hosts, which had declined in number from estimated values of 2559 to 1786. This explanation is thrown into some doubt by the fact that the relative increase in the Nagupande catches had started three months before the onset of hunting, and continued for only two months thereafter (Fig. 6).

Between November 1962 and March 1964 the catches in the Nagupande area declined exponentially relative to the control, from a peak of 132% to less than 2% (Fig. 6). During this period, host numbers decreased to an estimated 583. In the next year this figure declined to 234

Figure 5.   **Starvation vs hosts and search efficiency**

a) Probability of starvation for different search efficiencies. *I* = 6 days

b) Daily mortality due to starvation
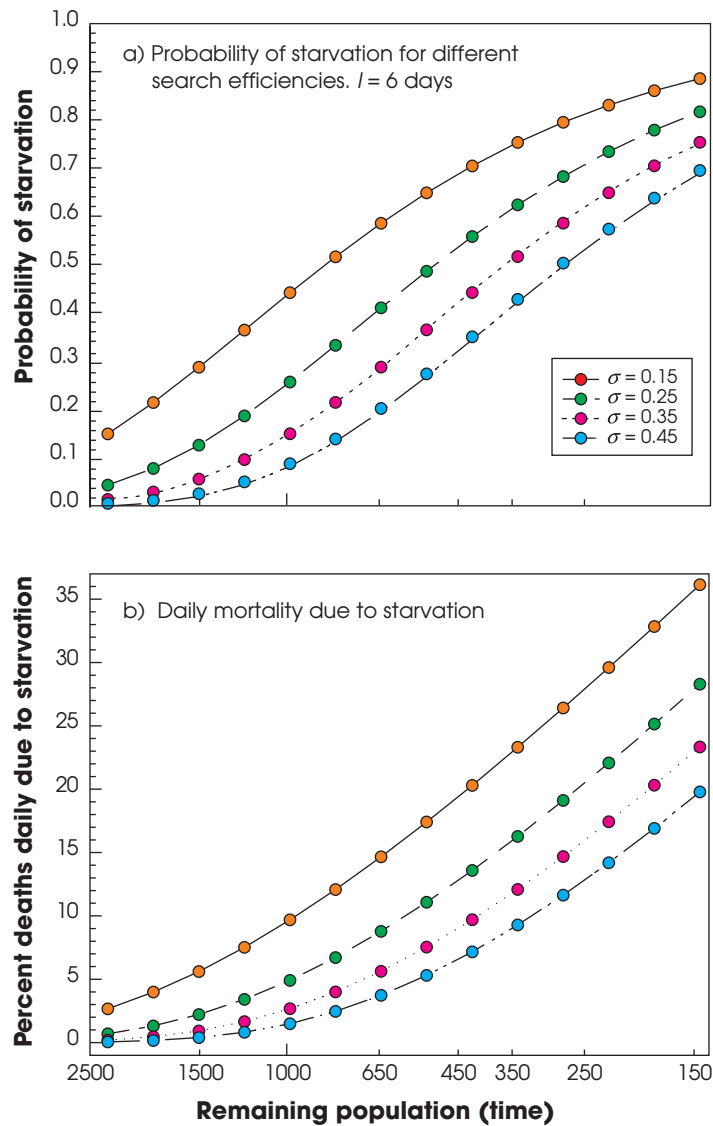
Effect of host density on a) the probability of starvation and b) the daily mortality due to starvation for flies that can survive a maximum of six days without feeding. The estimates are made for different assumed values of σ, the probability that an active fly finds and feeds on a single host in a 1 km^2 area in one day. Nagupande experiment.

Table 4. **Killing rates and number of hosts**

r	$K = r - k_2$	$N(3) = -k_1 k_2 / K$
0.000	0.0707	2214.1
0.001	0.0717	2183.2
0.002	0.0727	2153.2
0.003	0.0737	2124.0
0.004	0.0747	2095.5
0.005	0.0757	2067.9
0.006	0.0767	2040.9
0.007	0.0777	2014.6
0.008	0.0787	1989.0
0.009	0.0797	1964.1
0.010	0.0807	1939.7
0.011	0.0817	1916.0
0.012	0.0827	1892.8
0.013	0.0837	1870.2
0.014	0.0847	1848.1
0.015	0.0857	1826.6

Monthly killing rates (K) and number ($N(3)$) of hosts present at the start of December 1962 estimated for various assumed levels of the monthly growth rate (r).

but there was no further reduction in tsetse numbers. Since tsetse populations to the west, north and east of Nagupande were not subject to control operations it seems likely that the population had reached a stable equilibrium in which small numbers of immigrant tsetse were able to survive temporarily on the remaining hosts.

After March 1965, the relative catches in Nagupande increased over a six-month period (Fig. 6) due, in part, to the introduction of cattle. The further decline in Nagupande catches, starting in October 1964, may be attributed to changes outside the study area. Following the success of the Nagupande experiment, the government had decided to introduce selective hunting in all operational areas. Accordingly, in October and November 1964, hunting began in all areas adjoining Nagupande. By February 1966 there were an estimated 200 wild hosts in the study area and tsetse catches had declined to approximately 0.4% of those in the control area.

As expected, the proportion of hunted hosts in blood-meal identifications decreased, but this proportion never fell below 50% (Fig. 7), consistent with the indications from Fig. 6 that there were still appreciable numbers of the favoured hosts in the area.

Figure 6.   **Fly-round catches as percentage of control**
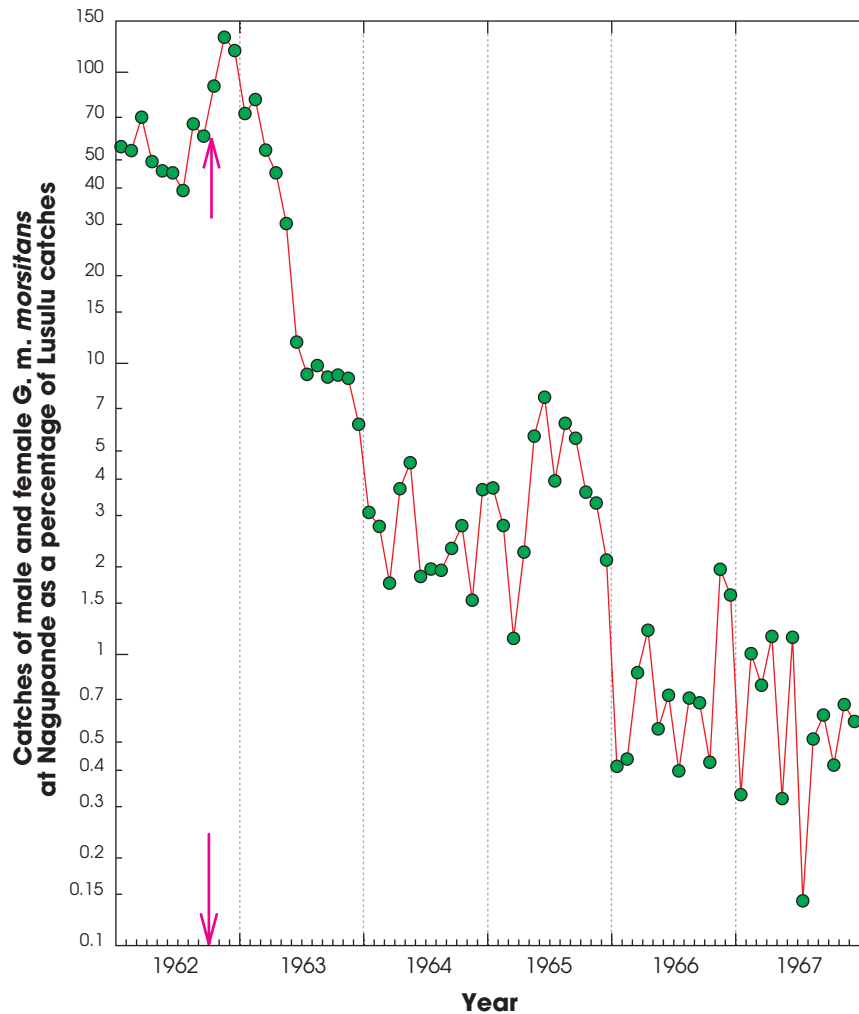
Monthly fly-round catches of male and female *G. m. morsitans* in the Nagupande area, expressed as a percentage of similar catches in the control area at Lusulu. The arrows indicate the onset of hunting.

Modelling the changes in populations of tsetse and hosts

The simulation technique outlined in Appendix 4 was used in Microsoft® Excel to model the changes in tsetse populations during the Nagupande experiment. The block over which the modelling was carried out (Fig. 2) was split into four areas:

Figure 7. **Percentage of meals from six hosts**
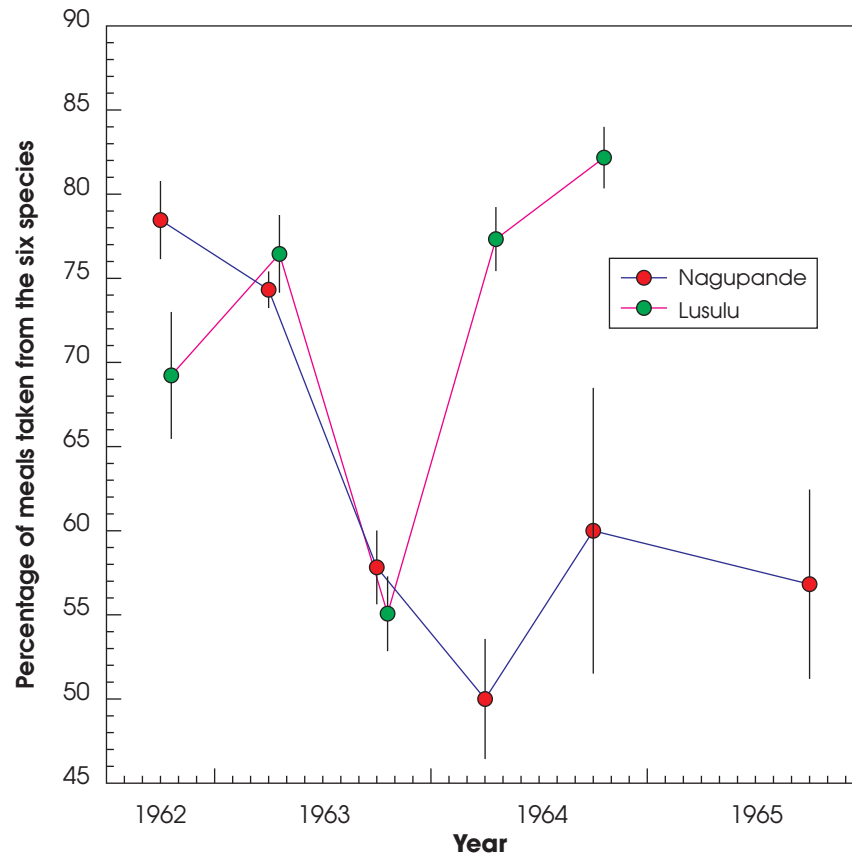
Percentage of the six host species in the blood-meal identifications for *G. m. morsitans*. Nagupande experiment.

1. Nagupande hunting area
2. Game areas to the north (Zimba) and west
3. Mzola to the south
4. Areas to the east of Nagupande

These areas differed in their 'normal' levels of game and, hence, in the abundance of the tsetse that they supported.

Preliminary simulation studies were carried out using the estimated change in host numbers shown in Fig. 4 and the resulting estimates of starvation mortality shown in Fig. 5. These fits to the

data, in which parameter values were varied by trial and error, provided reasonable starting values for use in an optimised simulation. In carrying out this procedure, the fit was optimised with respect both to the number of *G. m. morsitans* caught on the fly-rounds and to the number of host animals shot monthly in Nagupande.

Given that the host data were also fitted, it was necessary to include variables defining the growth, movement and rate of attrition of host populations. It was allowed that the rate at which hosts were killed varied with time (as shown by Fig. 3) and that hunting was suspended at some times, and later extended to areas outside Nagupande.

Reasonable fits to the data on tsetse and on their hosts were achieved in the same simulation run (Fig. 8). The input data used to achieve these fits are shown in Table 5. Further work is required to improve the model and it is acknowledged that many of the parameters may be set at unrealistic levels. It is currently being assumed, for example, that the growth rates and carrying capacities for the hosts were uniform in space. This is clearly unrealistic since the Mzola area to the south had been extensively hunted prior to the start of the Nagupande experiment. The assumption may be irrelevant, however, since it was also assumed that the Nagupande area was closed to immigration, and the fly population in the Mzola area was 'forced' to remain at a low level by reducing the growth rate and carrying capacity in that area. Tsetse populations to the east of Nagupande were, similarly, kept at reduced levels in keeping with the less favourable habitat in that area. In contrast, Zimba, to the north and west, was well stocked with game and tsetse. Growth rates and carrying capacities were accordingly set at levels similar to those for Nagupande.

The long-term intention with this work is to refine the model by including the effects of season and temperature, using meteorological data from Lusulu. The fly-round catches from Nagupande and Lusulu will then be included separately, rather than expressing the former as a percentage of the latter.

Conclusion

The fit to the data shown in Fig. 8, despite its preliminary nature, shows that the selective hunting approach was not going to eradicate tsetse in Nagupande. In the first place the level of hunting was never sufficient to remove all of the favoured hosts – flies were still taking the majority of their meals from these animals (Fig. 7). Moreover, even if all the favoured hosts *had* been removed, any reduction in the hunting pressure thereafter would ultimately have resulted in re-invasion by hosts and then by tsetse from the north and west. The problem of re-invasion of areas where tsetse have been controlled, or even eradicated, will be a recurrent theme in this report, and was recognised at the time of the Nagupande experiment. It was intended to use other means to 'mop up' the residual tsetse population and invaders. In the event, the successful development of ground spraying led the

Figure 8.   **Fly-round catches and kills of host species**

a) Fly-round catches of *G. m. morsitans*

b) Host population and number shot
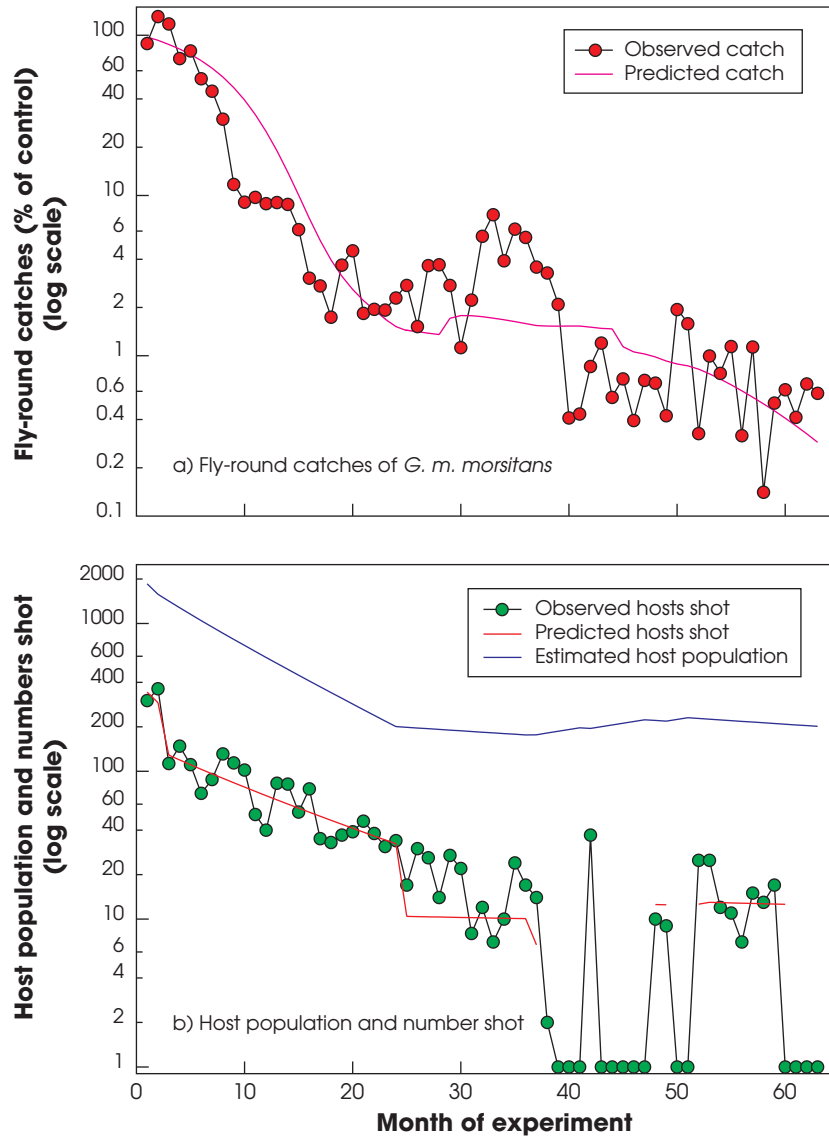
Results of applying optimised simulation to data from the Nagupande experiment on a) fly-round catches of male and female *G. m. morsitans* and b) monthly kills of six host species. Nagupande fly-round catches were expressed as a percentage of simultaneous catches from the control area at Lusulu.

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Table 5. **Input data**

Parameter	Period (days)	Areas			
		Nagupande	Zimba	Mzola	East
Hosts					
Growth rate	All	0.001	0.001	0.001	0.001
Carrying capacity	All	2195	2195	2195	2195
Initial population	All	2195	2195	2195	2195
Immigration rate	All	0	0	0	0
Hunting rate	1–60	0.0057 (0.0016)	0	0	0
	61–720	0.0028 (0.0006)	0	0	0
	721–1230	0.003	0.003	0.003	0.003
	1231–end	0	0	0	0
Flies					
Growth rate	All	0.01	0.015	0.001	0.005
Carrying capacity	All	100	100	100	10
Diffusion coefficient	All	0.02	0.02	0.02	0.02
Search efficiency	All	0.331 (0.283)	0.331 (0.283)	0.331 (0.283)	0.331 (0.283)
Days to starvation	All	7	7	7	7
Non-feeding period	All	3	3	3	3

Input data used for the simulation run which resulted in the fits to tsetse and host data shown in Fig. 8. Figures in parentheses in the body of the table are standard errors of the corresponding parameters.

Zimbabwean authorities to concentrate on this new technique. It will be seen below, however, that game destruction was used as an adjunct to spraying and that the combination of the two techniques was sufficient to allow the eradication of tsetse from large parts of Zimbabwe.

2.2 Bush clearing

While selective hunting in areas prone to re-invasion by hosts and tsetse could not be used to eradicate the flies, the wholesale slaughter of game in areas where the tsetse population is isolated, as in the Shinyanga experiment, certainly did result in eradication.

Despite this successful result, and the fact that Potts and Jackson (1952) estimated that it would have been more expensive to use bush clearing to eradicate the same population, they were pessimistic about the prospect of using game destruction in other settings. Their reasoning was that

game destruction alone had been successful only because it had been applied against an isolated tsetse population. If the area had been subject to re-invasion it would have been necessary to provide wide, costly 'fly-proof barrier clearings'. They concluded that 'though discriminative bush clearing costs initially more, it is greatly to be preferred *wherever it is practicable and can assure success*' (my emphasis). The words in italics are critical, however, since 'practicability' and 'success' in many tsetse control operations are only evident in retrospect. The aim of the present modelling approach is to allow us to predict with greater confidence just what is practicable and where success will indeed be assured.

2.2.1   Total clearing

In considering bush clearing one must be careful to distinguish between *total* and *discriminative* bush clearing. According to Ford *et al.* (1970) 'Total, sheer or ruthless clearing means the destruction of all trees and shrubs in the area treated. It is a completely effective method of eliminating *Glossina*, and the oldest'. The problem is that it is almost impossible to separate the effects of this extreme method from the effects of game destruction. By removing all of the vegetation, one is removing not only the supposed 'home' of the tsetse fly, but also the habitat of the animals essential for the fly's survival.

Whereas total clearing may be an effective means of tsetse eradication, many in the modern world would regard it as deeply repugnant. It is a sobering thought, however, that where land is being cleared for crops, both game elimination and total bush clearing will occur anyway – either as a means to eradicate tsetse or as a consequence of an eradication programme. Ford *et al.* (1970) go further: 'Where land is to be freed of tsetse in order to assist farm development, total clearing has great advantages. It is effective as an anti-tsetse measure; it relieves the future occupiers of the great burden of bush clearing, and, provided that subsequent usages follow a properly designed rotation, pasture is greatly improved'.

The problem in such cases does not concern the desirability of the *method* used to remove tsetse. The question is whether the fly's removal is anyway economically necessary and ecologically desirable. This issue will be taken up further in the discussion.

2.2.2   Partial, selective and discriminative clearing

Ford *et al.* (1970) give a full review of bush-clearing techniques that avoid a ruthless removal of all vegetation. They quote examples where tsetse species have been eradicated from rivers and streams in Nigeria and Ghana by removing part of the vegetation – generally, most of the short bush and trees with low branches. Distinctions between the various types of clearing are not very well marked. When partial clearing involved the removal of particular species of vegetation it was called 'selective'

clearing; when it involved 'the removal of all woody vegetation from certain plant communities' it became 'discriminative' clearing. As Ford *et al.* point out: 'Since the procedure involves the removal of all woody vegetation within definable zones, it lends itself to mechanical methods' though many countries could not afford the expensive equipment required for this process. Jordan (1986) gives a recent account of the eradication of sleeping sickness in the Anchau corridor of northern Nigeria using such methods.

An oft-cited example of the success of discriminative bush clearing is the work performed between 1936 and the early 1950s around Mbala, Zambia (then called Abercorn, Northern Rhodesia) on the southern shores of Lake Tanganyika. A mere 3% of the vegetation was removed in a total area of around 725 km². Within five years, catches of *G. m. morsitans* by men at stationary pickets on roads in the area had declined to near zero, and by the early 1950s the area had been declared free of tsetse (Fig. 9).

Given the very small area that had been cleared of vegetation, it was never certain why the intervention seemed so successful. In making this point, Buxton (1955) notes that 'as a measure against outbreaks of rinderpest, game destruction was being practised on the edge of the experimental area' but he gives no reference to support this assertion.

It still seems uncertain, to this author at least, why discriminative bush clearing was abandoned as a method of control. It may have been due, in part, to the evidence which began to emerge from Zimbabwe in the late 1960s indicating that the theory which under-pinned discriminative bush clearing as a means of tsetse control was based on a crucial misunderstanding of the fly's behaviour and ecology.

It had long been held that particular vegetation types provided an essential part of tsetse habitat. Jackson (1941, 1944, 1948) gave this idea a more formal foundation when he concluded from a long series of mark–recapture experiments that tsetse had distinct 'home' and 'feeding' areas and that the flies necessarily made directed movements between these two habitats. If the flies were as dependent on the woodland habitat as Jackson supposed, then its destruction should control or even eradicate tsetse.

When Pilson and Pilson (1967) began to use stationary oxen to catch fed tsetse in Zimbabwe, however, they found evidence to suggest that there were many more tsetse in the seemingly inhospitable scrub vegetation and mopane woodland than had been apparent from man fly-rounds. Bursell (1966), in an allied study carried out in the same area, found that when oxen were used as bait on fly-rounds, rather than just a cloth screen carried by men, tsetse caught in the dry season in the leafless mopane showed no signs of nutritional stress. There was, therefore, nothing to suggest that they were in any sense 'lost' from their true home in the riverine woodland. Furthermore the tsetse population in the mopane differed significantly in size and fat content from

Figure 9. **Discriminative bush clearing**
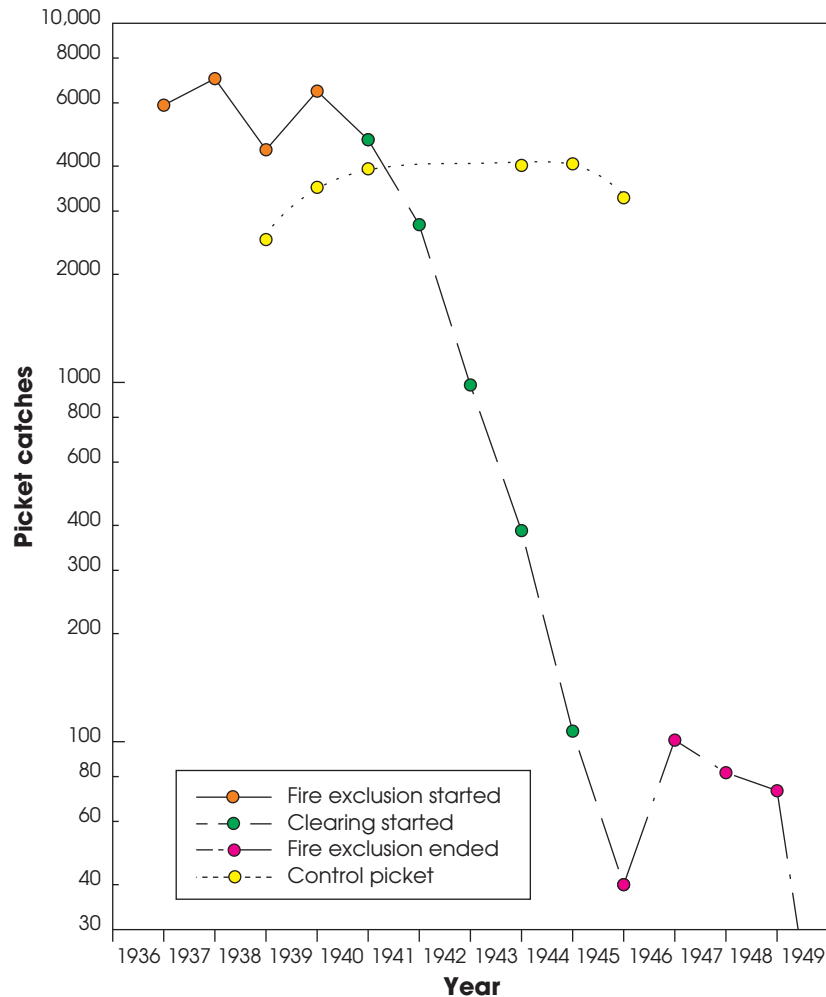
Catches of tsetse, *G. m. morsitans*, at pickets around Mbala in Zambia, and at a control site (Malombe) more than 10 km southwest of the edge of the cleared areas.

populations in nearby riverine woodland. It seemed therefore to be a separate, self-supporting population, and would not be eradicated simply by the removal of the semi-evergreen vegetation in the distant riverine woodland.

Bursell (1970a) also refuted Jackson's implied notion of the directed movement of the fly between home and feeding ground. Bursell proposed instead that tsetse actually moved at random. He suggested that Jackson's model, and by implication the whole principle of discriminative bush

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clearing, was based on data from man fly-rounds which were associated with 'vicious sampling bias, almost reaching the dimensions of a practical joke'.

In reaction to these findings, Ford *et al.* (1970) argued that it 'may be that the original theory on which partial clearing was based is incorrect but the fact that this method has been so successful in so many different areas is proof that, in some way not yet known, the concentration areas are parts of the habitat essential to the fly in some period of their life history'. They continued: 'The results of one, admittedly biased, method of sampling cannot be said to be refuted by the results of another biased method until that has been tested objectively and over a wider range than has yet been done.'

In the event, such tests were never conducted and in the 1970s, bush clearing began to disappear from the repertoire of tsetse control. This was not because it was inefficient, nor even apparently because of its ecologically undesirable nature, but more because of the advances being made with the cheaper ground spraying technique using organochlorine compounds such as dieldrin and DDT.

Few data are available on changes in tsetse populations resulting from bush clearing and thus there is little scope for modelling this technique. A more important constraint to modelling is our ignorance of exactly how or why the technique appeared to be successful. One obvious possibility is that the habitats destroyed in fly concentration areas are as important, if not more so, for the hosts of tsetse as they are for the fly itself. Whatever the truth of the matter one must agree with Bourne *et al.* (2001) that a combination of bush clearing for the purposes of developing fields for agriculture, and hunting game for food, provide effective tsetse control as a consequence rather than as a direct aim of these pursuits.

2.3   Ground spraying

Jordan (1986) describes ground spraying campaigns in northern Nigeria as 'the most extensive, and amongst the most thoroughly planned, operations of their kind anywhere in Africa'. The result was that between 1955 and 1978, approximately 200,000 km^2 of land was cleared of tsetse, 94% of which was achieved by ground spraying and the remainder by helicopter spraying. The operations consumed around 570 tonnes of DDT, 176 tonnes of dieldrin and 77 tonnes of endosulfan (Putt *et al.*, 1980). Additional aspects of the campaign are described by Davies (1964, 1971a, 1971b, 1977) and Davies and Blasdale (1960).

Ground spraying has also been successfully employed for many years as a tsetse eradication technique in Zimbabwe. During the 1960s and early 1970s, over 10,000 km^2 of country were cleared in the Sabi-Lundi drainage system, in a joint control operation with the governments of Mozambique and South Africa. The technique was also used to good effect in the northern fly belts

in Zimbabwe but, in that area, eradication eventually involved the joint use of a number of techniques, discussion of which is deferred (see Section 2.9). It is clear from the Nigerian and Zimbabwean results, however, that ground spraying, when pursued with sufficient vigour and determination, can be used to eradicate tsetse. The problem, as always, is to prevent re-invasion.

Lack of time, and the difficulty of accessing suitable data, has prevented the inclusion of modelling of ground spraying operations in this report. In most ground spraying operations, certainly for those carried out in Zimbabwe, surveys usually started after the spraying season, and there are no data relating to the rate of decline of the tsetse population during the spraying operation itself. An exception exists in work supervised by D.F. Lovemore (personal communication) in the Doma area of northern Zimbabwe. Lovemore was struck by the gradual decline in trap catches of *G. morsitans* and *G. pallidipes* during this ground spraying campaign, suggesting a small daily kill rate maintained for long periods. Hence, the population changes might be viewed as somewhat similar to those occurring when 'bait' systems are used (see Section 2.4).

It is proposed to model these ground spraying data in a later review. It is anticipated that such modelling will be complex, however, since the kill rate is a function of the weather – in particular the 'refuge seeking' behaviour of tsetse at high temperatures (Vale, 1971).

2.4   Bait technology

Game and habitat destruction and the spraying of large areas with chlorinated hydrocarbons were, for a long time and in many circumstances, the only necessary and sufficient means of tsetse eradication. None of these methods is ecologically desirable. They also require a high level of centralised organisation and are becoming increasingly expensive. These concerns have led to the search for simpler, cheaper and less damaging techniques. In particular, there has been renewed interest in the use of devices that can be used to kill or sterilise tsetse in the field. In principle, and if properly carried out, these methods should allow the eradication of tsetse without the need to remove hosts or vegetation and without depositing large quantities of toxic chemicals in the environment, sometimes with long-term residual effects.

Initial interest was in traps, then in insecticide-treated 'targets' or 'screens' (*écrans* in French). Later, it also appeared that modern pyrethroids were better suited for use as sprays or dips for cattle than previous generations of insecticides, such as the chlorinated hydrocarbons.

Interest in bait technology was stimulated by discovery of the low reproductive rate in tsetse, which implies that even small (*c.* 4% per day) additional death rates of adult females, if *sustained*, will eradicate a closed population, regardless of any density-dependent resilience (Hargrove and Vale, 1979; Rogers *et al.*, 1984; Hargrove, 1988).

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Fly capture had first been used in the eradication of tsetse on the island of Principe, where *G. palpalis* Robineau-Desvoidy was removed in the early 20th century. Tsetse were caught using hand-nets, or on sticky panels fixed to the backs of workers. This early, simple, well-defined example illustrates two of the main principles and problems associated with tsetse eradication and its analysis.

First, it is often unclear what contribution a given intervention has made to the overall process of control or eradication. In the case of Principe, in addition to trapping, many of the island's wild pigs and dogs were shot (Leak, 1998). It is not clear, therefore, whether the trapping exercise by itself would have resulted in eradication.

Second, the exercise underlined the problem of re-invasion, even on an island. Even though Principe is over 200 km from the nearest population of tsetse (on Fernando Po) the island was re-invaded by tsetse in the 1950s (Glasgow and Potts, 1970).

2.4.1   Traps and targets

Harris' control of G. pallidipes *in Umfolosi using traps*

Harris (1932, 1938) carried out the first large-scale control campaign using traps in the Umfolosi game reserve in Zululand, South Africa. As with the Nagupande hunting experiment, the study is often quoted but has never been analysed in any detail.

In the late 1920s, populations of *G. pallidipes* around the Umfolosi game reserve caused problems in cattle, particularly among those owned by settler farmers to the south of the reserve. The campaign against this tsetse population had two phases. In 1929 and 1930, host animals were killed in the areas surrounding the reserve; thereafter (between 1931 and 1938) Harris traps were deployed in the reserve and perhaps in part of the area outside. This much is clear, but other details of the operation are less apparent.

Thus, while Harris (1938) provided monthly totals of catches, these were not split into catches from the various areas. Buxton (1955) notes that much greater detail of catch and trap distributions is provided in a typed supplement to the 1932 paper, but these data could not be found for this report. He also notes that it is not clear over what area the traps were deployed. The Umfolosi game reserve is quoted as covering 70,000 acres (*c.* 280 km^2) but Harris (1932) states that the 'traps are erected here and there over more than 200 square miles' (*c.* 520 km^2).

An additional problem arises in the continuity of the data, as Harris (1932) laments 'the financial stringency which caused the work to be stopped in early January, 1932…for three months the traps were unattended'. Nonetheless, the traps were still operating and killing tsetse, even if not always with optimal efficiency. All of these uncertainties make modelling difficult, and the analysis provided here is therefore only provisional.

There has also been some confusion over the relative effects of game destruction and fly trapping on the tsetse population. Buxton (1955) concludes that the shooting 'appeared to lead to a reduction in the number of flies (Harris, 1932). It is not possible to discover for how long the shooting of game continued or whether it was renewed at a later date; it may be that some of the reduction in numbers of tsetse caught in the traps was due, in part, to the game destruction'.

Harris (1932) states unambiguously, however, that as 'it would have been impossible to concentrate and confine the enormous numbers of animals from the surrounding country within the confines of the Umfolosi game reserve…it became essential to work from the outermost boundaries of the game and fly area concentrating towards the sanctuary, destroying the animals that were found in the buffer zone, in order to reduce the numbers of those which would be driven into the reserve'. The hunting was carried out 'from May, 1929 to November, 1930. During this period, 26,000 head of game was destroyed in the Umfolosi buffer zones alone…'. He states, specifically, that hunting operations were stopped for financial reasons and that this move was followed by 'one of the worst droughts in the history of the country. The Umfolosi game reserve became a wilderness and was gradually deserted by the majority of the game'.

The hunting operation was thus complete before the traps were deployed in the Umfolosi game reserve in January 1931 and there is no suggestion of hunting in this area, either before or during the trapping operation. The changes in fly numbers within the reserve may therefore be attributed almost entirely to the effects of trapping. What the hunting operation will undoubtedly have achieved is a massive reduction in fly numbers in the buffer zone, thereby reducing, but not entirely preventing, re-invasion of the trapping area.

Given these considerations, the data on fly catches were modelled below as if the declining levels were due entirely to increasing trapping pressure. The effects of the hunting were also included, however, in assuming that in the area surrounding the reserve, initial tsetse population levels, growth rates and carrying capacities were all much reduced.

Modelling

As with the modelling of the Nagupande experiment and other work covered in this report, the Fisher equation was used to model changes in the tsetse population. Figure 10 shows the number of traps deployed each month and the catches of tsetse per trap per day. The very rapid decline in catches at the end of 1931 draws immediate attention to a deficiency in the experimental design: Harris did not use an 'objective' means of assessing the decline in tsetse numbers in the Umfolosi area as a whole. For instance, his traps were used simultaneously as control and sampling devices. This problem was compounded by the fact that Harris moved the traps 'from one section to another if the average number of flies per trap in a section showed a heavy decrease from the

previous month'. Clearly, the trapping effort was not constant in any particular area, or across the reserve as a whole. The very high catches in 1931 presumably reflect the fact that Harris initially deployed traps in the areas where he judged fly populations to be highest. What the trap catches measured, therefore, was a local decline rather than an overall reduction in the *G. pallidipes* population.

The trap catches are not therefore an entirely reliable indication of *detailed* population changes. Nonetheless, the decline in mean catch per trap per day over the seven years of the experiment amounted to about five orders of magnitude and it is this overall change that should be reproduced via the modelling process. A reasonable fit to the data was achieved when it was assumed that each trap killed approximately 0.225% per day of the female population within a 1 km^2 neighbourhood of the trap (Fig. 10).

The numbers of traps deployed increased, somewhat unevenly, until 11,020 traps were being used simultaneously at a mean density of $11,020/280 \approx 40$ per km^2. The maximum imposed daily death rate would thus be approximately $40 \times 0.225 = 9\%$ per day if all traps acted independently. In fact, a uniform grid with traps at this density means that there would only be 150 m between each trap and there might well have been some interference between traps. The distance between some traps would be less than this if, as Harris states, traps were only placed in what was deemed to be suitable habitat. Conversely, the inter-trap distance would have been greater if the area over which they were deployed was actually 520 km^2 (see above).

Tsetse population levels in the Umfolosi area can be estimated from the results of the modelling. If each trap kills a constant proportion p of the tsetse flies in a 1 km^2 neighbourhood, and if traps catch an average of n_i flies on day i, then the population density may be estimated as n_i/p. With maximum catches of 87.7 flies per trap per day, and with p estimated as 0.00225 from the modelling, this gives a population density of *c.* 39,000 *G. pallidipes* per km^2 and a total population for the whole game reserve of around 11 million if it is assumed that the traps were deployed over an area of 280 km^2. Vale *et al.* (1986), using similarly approximate techniques, estimated a population of around 9 million for the Rifa Triangle within an area of approximately 600 km^2.

As emphasised above, the estimates for capture probability and total population for Umfolosi are only first approximations. Better estimates from Zimbabwe for the proportion of female *G. pallidipes* killed daily by a single odour-baited target suggest a value of 2–2.5% (Vale *et al.*, 1986; Hargrove, 2003). This suggests that the kill rate of *G. pallidipes* by a target is an order of magnitude greater than by a Harris trap. In accordance with this view, Vale and Hargrove (1979) found that less than 50% of tsetse approaching mechanical traps were actually captured, whereas all flies contacting insecticide-treated targets are killed. Moreover, adding odours to the targets is

Figure 10. **Harris trap catches, South Africa**
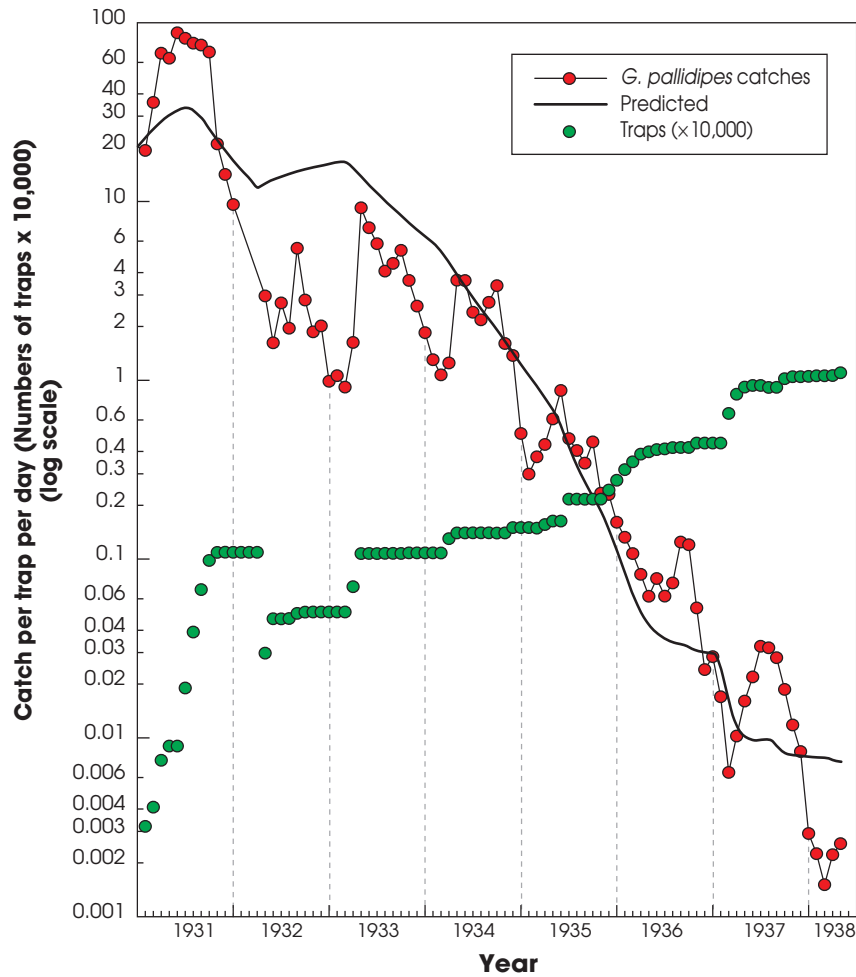
Harris trap catches of *G. pallidipes* in and around the Umfolosi game reserve, Zululand, South Africa. Constant growth rates of 0.75 and 0.1%/day and arbitrary carrying capacities of 100 and 1 were assumed for the areas inside and outside the reserve, respectively. The diffusion coefficient was set at 0.2 km day$^{-1/2}$ in all areas. Each trap was assumed to act independently and to kill 0.225% per day of the female population in a 1 km^2 neighbourhood.

estimated to increase the number of flies visiting them by a factor of six (Vale, 1993). The combination of these two factors may therefore be expected to result in an order of magnitude increase in the killing rate.

Du Toit (1954) argued that the Harris traps were successful because the campaign was preceded by a game elimination exercise and three years of severe drought, a line of argument repeated by Glasgow and Potts (1970). No arguments or data were advanced to substantiate this claim and the present analysis suggests that the decline in catches over the seven years of the campaign was entirely consistent with the predicted effect of the traps.

What is evident from the results is that, despite the fact that the trap density was 20–40 per km^2 by 1938, the population had still not been eradicated and this feature is predicted by the modelling. The problem lies in the fact that the area treated was small and that a residual tsetse population surrounding the reserve formed a source of re-infestation.

Similar attempts to use traps in tsetse control operations in West Africa were even less successful (Morris and Morris, 1949) and interest in this method waned for many years until Vale's (1974a, 1974b) discovery of the importance of odour in attracting some species of tsetse. This finding changed the entire dynamics of the use of traps and targets for tsetse control and eradication. If odours could increase the numbers of tsetse visiting a target, then it would be possible to achieve eradication with much smaller bait densities.

Antelope Island experiment

The first operational trial of odour-baited devices for tsetse (Vale *et al.*, 1986) was performed on Antelope Island, Lake Kariba, Zimbabwe between 1980 and 1984, against populations of *G. m. morsitans* and *G. pallidipes* introduced as pupae to replace the former natural population that had previously been subject to control using a combination of aerial spraying and SIT in the late 1960s (Dame and Schmidt, 1970). Intensive mark–recapture experiments were carried out so that odour-baited traps and 'targets' could be tested against tsetse populations whose numbers were estimated using the methods of Jolly (1965) and Seber (1965).

When the densities of the introduced populations were at or near their carrying capacities, a series of odour-baited devices – automatic sterilising devices, then traps and finally insecticide-treated targets – were ranged against the two species. The end result was that both species were eradicated from the island. A more precise idea of what is meant by the term *eradication* is developed below; from that development it may be stated that the probability that any surviving fly went undetected was <0.0001.

Hargrove and Williams (1998) have already modelled the growth and decline of the population of *G. m. morsitans* and these results are not repeated here. Suffice to say that it was possible to

provide a good fit to the data (Fig. 11) with a model that was simple enough to suggest that similar models might profitably be applied to field data from other, larger tsetse control campaigns.

The experiment demonstrated that odour-baited targets could be used to eradicate *closed* populations of *G. m. morsitans* and *G. pallidipes*; the more interesting point was how they would fare against populations subject to re-invasion. Following the success of the Antelope Island operation, Vale *et al.* (1988) proceeded to test the system against an open population of tsetse in the Rifa Triangle of Zimbabwe.

Figure 11. **Antelope Island experiment, Lake Kariba, Zimbabwe**
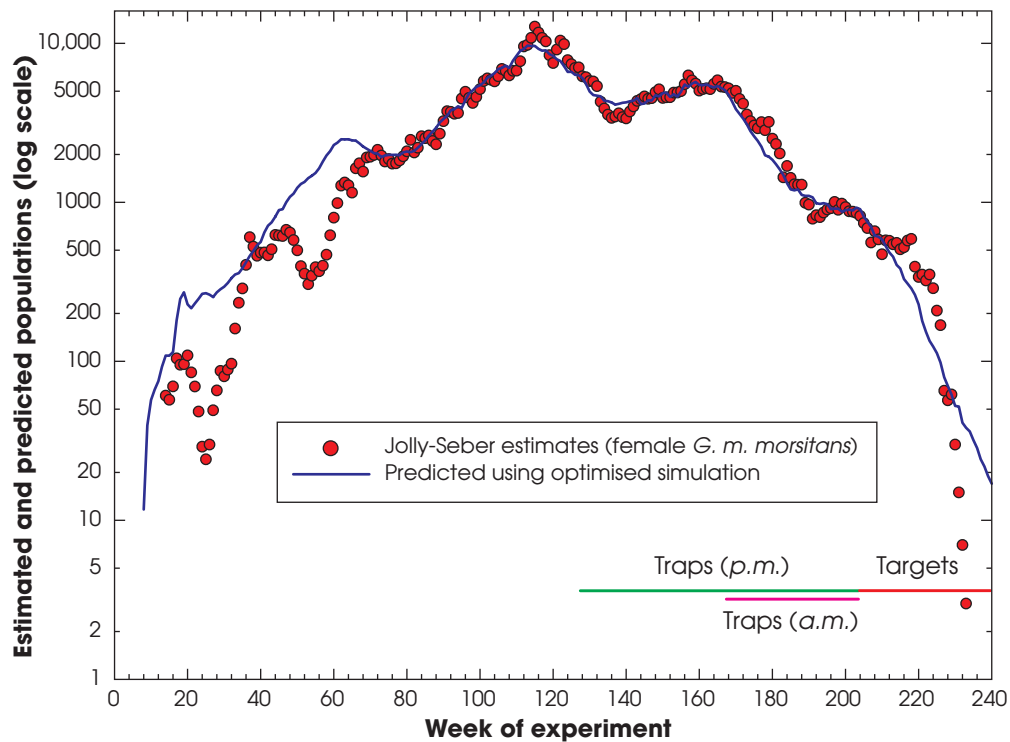
Estimated and predicted population of female *G. m. morsitans* on Antelope Island, Lake Kariba, Zimbabwe. The graph demonstrates the decline and ultimate eradication of the population after the deployment of odour-baited traps, followed by targets. Data were fitted as described in the study on optimised simulation by Hargrove and Williams (1998). The bars in the bottom right-hand corner of the graph indicate the periods when odour-baited traps or targets were deployed on the island.

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Rifa Triangle experiment

In 1984–1985, around 3000 odour-baited targets treated with insecticide were deployed in a 600 km² area known as the Rifa Triangle (or more simply 'the Rifa'), in the Zambezi Valley, Zimbabwe (Fig. 12). Changes in populations of *G. m. morsitans* and *G. pallidipes* were estimated over a two-year period from trap catches at sites inside and outside the control area (Vale *et al.*, 1988). The data have recently been analysed using the modelling techniques described in Appendix 3 (Hargrove, 2003). The results of that exercise are described here.

For modelling purposes the area was split into five zones (Fig. 12):

1. The main invasion area, comprising hunting areas and, beyond them, the Mana Pools National Park. No tsetse control was carried out in these areas.
2. The Rifa, where target density increased between March and October 1984.
3. The Zambezi escarpment, where no targets were deployed but an area of 1428 km² was ground sprayed with a 4% solution of DDT (183 gm active ingredient per ha) in September 1984.

Figure 12.   **Map of the Rifa Triangle and surrounding area**
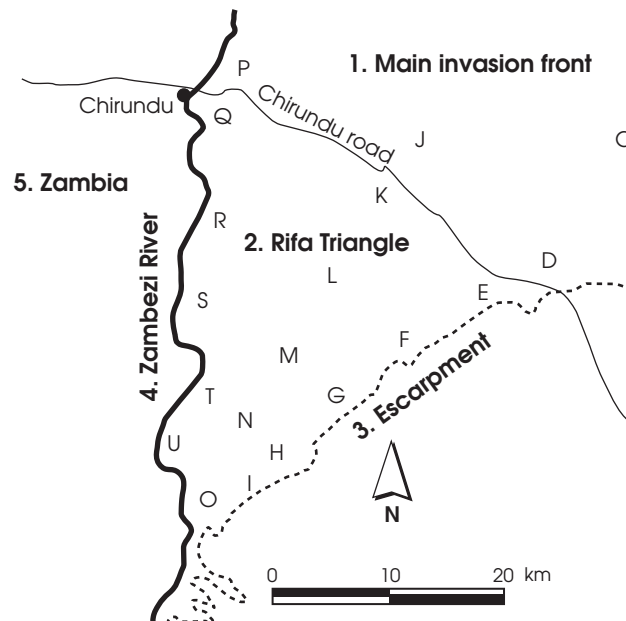
Letters in the body of the map denote sites where tsetse samples were taken using odour-baited traps. Catches were also made at two sites (A and B, not shown) near Rekomitjie Research Station, *c.* 25 km east of site D.

4. The Zambezi River, which may act as a partial barrier to the movement of tsetse between Zimbabwe and Zambia.

5. Zambia, in the area opposite the Rifa, where there had been extensive destruction of habitat and wild hosts, and where the tsetse populations are known to be lower than on the Zimbabwe side of the river.

The area was 'mapped' in Microsoft® Excel as a 50 km square where each cell represented an area on the ground of 1 km². Northeast of the Chirundu road, towards Rekomitjie Research Station, the block extended 12 km beyond the edge of the Rifa; west of the Zambezi and southeast of the escarpment it extended for at least 5 km; and south of the apex of the Rifa, along the Kariba gorge, it extended for 3 km. These limits were chosen after modelling indicated that, beyond them, the targets had no discernible effect on fly populations.

Odour-baited traps were used to catch *G. m. morsitans* and *G. pallidipes* at widely distributed sampling sites (Fig. 13), not all of which could be sampled simultaneously. Trap catches of *G. m. morsitans* were one or two orders of magnitude lower than those of *G. pallidipes* and were too small to allow meaningful modelling using optimised simulation. The results of applying this procedure to *G. pallidipes* were, however, useful in suggesting parameter values for fitting the *G. m. morsitans* data.

Reasonable fits to the *G. pallidipes* data were achieved by varying only the flies' rate of movement and the rate at which adults are killed by odour-baited targets. Thereafter, it was necessary to use optimised simulation to improve the fit and to find out which variables were required for the model.

The technique was used to provide improved fits to the *G. pallidipes* trapping data for all areas (Fig. 13). The most important variable accounting for the decline in tsetse numbers in the Rifa was, as expected, the effect of the targets; each target killed approximately 0.5% of the female *G. pallidipes* population in each six-hour period, which equates to 2% per day. Since each 1 km² cell eventually contained, on average, four targets, the imposed mortality in the Rifa was approximately 8% per day.

Ground spraying of the escarpment appears to have played an important part in reducing re-invasion from that quarter. The parameter estimate suggests that daily mortality in the escarpment increased by 8% after the onset of spraying. This result is in accord with the view expressed by D.F. Lovemore (see above) that ground spraying of tsetse leads to a relatively slow decline in fly populations, akin to the observed decline resulting from the deployment of odour-baited targets.

The likely time-course of the control of *G. m. morsitans* was modelled using information from the results for *G. pallidipes*. Many of the parameters, such as growth rates and carrying capacities, may be of similar magnitude for the two species, but there are likely to be larger

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Figure 13. **Mean daily catches of *G. pallidipes* in the Rifa triangle**
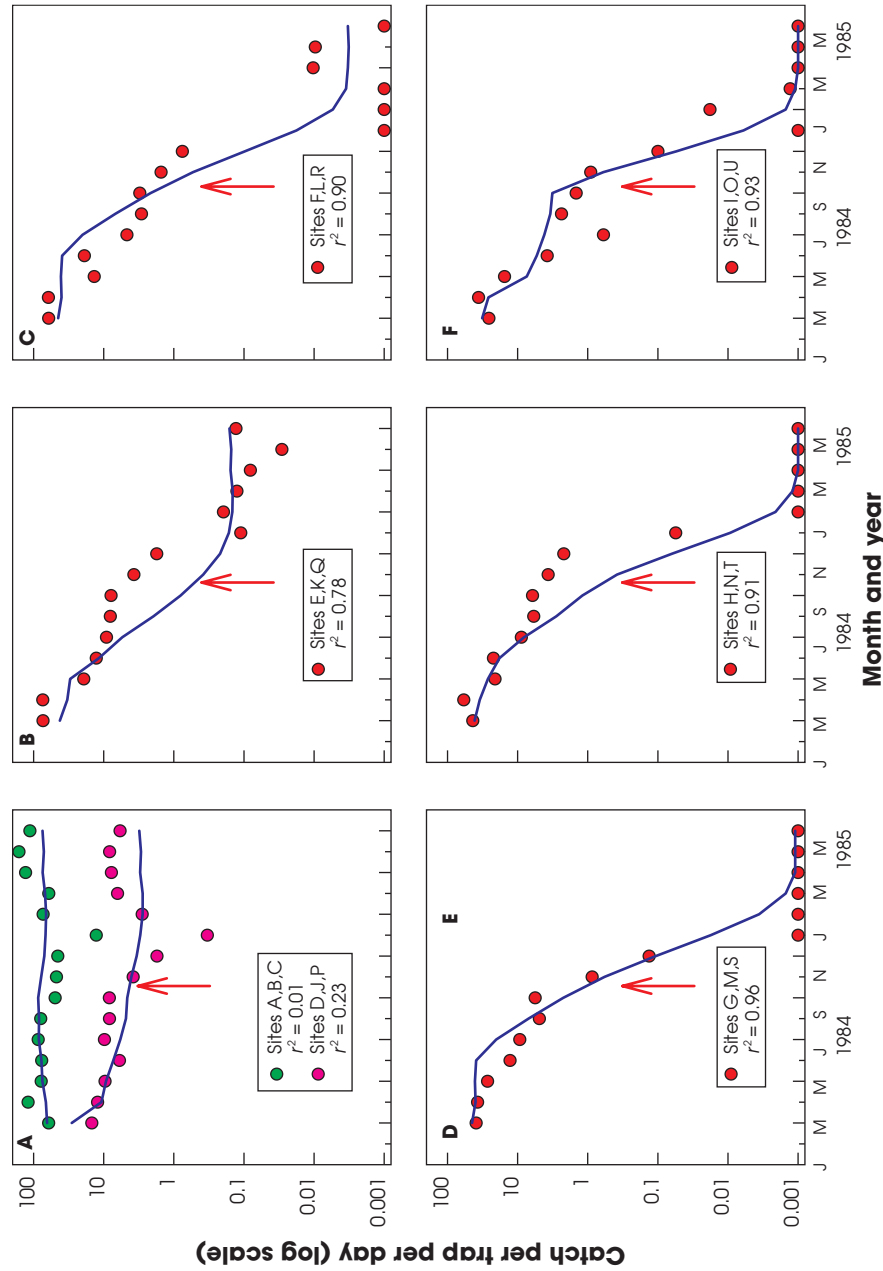
Mean daily catches of *G. pallidipes* in the Rifa triangle pooled over monthly trapping periods and over the sites shown in each graph. The plotted lines indicated the predicted population changes resulting from the optimised simulation described in the text. For the fit to all data combined, $r^2 = 0.93$. The arrow in each graph indicates the onset of the hot dry season. Catches were pooled from traps operated at approximately the same distance from the Chirundu road, which marks the boundary between the experimental area and the main source of tsetse invasion into the Rifa.

differences in terms of the rates of movement and the killing rate due to targets. *G. m. morsitans* appears to disperse more slowly than *G. pallidipes* (Vale *et al.*, 1984) and early estimates suggested a daily step length of not more than 200 m (Rogers, 1977; Hargrove, 1981) equivalent to $\alpha = (0.2 \times 0.2)/4 = 0.01$ km^2 per day, although the movement of females of this species may be markedly higher under some circumstances (Vale *et al.*, 1984). Vale *et al* .(1988) also estimated that, whereas the Rifa targets killed 10% of the *G. pallidipes* per day, the figure for *G. m. morsitans* was only 2%, although they regarded these as crude estimates derived from a variety of sources. Their estimate for *G. pallidipes* is nonetheless close to the present estimate of 8% for a situation where the target density is four per km^2 (see above). Accordingly, as a preliminary study of the likely time course of control, various simulation runs were carried out in which α was varied from 0.01 to 0.1 km^2 per day, and the imposed mortality due to targets varied from 2 to 8% per day. Further details of these other simulations are given by Hargrove (2003).

The results (Fig. 14), for reasonable values of the diffusion coefficient and for mortality caused by the targets, were consistent with the findings summarised in Fig. 13; simulation predicted that within six months flies would have virtually vanished from the Rifa – except on the boundary with the main invasion route. Reducing the diffusion coefficient by an order of magnitude made little difference to the predicted levels in the heart of the Rifa, but, as expected, numbers changed more sharply at the edge of the Rifa. As the modelled mortality due to targets was decreased, the population decline within the Rifa naturally became smaller until, when the additional mortality was only 2% per day, target mortality had little effect on the population in the middle of the Rifa.

Reduced populations at the left edge of each graph are due to the proximity to the escarp-ment where ground spraying had been carried out and the imposed mortality was high. A separate series of simulations was carried out (results not shown) in which no mortality was imposed in the escarpment. Then, of course, populations were always higher, at every stage and throughout the Rifa.

The results of these simulations were used to gauge, very roughly, the mortality that was being imposed by the targets on the *G. m. morsitans* population. Because of the small numbers of *G. m. morsitans* trapped, catches were pooled over two months and over all trapping sites within the Rifa. These catches were then expressed as percentages of the catches at Rekomitjie Research Station (Fig. 15a). By way of comparison, similar means were calculated for *G. pallidipes* (Fig. 15b).

Comparisons with simulated results were made by taking cuts across time, instead of space (as in Fig. 14), using the predicted populations along a line between site J and the apex of the Rifa adjacent to site O (Fig. 12). For *G. m. morsitans*, up to the time when the escarpment was sprayed, the data are consistent with the results when it was assumed that $\alpha = 0.01$ and that the additional daily female mortality (μ) in the Rifa was 1% (Fig. 15a). Thereafter, when an additional mortality

Figure 14. **Predicted control using targets in the Rifa Triangle**
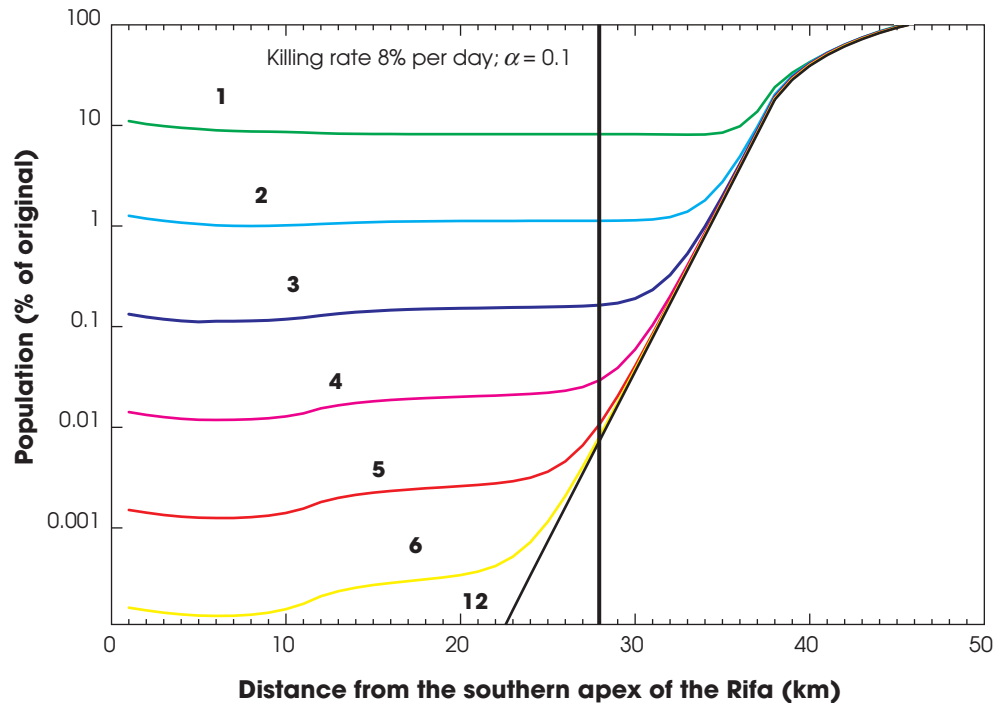
Predicted population levels in the Rifa Triangle as a function of the mortality imposed due to targets and as a function of the diffusion coefficient (α). Each trajectory shows the predicted population along a line between site J and the apex of the Rifa adjacent to site O (see Fig. 12). The vertical line in the body of the graph indicates the edge between the Rifa and the main invasion area. Numbers in the body of the graph indicate months after the start of the control operation. A constant 8% daily mortality was assumed in the escarpment.

of 8% per day was assumed in the escarpment, it was only necessary to assume that μ increased to 2% per day to account for the more rapid decrease in trap catches.

For *G. pallidipes*, a good fit could be achieved for the pre-spray data if $\alpha = 0.1$ and $\mu = 2\%$ per day (Fig. 15b). Thereafter, it was necessary to increase μ to 8% per day. More rapid decreases in trap catches of both species from October onwards, presumed to reflect changes in the actual populations, are due in part to the effect of the spraying in the escarpment, which reduced the invasion pressure along one side of the Rifa. Note that μ is the total additional mortality in the Rifa. The increase in μ after September was due in part to the increased numbers of targets deployed by

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Figure 15. **Decline in catches, Rifa Triangle**
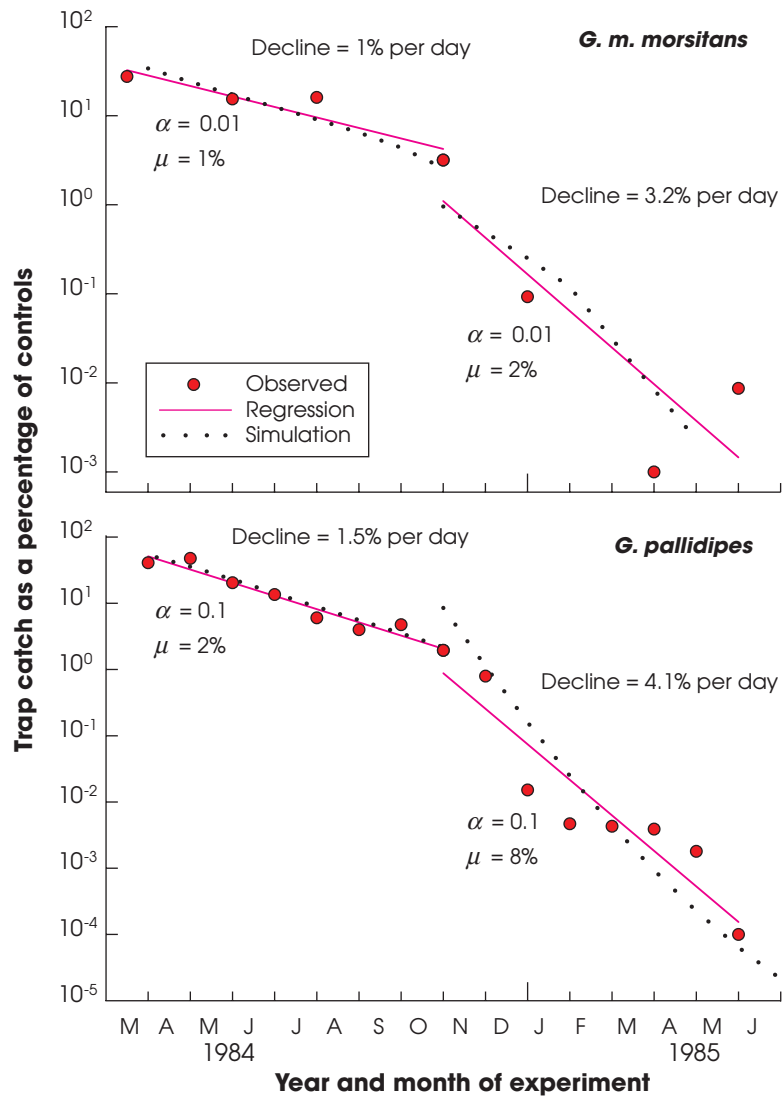
Mean observed and predicted trap catches of a) *G. m. morsitans* (bi-monthly) and b) *G. pallidipes* (monthly) plotted against the month of the trial. Solid lines fitted by linear regression, dotted lines by simulation using the given input values for the diffusion coefficient (α; units km^2 per day) and the additional mortality (μ; units % per day) in the Rifa Triangle.

this time, but, presumably, also to the onset of the hot season. If seasonal effects are assumed to be broadly similar for both species, then the kill rate due to the targets was smaller for *G. m. morsitans* than for *G. pallidipes*, in support of earlier estimates (Vale *et al.*, 1986, 1988).

This difference between the species has important implications for the outcome of eradication campaigns. For *G. m. morsitans*, if target effectiveness is halved, due, for instance, to the absence of odour sources or a decline in insecticide efficacy, the results suggest that the rate of population decline would be so slow that eradication would be unlikely. The same level of target deterioration would mean that 4% per day of the female *G. pallidipes* would still be killed, however, and this should result in eradication in all areas removed from the invasion front.

The progress of the Rifa experiment can be readily visualised using an Excel sheet where the population levels are colour-coded (Fig. 16). After 24 months of target action the simulation predicts that tsetse have been eradicated in the centre of the Rifa. Moreover, tsetse densities in Zambia are predicted to have declined.

Figure 16. **Rifa Triangle simulation**
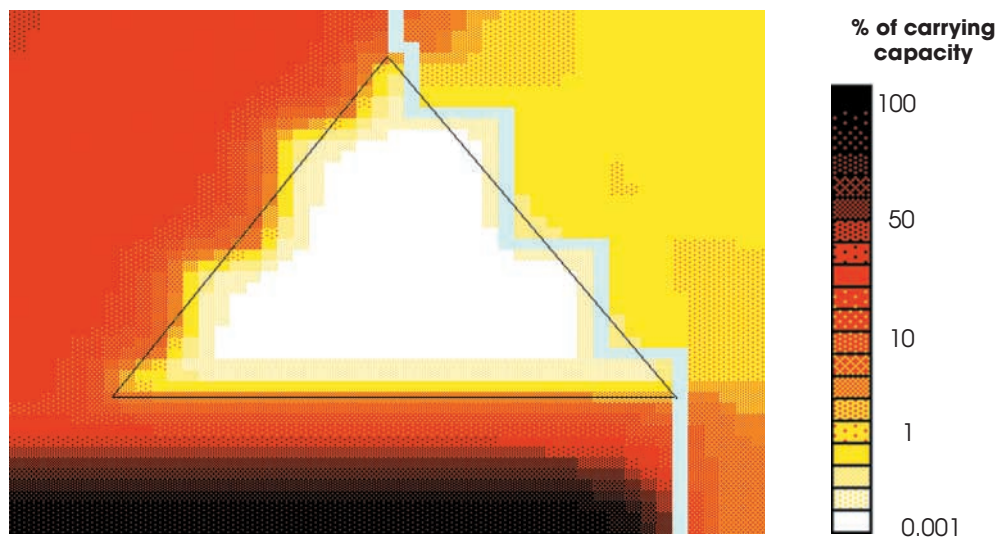
Colour-coded output resulting from a Microsoft® Excel run simulating the Rifa Triangle experiment. The broad blue line indicates the Zambezi River with Zambia to the right and Zimbabwe to the left. The colours in the remainder of the map represent the *G. pallidipes* population levels, as a percentage of the assumed carrying capacity, 24 months after the start of the experiment. In this simulation, no added mortality is assumed for the escarpment region. Note that the orientation of the 'map' was determined by the convenience of drawing it in Excel; the appropriate geographical orientation is shown in Fig. 12.

Note, however, the high densities of *G. pallidipes* indicated at the bottom of the map, towards Rekomitjie Research Station. Any relaxation of the control effort in the Rifa would quickly lead to re-invasion from this area of high fly density, and this has indeed now happened following the removal of targets from the Rifa Triangle.

Other tsetse control campaigns using odour-baited targets and traps

After the successes of the Antelope Island and Rifa Triangle experiments, a number of other attempts were made to use odour-baited targets to control or eradicate tsetse in different parts of Africa. Some of these efforts are summarised in Fig. 17; odour-baited targets were used in all the operations except Nguruman.

What is noteworthy here is the similarity of all time-courses of the target operations; in each case, tsetse became undetectable within a year. In the case of the Umfurudzi in northeast Zimbabwe, *G. m. morsitans* was eradicated from the area by the end of 1987 and no tsetse have been caught there since.

In Sioma, Western Province, Zambia, following the success of the pilot operation summa-rised in Fig. 17, targets were deployed over large areas adjacent to the trial block. When Knols *et al.* (1993) attempted to eradicate *G. m. centralis* using lower target densities (1–2 per km^2) they experienced difficulties and ultimately had to deploy extra targets to achieve their objective. Continuing operations in the province have met with considerable success. According to Thakersi (1997) 'to date c. 11,500 km^2 have been successfully treated with targets and a 200 km long barrier protects the cleared area from re-invasion and some 50,000 cattle from trypanosomiasis. Whilst there is every reason to believe that it is successful, the lack of regular monitoring services in the area means that it is not certain'.

There is an obvious, marked difference in Fig. 17 between the results of operations where insecticide-treated targets were used and the Nguruman operation, where tsetse were caught and killed in mechanical traps. This is due partly to differences in the baits used. Whereas all flies that touch an insecticide-treated target will die, large proportions of tsetse may fail to enter a trap. Moreover, in the Zimbabwean and Zambian operations, targets were always baited with acetone and, except on Antelope Island, also with 1-octen-3-ol (octenol). In the Umfurudzi and in Zambia, but not on Antelope Island and in the Rifa, a mixture of two phenols was also used. At Nguruman, the only bait used in the control traps was bovine urine.

The other cause of the difference relates to the size, shape and degree of isolation of the areas treated. Antelope Island, while only 5 km^2, was not subject to any re-invasion. The Rifa and Umfurudzi are both approximately 600 km^2 in area; the former was only subject to serious re-invasion on one side of the triangle and the latter was isolated due to the prior removal of flies

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Figure 17. **Results of selected target and trap trials**
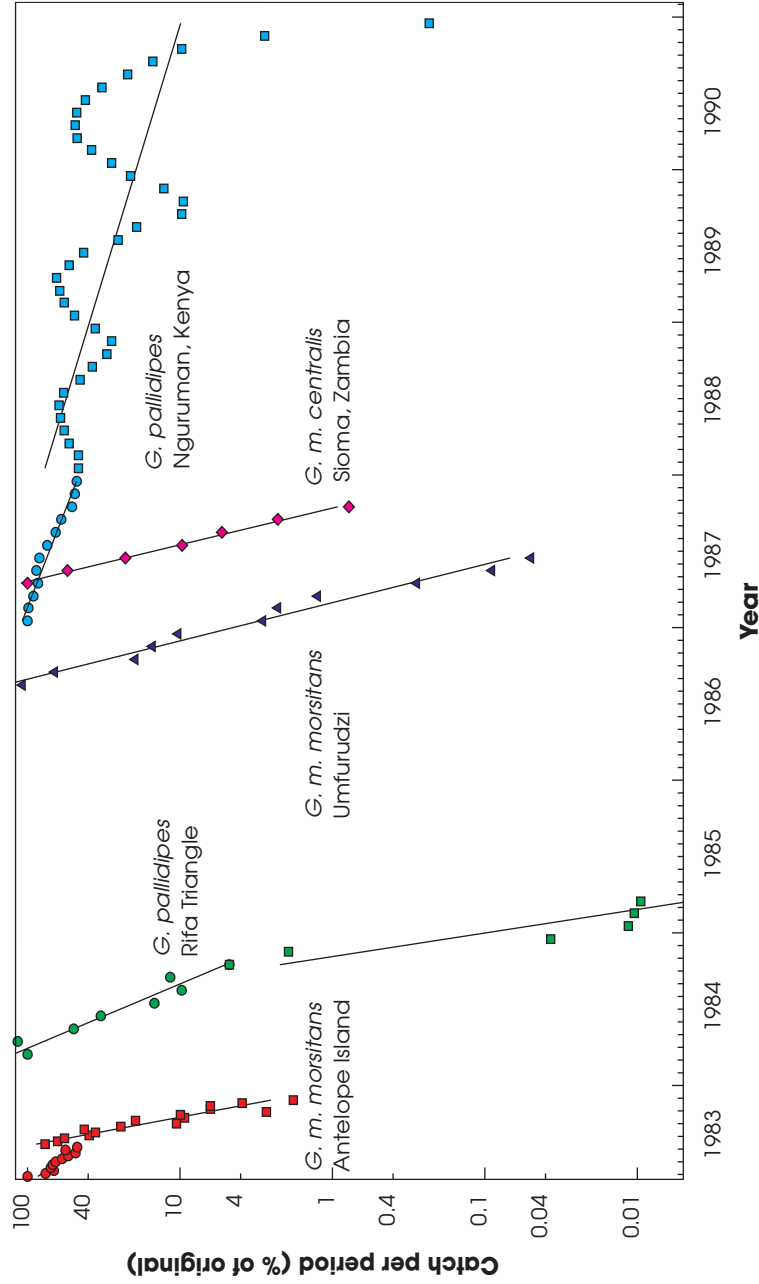
The time course of operations where odour-baited targets and traps have been used to control or eradicate tsetse in Zimbabwe, Zambia and Kenya. Data: Antelope Island (Hargrove and Williams, 1998); Rifa Triangle (Vale *et al.*, 1988); Umfurudzi (unpublished data); Sioma (Willemse, 1991); Nguruman (Brightwell *et al.*, 1997). Note that, although the Nguruman population declined rapidly in 1990, it recovered again in 1991 and has never been eradicated.

from the surrounding areas. The trial block at Sioma was only 500 km^2 and was subject to re-invasion. As soon as the trial was seen to be successful, however, target operations were started in contiguous areas and the invasion pressure was greatly reduced.

In Nguruman, the situation was quite different. The total area covered by traps was never more than 200 km^2 and approximated the shape of a 25×8 km rectangle subject to rapid invasion of flies at certain times of the year. As with Harris' trial, there were annual cyclical variations in trap catches (Figs 10 and 17). These cycles do not appear in the data from Zimbabwe and Zambia because in each case the populations virtually disappeared within a single year.

Differences in the time course of changes in tsetse populations between the Nguruman and Umfolosi cases on the one hand, and the odour-baited target campaigns on the other, are due both to differences in the kill rate and to issues of re-invasion. The latter relate to the scale of the operation, the shape of the control area and the presence or otherwise of tsetse populations in adjacent areas.

Similar considerations are naturally important in all tsetse control operations, regardless of the control method used. Their importance is particularly evident in bait systems of tsetse control which, by their nature, tend to induce gradual and easily measurable changes in tsetse populations. Further examples are seen in operations where insecticide-treated cattle have been used to control or eradicate tsetse.

Traps and targets used against riverine and forest species of tsetse

It has been emphasised above that small-scale operations involving traps and targets are liable to fail as a consequence of invasion pressure. An exception to this rule is the situation where a small population is effectively closed – for instance with island populations. Rather less obvious 'islands' of tsetse also exist in isolated patches of forest or riverine woodland. These include riverine species of tsetse such as *G. palpalis palpalis*, which tend to inhabit narrow bands of riparian vegetation. Re-invasion pressure from this species thus tends to come along a narrow front that can easily be guarded. It was in such settings that the use of traps and then targets first saw a resurgence in the 1970s. The change was motivated by the development of the biconical trap by Challier and Laveissière (1973). Traps and targets were being used in tsetse control operations in West Africa by the end of the 1970s (Laveissière *et al.*, 1980; Laveissière and Couret, 1981) and have been used successfully in various campaigns since that time (Filledier and Politzar, 1985; Merot and Filledier, 1985; Dagnogo *et al.*, 1986; Takken *et al.*, 1986).

Data from these campaigns were not available to the author and modelling of their out-comes was thus not possible. Nonetheless it is recognised that, where data are available, they would provide a valuable opportunity for assessing the efficacy of using baits to control riverine and forest species of tsetse.

Limitations of odour-baited targets

The previous sections review a number of campaigns where odour-baited targets have been used successfully to control and even eradicate populations of tsetse. However, the method has not been used as widely as might be expected. This is due partly, as discussed in the previous section, to a failure to appreciate the effects of scale and the attendant problem of invasion. There is a further problem – when applied on the scale for which the method was originally designed in Zimbabwe, there is a requirement for an efficient infrastructure of trained personnel, supplied with well-maintained fleets of vehicles. This requirement, which is also needed for ground spraying operations, is hard to achieve in most African countries. In addition, targets are seen as valuable items, and when there are large numbers of poor people in the area where targets are deployed, many may be stolen and the control campaign may be severely disrupted. Hence, the method has met with disenchantment in many settings.

2.4.2   Insecticide-treated cattle

The use of targets has perhaps been overshadowed by the almost simultaneous development of a method whereby insecticide is applied to livestock, rather than to targets. In areas where there are large numbers of cattle, this is the cheapest, simplest and most effective method of vector control available. The method has been used, with varying degrees of success, to control tsetse in Zimbabwe (Thompson *et al.,* 1991; Thomson and Wilson, 1992a, 1992b; Warnes *et al.*, 1999), Zambia (Chizyuka and Liguru, 1986), Tanzania (Fox *et al.,* 1993), Kenya (Stevenson *et al.*, 1991), Burkina Faso (Bauer *et al.,* 1992, 1999a, 1999b) and Ethiopia (Leak *et al.*, 1995; Rowland *et al.*, 2000).

The principle of the method is the same as with odour-baited targets; it is only necessary for the cattle to kill more than 4% per day of the female tsetse population for that population to decline. If this kill rate is maintained over an *entire, closed* population of tsetse then that population will eventually be eradicated.

As with operations involving the use of traps and targets, however, problems arise when only part of the tsetse population is being treated, when the kill rate is too low, and when the population is subject to re-invasion. The operations are also more difficult to control than those where only stationary baits are involved. Targets and traps can be deployed wherever, and at whatever density, they are required, but the density, placement and movement of treated livestock is decided by factors that may have little to do with the needs and desires of the average tsetse control official. These problems are illustrated here with reference to three campaigns, two from Tanzania and one from Zimbabwe, where insecticide-treated cattle were used to control tsetse. The results of these operations were first presented by Warnes *et al.* (1999) and Hargrove *et al.* (2000) and have been analysed in more detail by Hargrove *et al.* (2003).

Mkwaja Ranch, Tanzania

Mkwaja is a 250 km^2 ranch on the Indian Ocean coast south of Tanga, Tanzania. The ranch has had a long history of trypanosomiasis problems caused largely by *G. pallidipes*, though populations of *G. m. morsitans*, *G. brevipalpis* and *G. austeni* are also present. The problems are largely unresolved to this day – despite the fact that the ranch has been used as a laboratory for testing techniques as diverse as bush clearing, trypanocidal drug treatments, SIT and now the use of insecticide-treated cattle.

Between 1989 and 1999, the population of Zebu Boran cattle varied from around 6000 to 14,000 animals. At night the cattle were kept in kraals, each holding 150–1700 animals. For grazing purposes, the animals from each kraal were divided into herds of 150 animals and these were grazed separately between 0700 hours and 1800 hours with the aim of providing an even coverage over the limits of the ranch. Surveys suggested, however, that 38% of the 1 km^2 cells on Mkwaja had at least a 20% chance of having a herd of 150 insecticide-treated cattle grazing on them, but 43% of the cells had less than 13% chance. The patchy cover resulted from the presence of considerable areas of dense thicket that were impenetrable to the cattle but were inhabited by game animals such as warthog (see Fig. 5 in Hargrove *et al.*, 2000).

Modelling of observed changes in the apparent density of *G. pallidipes* was carried out in the usual way (Appendix 3). It was estimated that female *G. pallidipes* had a daily probability of 0.22 of contacting one of the above herds, if it was present in a 1 km^2 cell on a given day. Other input parameters used in the modelling are given in the legend of Fig. 18. After a year of control, the predicted numbers of tsetse declined by over 90% in the areas of heavy grazing (Fig. 18). Elsewhere, particularly over much of the periphery of the ranch, predicted numbers declined by only 20–60%.

The geometric mean of the tsetse population, calculated over approximately 90% of the ranch (Fig. 18), was used as a measure of the overall effect of the treated cattle. The predicted decline in this mean is consistent with the data of Fox *et al.* (1993) for *G. pallidipes* and with their observations of a substantial improvement in the trypanosomiasis situation and a significant improvement in herd health. Despite the undoubted benefit of the insecticide treatment on disease levels, however, the predicted effect on the tsetse population fell far short of eradication, and was consistent with the continuing tsetse and trypanosomiasis problems experienced on the ranch (Hargrove *et al.*, 2000).

Reduced efficacy of control was due partly to the declining numbers of treated cattle on the ranch. Many cattle were sold and the total herd size fell from 13,900 in September 1991 to 11,000 by September 1995, then sharply to less than 9000 by the end of that year (Hargrove *et al.*, 2000). The model predicts that, with a natural growth rate of 1.5% per day, the 1991 tsetse population should fall to a new equilibrium level of about 10% of carrying capacity. In previous and in later

Figure 18. **Tsetse control using treated cattle, Mkwaja, Tanzania**
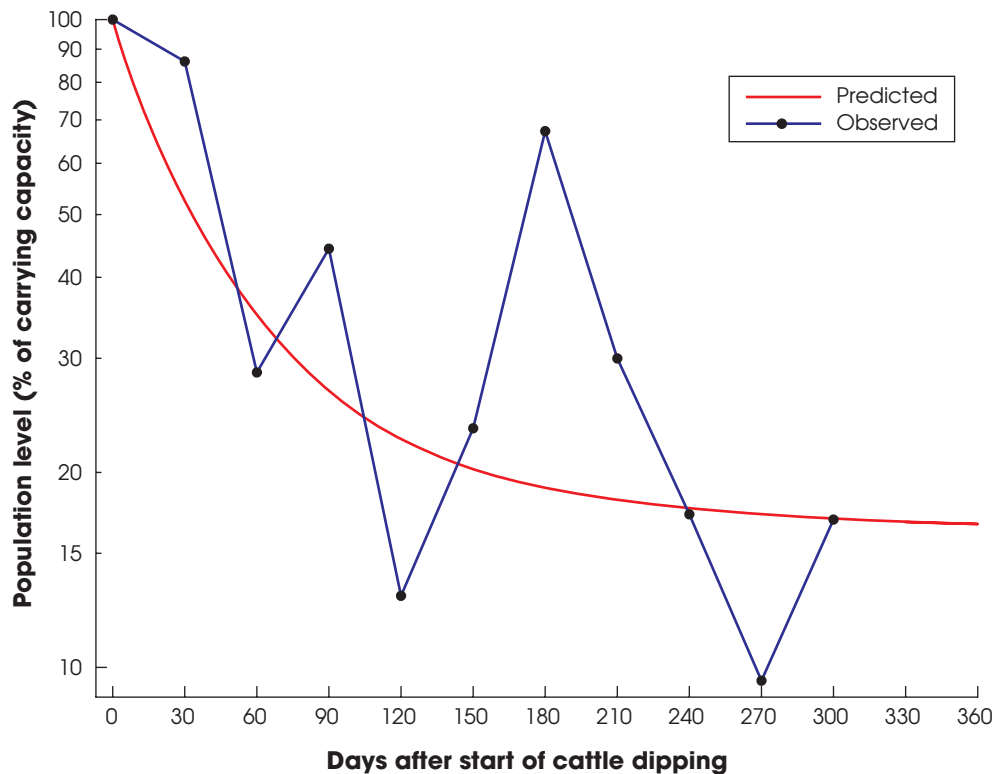
Observed and predicted rates of decline of the population of *G. pallidipes* following the introduction of insecticide-treated cattle in 1989 at Mkwaja Ranch, Tanzania. Input parameters: diffusion coefficient = 0.08 km^2 per day; growth rate = 1.5% per day; imposed mortality = 22% per day, given the presence in a given cell of a herd of 150 cattle.

years, when there were fewer cattle than in 1991, the decline in the tsetse population was not as great. In 1989 and 1990, for instance, the new equilibrium was closer to 15%. However, the rates of decline during 1991, when the herd was largest, suggest that a reduction in herd size did not have a major impact on the levels of suppression. The problem was more related to the distribution of the cattle, while the scale and presence of untreated foci of tsetse on the ranch added to the problem of invasion from outside the ranch boundaries.

Input parameters for the model were varied in an attempt to see whether enhanced control, or even eradication, might be achieved by simple changes in the treatment regime. Levels of control were indeed found to be a function of assumed killing rate due to each livestock unit, their grazing pattern and the size of the grazing herds, and also of the flies' assumed rates of population growth

and movement. The judicious use of odour-baited targets, in conjunction with treated cattle, could have reduced the tsetse population to 1% of its original carrying capacity and probably allowed the management to stop using Samorin® as a prophylactic against trypanosomiasis – but the modelling suggests very strongly that it would not have removed the trypanosomiasis problem entirely.

For all configurations of the model, tsetse numbers increased rapidly with increasing distance from the ranch boundary, in accordance with the results of the use of odour-baited targets in the Rifa (see above). This provides evidence for strong re-invasion pressure, indicating that control operations restricted to the ranch alone would not provide satisfactory relief from trypanosomiasis. The overall message arising from this operation is that treated cattle, when used over small areas that are subject to re-invasion (as in Mkwaja), will not provide adequate relief from trypanosomiasis and will, therefore, be of questionable economic value in the long term. This should serve as a severe caution to those who advocate the use of treated cattle on even smaller scales and with no target reinforcement.

In the following example, insecticide-treated cattle were used to much better effect. Viewed in conjunction with the Mkwaja experience, this shows clearly that each situation will vary and needs to be analysed on its own merits.

NARCO Ranches, Kagera Region, Tanzania

The Kagera Region in northwest Tanzania is home to several large ranches belonging to the National Ranching Company (NARCO). Like Mkwaja, this region has experienced a long history of tsetse problems. In the past, bush clearing and ground and aerial spraying campaigns have been carried out in attempts to eradicate the fly, all to no avail. The improvement in herd health resulting from the use of insecticide-treated cattle in Mkwaja led the NARCO management to try the same technique on their ranches. The results were spectacularly more successful in this setting and it is instructive to consider why.

No detailed data on cattle distribution in Kagera are available, but the potential area of tsetse infestation is a rectangle measuring approximately 100×25 km (Fig. 1 in Hargrove et al., 2000). To the west lies the Karagwe escarpment, and to the east dense banana plantations; neither habitat is suitable for tsetse. The only sources of re-invasion lie to the south, and to the north from across the border with Uganda. In each case, the invasion front is only about 25 km long. The proportion of the perimeter open to invasion is thus $50/250 = 20\%$ (cf. >80% on Mkwaja).

In the two years after the introduction of dipping with pyrethroids in 1991, cases of trypanosomiasis in the region dropped by more than an order of magnitude (Fig. 19; see also Hargrove et al., 2000). On one of the NARCO ranches, where pyrethroid treatment was most extensively and rigorously applied, the decline approached two orders of magnitude over a similar period.

Figure 19. **Trypanosomiasis control, Tanzania**
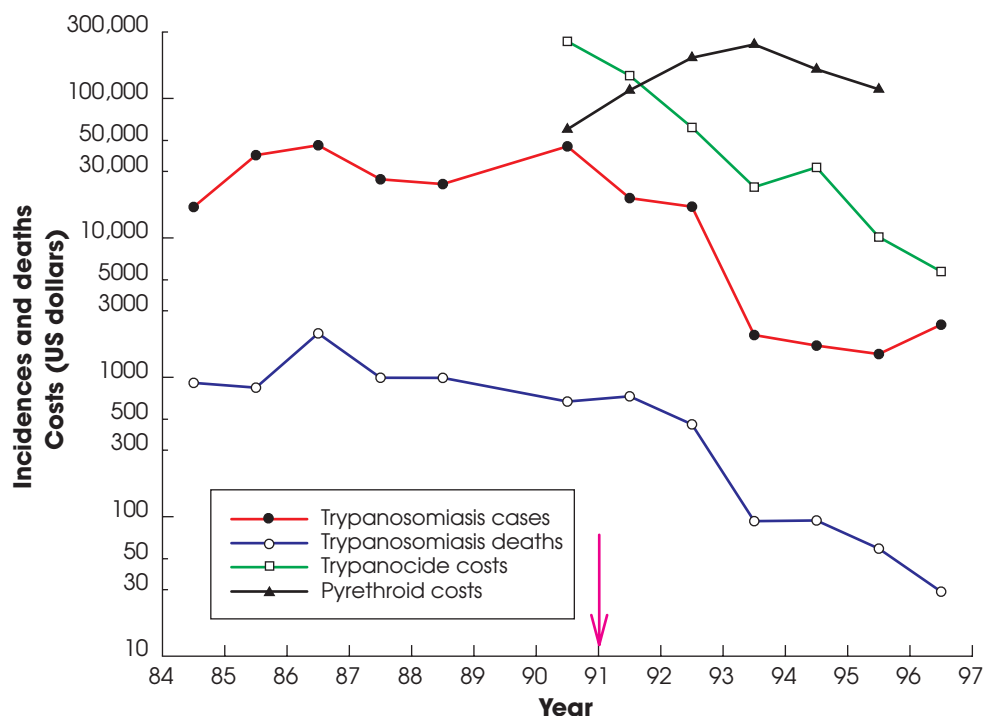
Trypanosomiasis control and the consumption of trypanocidal drugs and synthetic pyrethroids in Kagera Region, Western Tanzania. The arrow on the abscissa denotes the start of dipping with pyrethroids.

The tsetse population must have declined by at least this amount, but there are no hard entomological data that can be used to model the process. There is also uncertainty about the numbers of indigenous cattle that were treated with pyrethroids and there is no information on the grazing patterns for the various animals. Nonetheless, data from the Kagera Livestock Development Project (KALIDEP, 1996) show that there were approximately 27,000 cattle on the NARCO ranches and over 250,000 in the Bukoba and Karagwe districts of the region. The number of insecticide-treated cattle in the area at any given time therefore lies somewhere between these very broad limits.

As a start to the modelling process, the lower limit was chosen and it was assumed that the cattle were split into 180 herds of 150 animals that grazed in a uniform distribution over the whole 2500 km^2 rectangle surrounding the NARCO ranches. This means that on a given day there is only a 7% chance that a herd will be in a given 1 km^2 cell. This is a markedly lower mean grazing density

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Figure 20.   **Tsetse control using insecticide-treated cattle, Tanzania**
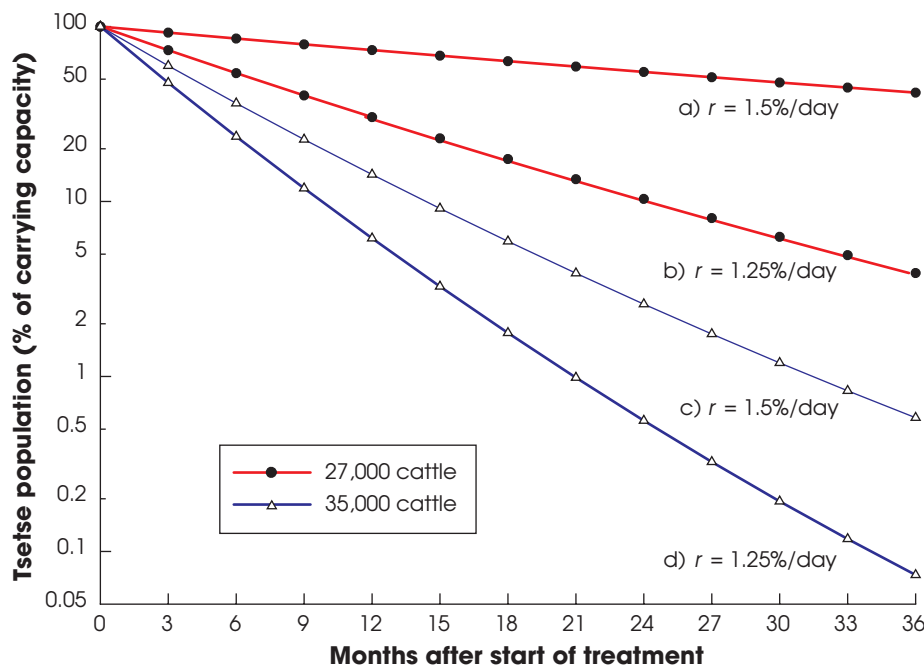
The predicted effect of using insecticide-treated cattle as a means of tsetse control in the Kagera Region, Tanzania. See text for details of cattle distribution within a rectangle of 2500 km².

than in Mkwaja and the predicted rate of tsetse population decline is therefore lower, assuming identical tsetse population growth rates (Fig. 20; curve a).

However, when the number of treated cattle was assumed to be 35,000, an increase of only 30%, the predicted tsetse population fell by over 99% in three years of treatment (Fig. 20; curve c). Notice that there is now a 9% chance that there will be a herd in a given cell, still much lower than the mean figure for Mkwaja. The key difference is the lower rate of re-invasion in the Kagera region. This factor also means that, whereas in Mkwaja the introduction of insecticide-treated cattle saw a new tsetse population equilibrium set up within a year, in Kagera the mean population continued to decline for over three years (Fig. 20).

Hargrove *et al.* (2000) suggested that the difference in impact of insecticide-treated cattle in Mkwaja and Kagera could be due to variation in the natural growth rates of tsetse in the two areas. Simulation indicates that the tsetse population in Kagera is much more sensitive to changes in its

assumed natural growth rate. In Mkwaja, halving the growth rate saw only a modest improvement in the control situation. By contrast, in Kagera, a much smaller decrease in growth rate, from 1.5 to 1.25% per day, saw an order of magnitude difference in predicted population after three years (Fig. 20, compare curves a with b, and c with d).

Effects of shape and scale of operational areas on tsetse control

The tsetse control operations in Tanzania underline the importance of invasion as the major factor frustrating effective tsetse control. Two simple geometric factors are particularly noteworthy. First, for any given shape, the area:perimeter ratio of a control area increases with size. Consequently, the relative length of the perimeter is greater with small areas and invasion is inevitably a bigger problem. The greater level of control achieved in Kagera compared to Mkwaja may be attributed partly to this difference in scale, combined with the fact that invasion pressure was restricted to the short borders to the north and south of the ranches. Second, the inevitably patchy distribution of insecticide-treated cattle means that areas treated using this technique will tend to have an irregular shape. In contrast, operations using odour-baited traps or targets have fairly regular, compact shapes (Vale *et al.*, 1988; Willemse, 1991). Irregular shapes will tend to have longer perimeters, thereby increasing the area at risk from invasion. Modelling of the results of the Rifa experiment showed that the odour-baited targets could not prevent the invasion of small numbers of flies up to 5 km from the edge of the treated area. The proportion of an area that is within 5 km of the invasion front thus gives a good rule of thumb for the invasion problem to be expected in a control operation.

The latter effect is aggravated by the fact that, as in Mkwaja, relying on treated cattle can result in the presence of untreated 'islands' of tsetse within the treated area. In contrast, when artificial baits are used, the operator can ensure that the entire area is covered. The consequence is that small areas controlled using insecticide-treated cattle are inherently more susceptible to invasion than an equivalent area controlled using targets. This problem is further exemplified below, by a trial in Zimbabwe where an attempt was made to replace a target barrier with a 'living barrier' of treated cattle.

The Mudzi barrier experiment

Mudzi District lies in northeast Zimbabwe, on the border with Mozambique. Tsetse were eradicated from the district in the late 1980s using odour-baited targets and insecticide-treated cattle. The area is, however, subject to re-invasion from Mozambique (Shereni, 1990) so that a combination of odour-baited targets (Vale *et al.*, 1988) and insecticide-treated cattle have been deployed along the border to prevent re-infection with trypanosomiasis. In 1996, the targets were removed from

around 40 km of the barrier for a trial period of six months, to assess the effectiveness of using approximately 6000 insecticide-treated cattle as a 'living barrier' (Warnes *et al.*, 1999).

Insecticide-treated cattle were also used in an area of approximately 165 km^2 of Mudzi District, as part of a much bigger operation using treated cattle all along the northeast border of Zimbabwe. When odour-baited targets were present they were deployed at a density of four per km^2 in a band 10 km broad running through the District, and extended to the north and to the south of the area in which cattle were treated with insecticide. The target barrier had been in place for some years prior to the onset of the trial with insecticide-treated cattle and there had been no trypanosomiasis problem in the area. Accordingly, at the start of the simulation, it was assumed that the District was tsetse free. However, the model allowed a constant threat of re-invasion from across the border in Mozambique, where the tsetse population was assumed to start at 100% of carrying capacity.

Preliminary simulations were performed to assess the extent to which tsetse penetrated the target barrier. Simulation of a target-based operation in the Rifa Triangle of Zimbabwe (Hargrove, 2003) indicated that each target kills approximately 2% per day of the female *G. pallidipes* population. When the model was allowed to run for a year with this kill rate, there was little effective invasion into the Mudzi District. Tsetse penetrated a few km into the target barrier but did not reach the hinterland beyond. These results agree with the theoretical and practical work carried out in Zimbabwe on the efficacy of wide target barriers as agents against re-invasion (Hargrove, 1993; Muzari and Hargrove, 1996; Muzari, 1999).

The theoretical results (Fig. 21) predict that a tsetse fly has a probability of 0.001 of crossing an 8 km barrier of odour-baited targets deployed at four per km^2. After various trials at Rekomitjie Research Station, a full-scale field trial was carried out near Mushumbi Pools in the eastern Zambezi Valley. The results (Fig. 22) were in accord with the theoretical predictions. When an 8 km barrier was deployed at the edge of the fly-infested area to the west of Mushumbi Pools, trap catches on the eastern edge of the barrier rapidly declined to zero and no further flies were caught for a year, when the trial was concluded.

The target barrier in the Mudzi area was even broader than recommended and should thus have been expected to prevent re-invasion from Mozambique – assuming, as appears to have been the case for most of the time (G.A. Vale, personal communication), that the barrier targets were in working condition. When the target barrier was replaced with insecticide-treated cattle, simulation indicated that re-invasion from Mozambique would be substantial – and this was observed in practice.

In keeping with the actual findings of Warnes *et al.* (1999), the largest predicted tsetse populations were found close to the Mozambique border. The simulations suggest, however,

Figure 21.   **Protection by target barriers**
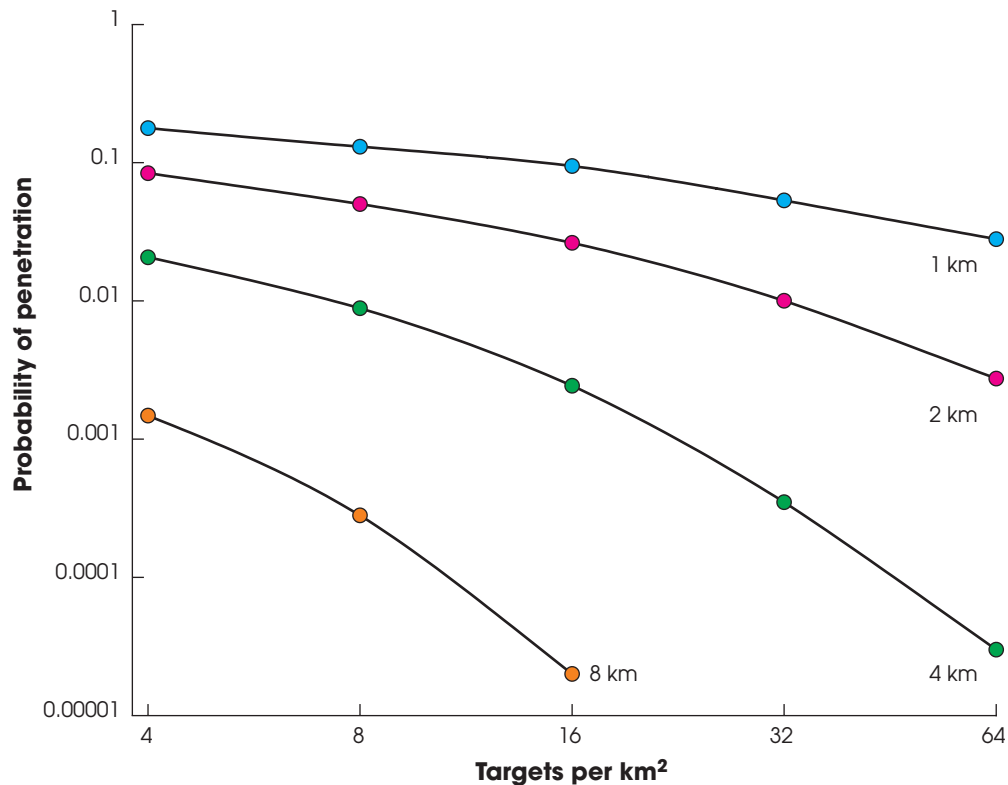
Probability that a tsetse fly will penetrate target barriers of varying widths and densities (Hargrove, 1993).

that if the insecticide-treated cattle trial had been continued any longer, tsetse invasion would have occurred deeper into Zimbabwe. In practice, the increase in cases of trypanosomiasis in early 1997 prompted the authorities to re-deploy the target barrier and the tsetse situation was brought rapidly under control.

If dictates of grazing, watering and other issues mean that the treated cattle are patchily distributed, then it is unlikely that they will provide an effective barrier to re-invasion. Moreover, forcing the treated cattle into a distribution convenient for tsetse control may not be possible, let alone economically sensible or desirable. That is not to say that cattle could not be used in an effective barrier. The above problems might be overcome, for instance, by the judicious deployment of targets, which plug the gaps in areas of low cattle density.

Figure 22. **The Mushumbi Pools target barrier experiment**
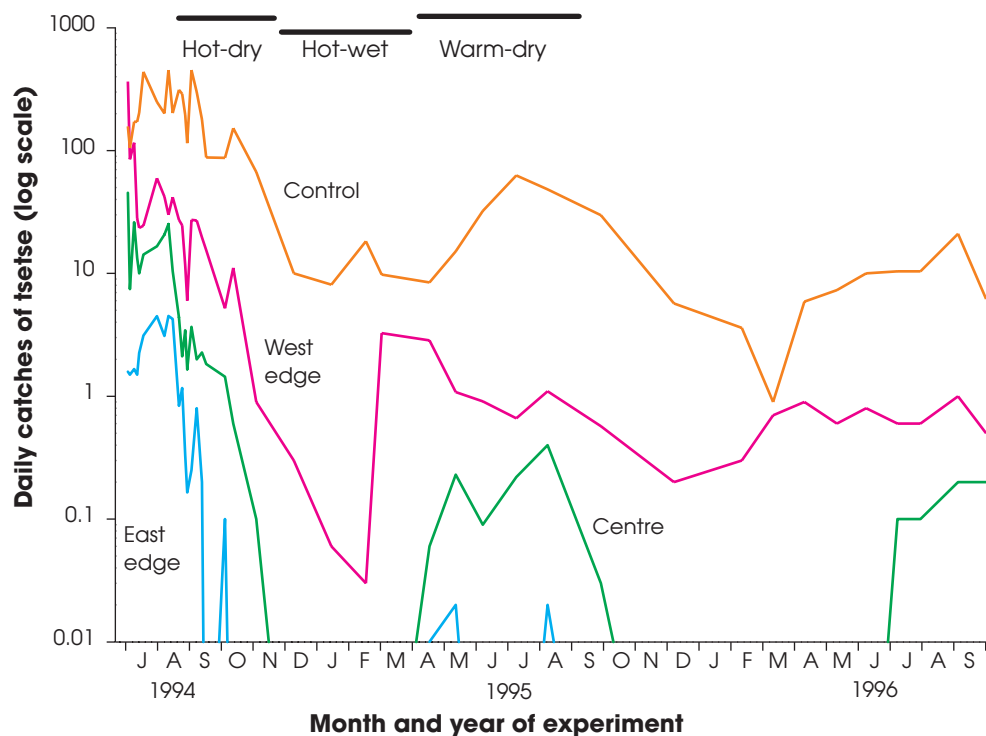
Mean daily trap catches of tsetse on the western (infested) and eastern (fly-free) edges, and in the centre, of an 8 km barrier of odour-baited targets deployed near Mushumbi Pools, northern Zimbabwe. Control traps were operated >5 km west of the edge of the barrier. Data from Muzari (1999).

Conclusion

Despite various problems associated with the method, the use of insecticide-treated cattle, in areas where livestock are abundant, promises to be a major force in tsetse control operations in the future. Recent work at Rekomitjie suggests, moreover, that the method can be made more effective and desirable (see Section 3). The method is the one means of vector control that may be expected to be attractive to stockowners since the treatment is applied solely to the owner's beasts. If carried out on a sufficient scale in areas with large numbers of cattle, however, the individual 'selfish' acts of many stockowners will provide mutual protection for entire areas.

2.5   Aerial spraying

2.5.1   Early success in South Africa

Control or eradication campaigns using bait technologies (and to a lesser extent ground spraying) involve a steady attrition of the tsetse population. A far more rapid population decrease can be achieved over large areas through the use of aerial spraying.

The technique was first used effectively in Zululand, South Africa (Du Toit, 1954) in a campaign that led to the permanent eradication of *G. pallidipes*. Although its success might be demeaned by the consideration that tsetse are at the edge of their range in this part of Africa, the massive trap catches that Harris (1938) reported are hardly suggestive of a population teetering on the edge of auto-extinction. A more important factor was that the population under attack was isolated. The major problem with aerial spraying is that there is virtually no residual effect of the insecticides. Thus, unless other techniques are used in combination with aerial spraying (see Section 2.5.3) there is nothing to stop flies invading from beyond the sprayed area. Equally, if there are any survivors left after the completion of the final cycle – either as adult flies or as pupae in the ground – then there is no hindrance to the growth of the population.

Eradication in the case of Zululand was certainly aided by the fact that much of the surrounding area was being developed for agriculture, and populations of wild hosts had been much reduced during the 20th century by hunting. Nonetheless, the campaign was notable for its vigour; there are numerous later examples of less vigorous campaigns that have produced rapid, impressive reductions in tsetse populations – followed by equally impressive recoveries.

2.5.2   Lambwe Valley, Kenya

Turner and Brightwell (1986) document such an instance for the Lambwe Valley in Kenya where, despite heavy applications of insecticide and 99% control overall, the population recovered to pre-spray levels in about a year (Fig. 23). The authors do not provide fine details of the eradication programme, but make it clear that much of the spraying was carried out before the ideal conditions of atmospheric inversion had set in at night, and that droplet size was not optimal. In this case, intensive trap sampling made it clear that eradication had not been achieved, since survivors were found after each spraying cycle. There was, therefore, no need to invoke re-invasion to account for the failure – although the recovery was so rapid that it is consistent with the idea that the population may have been augmented by immigration.

Figure 23. **Population recovery after aerial spraying**
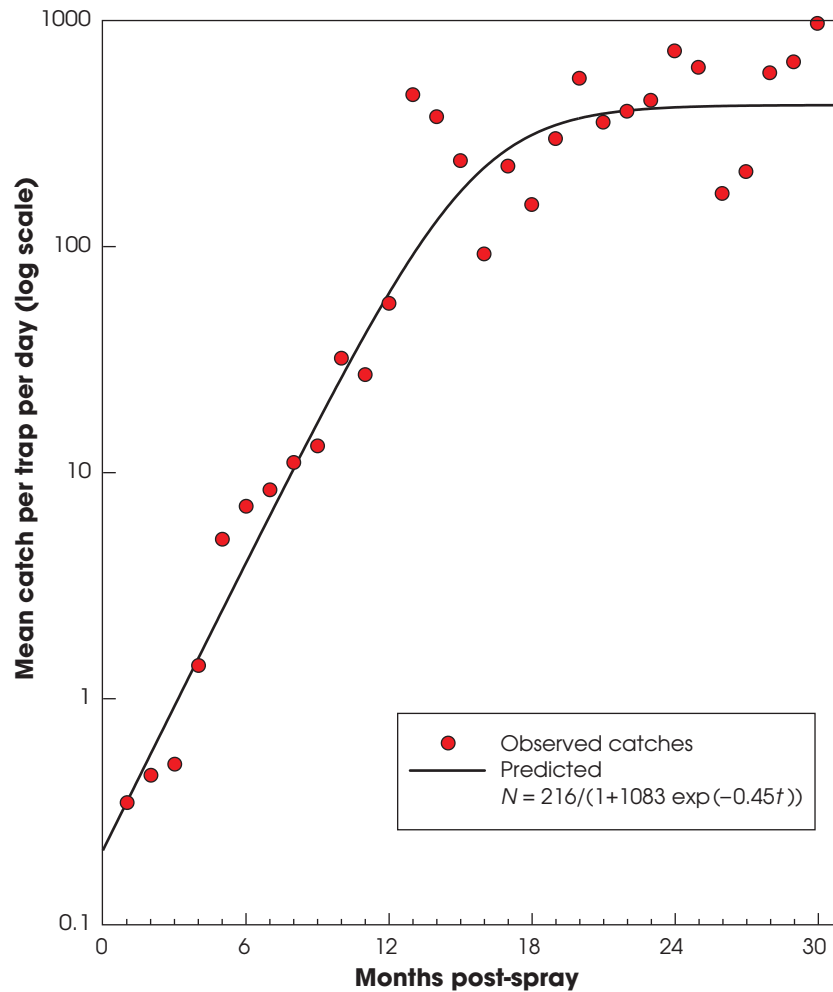
Growth of a *G. pallidipes* population in thicket habitat following an attempt to eradicate flies using aerial spraying, Lambwe Valley, Kenya. Redrawn from Turner and Brightwell (1986).

2.5.3   Operations in Botswana
Repeated operations 1973–1991

In other circumstances, re-invasion is a clear factor – regardless of whether the spraying has, or has not, succeeded in killing all tsetse in the area sprayed. A case in point is the Okavango Delta of Botswana, where the most prolonged and extensive aerial spraying exercises have been carried out.

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Figure 24. **Diagrammatic representation of aerial spraying in Botswana, 1973–1985**
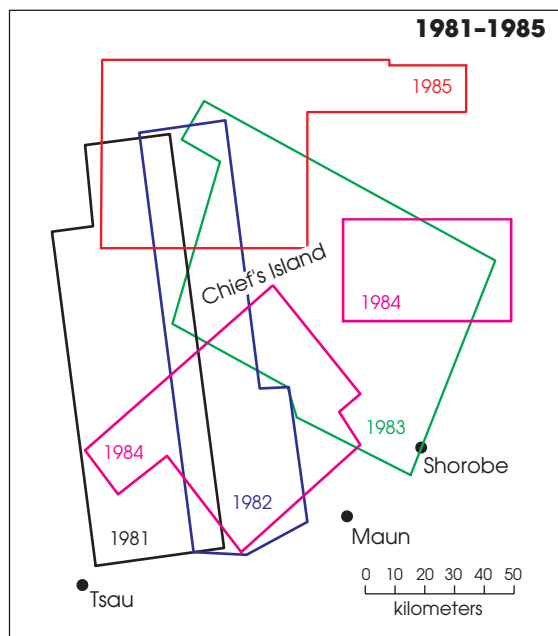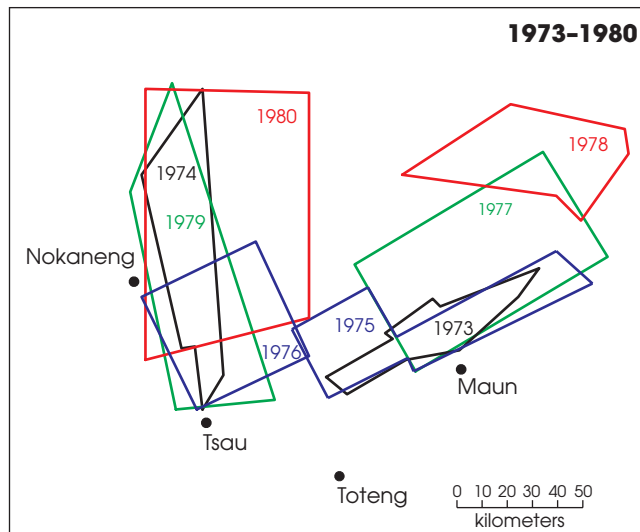
The entire area infested with tsetse (*G. m. centralis* in this case) was sprayed – often many times – in an unrelenting campaign between 1973 and 1991 (Figs 24 and 25). Regrettably, little detail on these campaigns has been published, and even less regarding actual catches in and around the sprayed areas.

Unpublished reports from relevant government ministries in Botswana do, however, refer to those years, e.g. 1981, 1983 and 1984, when it was not possible to catch any tsetse immediately after the spraying programme (Bowles, 1985). Since no details are given of the survey procedures, however, it is impossible to estimate the probability that the workers had failed to detect surviving flies. Nonetheless, at the end of the report it was stated that in 1986 it could be possible 'to eliminate the fly from the Kwando, thereby eliminating the fly completely from the country'. In a subsequent report (Bowles, 1987) it was stated that it 'was realised at the beginning of the 1986 spray season that, if successful, at the end of this operation most of the [Okavango] Delta and Selinda areas would be fly-free, with *only small isolated pockets remaining* [my emphasis], with the only major areas of infestation remaining being along the Kwando and Linyanti river systems, Botswana's border with the Caprivi Strip [in Namibia]'.

However, this plan required that the aerial spraying teams from Botswana should also fly over Namibia to remove tsetse from the part of the fly belt that lay across the border in the Namibian portion of the Linyanti Swamp. In the event, permission to carry out this international exercise was not forthcoming and the campaign was not able to remove the threat of re-invasion. Nonetheless, as Bowles (1985) pointed out, this part of the country is separated from the Okavango Delta 'by a relatively inhospitable area of the northern Selinda spillway'. It appears they believed that, if tsetse could be eradicated from the Delta, the spillway, aided by a chemical barrier, might be sufficient to keep the Delta fly-free.

Accordingly, aerial spraying operations continued in the Okavango Delta and in a report authored by Wooff (1992) it is stated that: 'Surveys and routine monitoring in the area…covered by last year's [1991] spraying operation was discontinued at the end of December, no tsetse having been caught there since 8 September. As that spray block had been designed to cover the only area in the Delta where tsetse had been detected earlier in 1991, *it was believed that the eradication of these flies from the Okavango had actually been completed* [my emphasis]. Attention was therefore given to the identification of potential re-invasion routes and a determination of how best these could be closed to tsetse movement'.

Survivors or invaders?

It quickly became apparent, however, that tsetse had not been eradicated from the Delta at all. Thus, while surveys in the 1990 spray block had 'been continued until the end of June 1991, without any further captures being made' (Wooff, 1992) more detailed surveys showed that there

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were tsetse present – as there were in the area sprayed in 1989 that was supposed to be fly-free. In fact 'a sizeable portion of the south western corner of the Delta was infested'. The situation deteriorated rapidly during the 1990s, despite the widespread use of odour-baited targets, and in 2001 aerial spraying was re-introduced (see below).

Before reviewing the later operations it is important to try to determine what went wrong with the earlier work. It may be that the reappearance of tsetse in the Delta was due their carriage, by game or traffic, from the Caprivi area. Other considerations suggest, however, that it is neither necessary nor reasonable to invoke this source of infestation – particularly when the first sign of the problem appeared in the *southwest* of the Delta (see above), the area furthest from the supposed source of invasion.

When the annual *pattern* of spraying over the period 1974–1991 is studied, it immediately becomes clear that there was never any real hope that the fly would be eradicated from the Delta. The areas sprayed were always too small and there was always the possibility that part of the fly population would move between the successively sprayed blocks, thereby avoiding treatment by any of the sprays.

The reader is left with the diverting exercise of pretending, with reference to Figs 24 and 25, to be a tsetse undertaking such avoiding action, albeit that the avoidance is presumed to result from random diffusion, not deliberate navigation. The challenge is not a difficult one. As a concrete example, consider that all tsetse residing in the 1981 spray block just north and east of the 1976 spray block will be free to move the distance (<10 km) into the latter block as soon as the 1976 operation is complete. They could also move a similarly small distance east into the 1975 spray block. Invaders that stay east of the 1979 block would not be sprayed again until 1981. Similar mind games can be played for the whole spraying period prior to 2001.

The proportion of the population that can move the required 10 km depends on the value of the diffusion coefficient (α). The results of Hargrove and Lange (1989) can be used to show that, if $\alpha = 0.04$ km^2 per day (equivalent to a daily step length, l, of 400 m) about 0.9% of the population just outside the sprayed block will move at least 10 km into the cleared area. While this may seem a small percentage, results developed below suggest that as few as 16 inseminated females may be sufficient to provide an effective pioneer population.

Moreover, a carefully conducted aerial spraying operation using a small block of woodland near Rekomitjie Research Station showed that female *G. pallidipes* and even *G. m. morsitans* were capable of moving substantially further than had been supposed from classical studies (Vale *et al.*, 1984). Whereas it had been thought in the past that females moved less than the male rate of a mere 150 m per day, the Rekomitjie experiment indicated that the daily rate for females might, in some circumstances, be 1000 m ($\alpha = 0.25$ km^2 per day) or even more. Under these circumstances,

Figure 25. **Diagrammatic representation of aerial spraying in Botswana, 1985–2002**
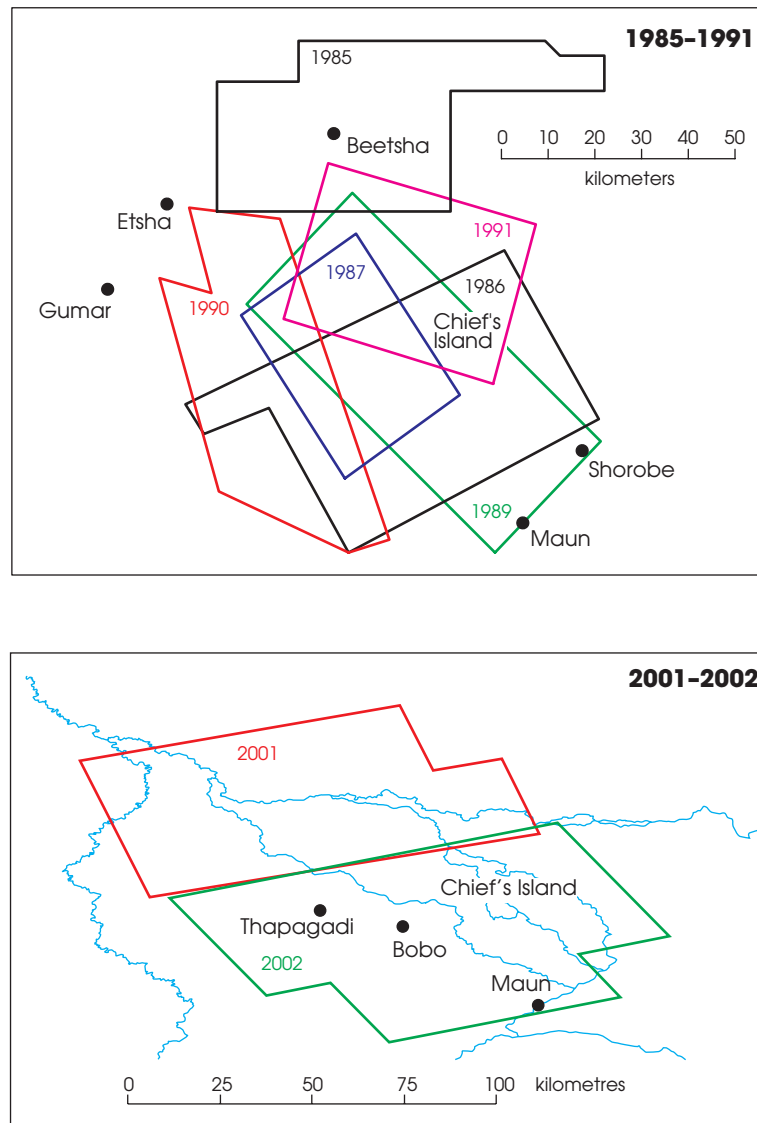
The lines in blue indicate the Okavango river and its tributaries.

nearly 30% of the population could travel 10 km in a year, and more than 3% could travel this distance in the 3 months while spraying is actually being carried out.

Regardless of the provenance of the tsetse populations in the Okavango Delta in the early 1990s, whether they were survivors or invaders, the flies rapidly became a serious problem. Attempts to use odour-baited targets to eradicate the population failed, and by the end of the millennium it was decided to revert to aerial spraying. It was appreciated by this time that much bigger areas needed to be treated if re-invasion was to be prevented.

Modern developments

Development of tracking systems linked to satellite cover made it feasible to spray larger areas in the confidence that the entire nominated area had indeed been covered. The areas treated in 2001 and 2002 are shown in Fig. 25. In both years, post-spray sampling failed to demonstrate the existence of any surviving flies in either block. These were extremely successful control operations and the failure to catch flies after the 2002 spray season may mean that tsetse have been eradicated from the Delta.

The very success of these operations means, however, that they are deserving of detailed study and attention, since any problems are likely to have more serious consequences in other operations that are not carried out with such vigour and thoroughness over such large areas. The following concerns, which the future may show to be groundless, are offered in this light.

First, Fig. 25 shows that there was almost no overlap between the spraying carried out in 2001 and that of 2002. This had not been intended, but the late detection in 2002 of tsetse in the southwestern Delta, close to Maun, meant that the spray block had to be expanded to take care of this problem. Given, however, that finances dictated a constant total area to be sprayed, this meant that the northern limit of the block had to be moved south and the planned overlap was lost (R. Allsopp, personal communication). This created a potential problem. As with the earlier spraying programmes, flies in the northern part of the 2002 block could move into the southern part of the 2001 block after the 2001 spraying – and would then be unlikely to be killed in 2002. This eventuality was catered for to some degree by the deployment of odour-baited targets along the southern boundary of the 2001 block. Given, however, that workers in Botswana have previously been unable to use targets to eradicate tsetse in the Delta this measure may not necessarily be foolproof.

Rates of development in tsetse and their effect on the choice of the spraying interval

A second worry concerns the timing of the spray cycles in 2002 and, more generally, the way in which decisions were taken on such timing. The idea behind aerial spraying is that every adult

tsetse in the area sprayed should be killed directly by the aerosol, on the night that the particular area is sprayed or, at worst, on subsequent days by any small residual effect. The spray has little or no effect, however, on flies in the pupal stage underground and which emerge as adults after the area has been sprayed. Hence, the spraying must be repeated at intervals for an entire pupal period to kill emerging females before they can replenish the protected pupal population. This means that the interval between successive sprays must be no more than 22–25 days, even at temperatures of 16°C, and not more than 18 days at a mean temperature of 21°C (depending on which estimates of the rate of physiological development are accepted).

Neither should the interval between spray cycles be much shorter than these values since this would increase the number of cycles and raise overall costs. This consideration is compounded by the fact that spraying must continue long enough for larvae deposited just before the start of the first cycle to have emerged *before* the final cycle, so they can be killed as adults. Thus, the timing of successive cycles is crucial.

Decisions on the timing (R. Allsopp, personal communication) are made using estimates published anonymously (Anon, 1955) but produced by C.H.N. Jackson (A.M. Jordan, personal communication). For simplicity, the resulting estimates are referred to below as 'Jackson's estimates'. The data relate to the relationship between temperature and the times that: i) a tsetse pupa spends in the ground (I_p) and ii) a tsetse female takes to deposit her first larva (I_0). The data in question were all derived from laboratory work carried out at constant temperature. To that extent, at least, they are not optimal since it is not clear how constant laboratory temperatures relate to the varying temperatures experienced by adult and immature tsetse in the field. Nor did the authors actually state the temperatures over which the experiments had been carried out. The study is also unsatisfactory in that it simply provides equations predicting I_p and I_0 without providing data or the mean periods from which the equations were derived. There is certainly no way to judge the variance of the estimated periods.

Later work has made good these shortcomings to some extent but the improved data have not been used in planning aerial spraying operations. Phelps and Burrows (1969a) repeated the earlier laboratory work on pupal durations (I_p) and these do indeed match the earlier estimates quite closely (Fig. 26). Phelps and Burrows (1969b) went further, however, when they measured the durations under field conditions. What then became clear was that, even when pupae were placed in the same situations at the same time, I_p varied substantially between individuals. Regardless of the validity of the predictive equations, therefore, one needs to allow for this variance in planning aerial spraying operations.

Differences in results between Jackson's and modern studies are more serious when we consider the predicted values for I_0. There are marked divergences between Jackson's predicted

Figure 26.　**Predicted and observed pupal durations**
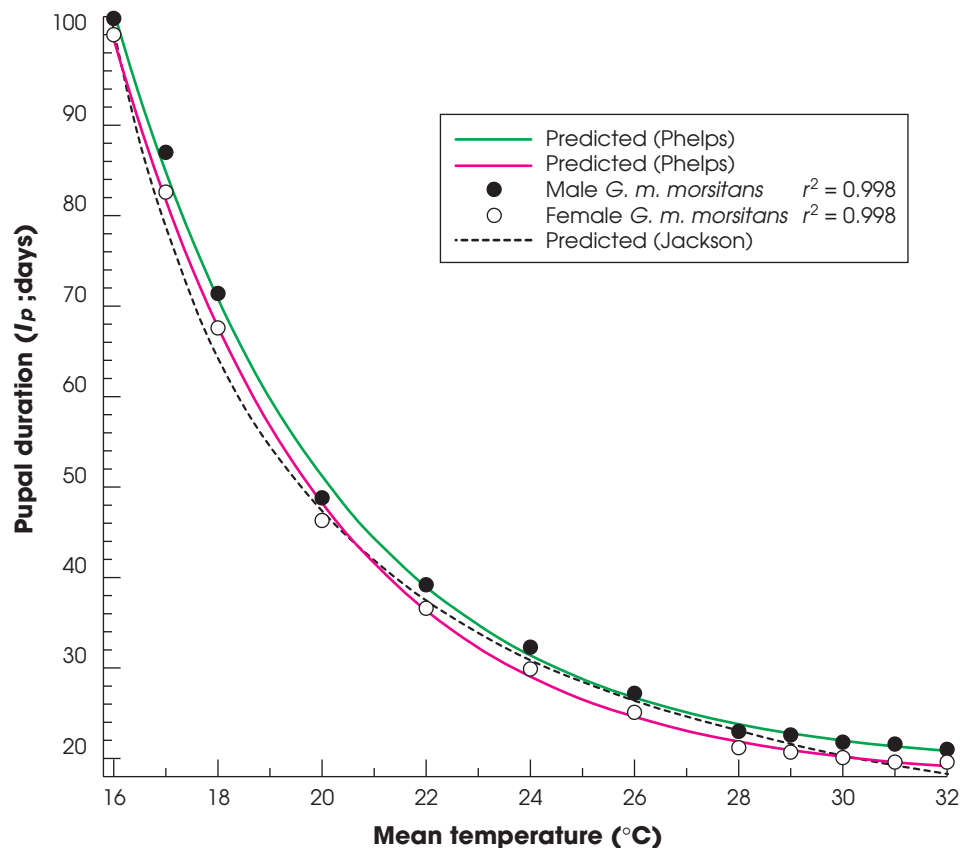
The effect of mean temperature on pupal duration for *G. m. morsitans* as predicted by the work of C.H.N. Jackson (Anon, 1955) and Phelps and Burrows (1969a). Jackson's estimated function for pupal duration refers only to females; he notes that the duration for males is *c.* 6% longer.

values and more recent estimates (Fig. 27). For temperatures in excess of 21°C, Jackson's predicted values of I_0 are up to three days shorter than Hargrove's (1994, 1995) estimates; at low temperatures the situation is reversed. It is these predictions at low temperature that are particularly worrying when considering aerial spraying operations, which are ideally carried out at the coolest times of the year when temperature inversion conditions set in at or around sunset.

As would be expected given normal biological variability and in accordance with Phelps and Burrows' I_p estimates, Hargrove's (1994) experiments also indicate that I_0 is not a fixed value at a given temperature. It varies between experiments carried out at similar temperatures, as measured in Stevenson screens. It also varies markedly between different locations for the same species. Thus the estimated values of I_0 for Redcliff Island were up to three days shorter than for those estimated at Rekomitjie Research Station (Fig. 27) and, more importantly, up to three days shorter than the predicted values from the fitted function. There is a difference between Stevenson screen tempera-ture and the temperatures experienced by a tsetse fly, and Hargrove's (1994) results might be explained quite simply if this difference were greater on the island than at Rekomitjie.

Figure 27. **Predicted and observed inter-larval periods**
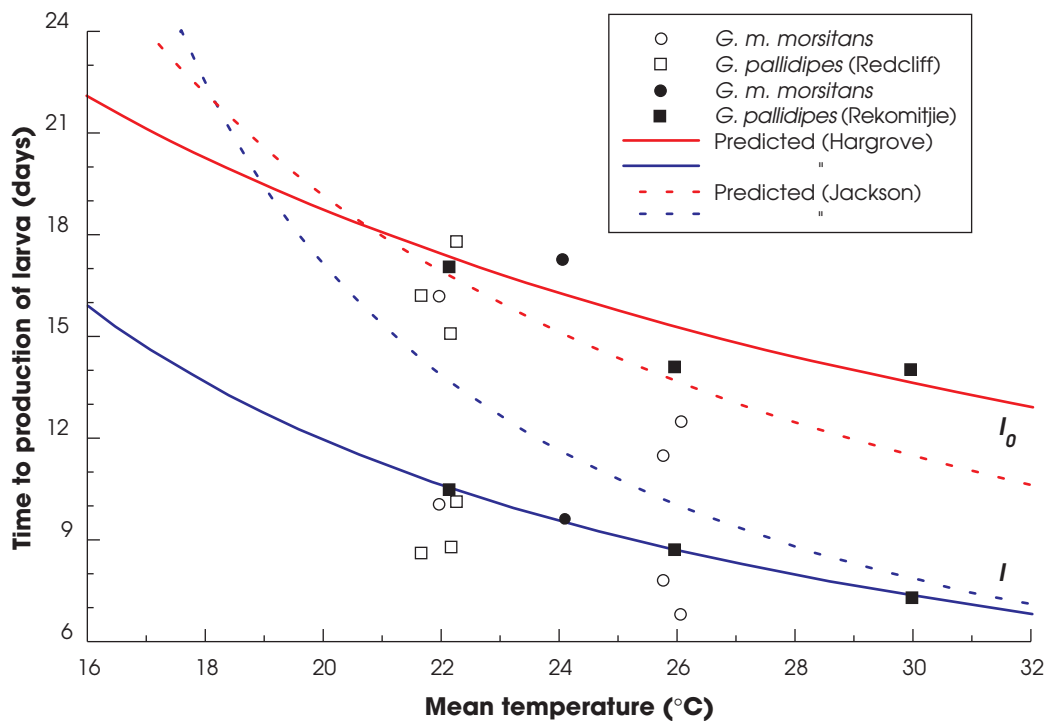
The effect of mean temperature on the age at which a female tsetse fly produces her first larva as predicted by the work of C.H.N. Jackson (Anon, 1955), working on *G. m. morsitans,* and Hargrove (1994, 1995), working on *G. m. morsitans* and *G. pallidipes*. I_0 is the expected time between the emergence of a female fly and the production of her first larva; *I* is the expected inter-larval period thereafter.

Whatever the reason for the difference, however, the variation in the results serves as a warning that the predicted values of I_0 can provide only a rough a guide for deciding the timing of aerial spraying cycles. For spraying in the Okavango, this is particularly germane since there are no field estimates of I_0 for the target species *G. m. centralis*.

Available estimates have been used here to predict the timing of emergence of pupae and the deposition of first larvae in the Okavango situation (Fig. 28) by calculating the daily proportion of development completed given the mean temperature on that day. Some potentially worrying facts have emerged. Both Jackson's and Phelps and Burrows' results suggest that the last fly to emerge

Figure 28.   **Timing of aerial spraying cycles, Botswana 2001**
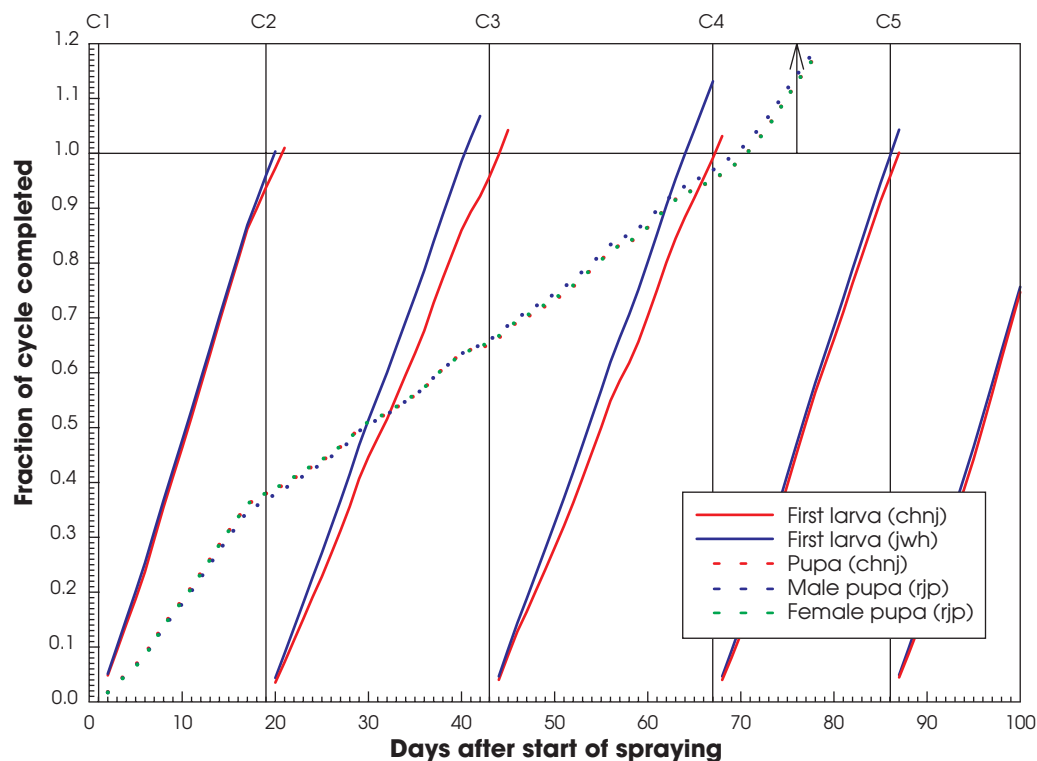
Predicted development patterns of mature larvae and adult female tsetse. In the legend: chnj = Jackson (Anon, 1955); jwh = Hargrove (1994, 1995); rjp = Phelps and Burrows (1969a, 1969b). The arrow in the body of the graph denotes the last capture of tsetse in the area, on day 76 after the start of the spraying operation.

from pupae that were in the ground before the first spray should have emerged on day 70 or 71 after the start of the operation. It is noteworthy that two young flies were caught in the Delta on day 76 – although none were caught after this. Where did these flies come from? If they simply reflect the natural variation in I_p suggested by Phelps and Burrows' results then there is no problem, since such flies would presumably have been killed by spraying in the fifth cycle. The alternative, that they were the offspring of undetected survivors after the first cycle, is a more serious concern.

When Jackson's estimates for I_0 were used, the timing of cycles two to five were such that newly emerged females *should* have been killed before they deposited their first larvae. Even with these estimates, however, the timing is rather 'tight'. Thus, for each cycle, any female that happened to deposit a larva just two days earlier than predicted would have done so before being killed by the ensuing spray. If Hargrove's (1994) estimates are appropriate, then the situation is even worse; they predict that, for cycles three and four, females emerging on the day after the previous cycle would be ready to deposit a larva three days before the next spray.

These potential problems are compounded by the selection of the temperature data used in estimating I_p and I_0, particularly the latter. This selection process presents a problem for the control officers on the ground because they obviously have to set, in advance, the date for the start of each cycle. For practical planning purposes, of course, they would like to set the timing of each cycle as soon as possible. They need to take this decision, therefore, before they can possibly know the actual prevailing temperatures that will decide the day on which a female is expected to deposit her first larva.

In the 2001/2002 Botswana campaign, meteorological records for previous years were used to predict the mean temperatures for each day of the spraying campaign (R. Allsopp, personal communication). The temperatures for May were based on ten-year averages in the Delta and those for June to August were based on the averages from Mombo, in the Delta, for 2001. Notice also that it is necessary to make an implicit assumption that the mean temperature, taken at a single site, applies equally over the whole area to be sprayed. The success of an operation would clearly be prejudiced if there were an unseasonably warm spell at any time, in any part of the area to be sprayed, during the whole period of the spraying campaign.

All of the above considerations suggest that the timing of the spray cycles leaves very little room for error and efficacy can easily be affected by natural variations in biological and meteorological parameters. These variations might explain the captures on day 76 and they suggest that some emerging female flies *might* have had enough time to deposit a larva before being killed in the next spray cycle.

Selection of spraying times and numbers of cycles to be carried out in such campaigns is influenced by the two opposing considerations of effectiveness and cost. The 2002 spraying

operation consisted of five cycles that started on days 1, 19, 43, 67 and 86 respectively. To achieve greater safety, particularly if Hargrove's (1995) estimates of I_0 are closer to the true mean, the projections in Fig. 28 suggest it would have been necessary to shorten the periods between cycles by about two, five, five and three days respectively. The first five cycles would then have started on days 1, 17, 36, 55 and 71 respectively. The last cycle would then, however, have been dangerously close to the limit imposed by I_p (Fig. 26) and it would have been necessary to have a sixth cycle starting on about day 87. If the cost of such an operation is proportional to the number of cycles, then the addition of a sixth cycle would have increased the cost by about 20%.

On one hand this significant extra spending is clearly not justified if the job can be (indeed perhaps has been) done using five cycles. On the other hand, if there are still flies in the Okavango as a consequence of cutting things too fine, then past experience suggests that the future cost of taking care of the progeny of those survivors will certainly be far more than 20% of the current operation. Indeed, it may ultimately be the cost of spraying the whole Delta – yet again.

In fairness, no flies have been caught anywhere in the Delta since day 76 (30 August 2002) and there is thus currently no evidence to suggest that eradication has *not* been achieved. Past experience advises caution in assessing the final result and extrapolating to other situations and times. There have been occasions (see above) when it was claimed that eradication had been achieved in all, or in very large parts, of the Delta – only for tsetse to be detected following more aggressive survey work. The flies captured in the southwest of the Delta in 1992 (Wooff, 1992) exemplify this problem.

How did tsetse evade detection so successfully in this part of the Delta? Moreover, given that they did so, when can we be sure that our failure to capture flies means that there are no flies present? In short, when can we be satisfied that all the flies are gone? A satisfactory answer can be given only by considering the probability of detecting a single fly surviving in an area from which tsetse have supposedly been eradicated. This problem, which applies to all methods of tsetse control, not just to aerial spraying, is considered in some detail in Section 2.8.

Of course, even if flies do survive the spraying campaign, they may do so in numbers so small that males and females never meet and the population is eventually extinguished anyway. Alternatively, even when populations are high enough to permit mating, the probability of insemination can be much reduced by, for instance, releasing large numbers of sterile males into the population, which compete for the favours of the surviving females. This method of achieving eradication is an example of the sterile insect technique (SIT) and deserves particular attention since it received prominence in the OAU Declaration (see Introduction).

2.6   Sterile insect technique

2.6.1   Early campaigns

The basic idea behind SIT, as currently applied to tsetse populations, is to release sufficient sterile males into a wild population so that the probability of a wild virgin female being inseminated by a surviving, fertile, wild male is drastically reduced. The wild population will then decline. The smaller the wild population, the fewer sterile males need to be released to swamp the wild males. Hence, it has long been recognised that SIT would rarely be effective as a stand-alone technique. Instead, it would generally be necessary to reduce the target population as much as possible using a more conventional technique before releasing sterile males.

SIT was first used by Dame and Schmidt (1970) against a natural population of *G. m. morsitans* on Antelope Island, Lake Kariba, Zimbabwe. Two aerial applications of lindane were used to suppress the population prior to the release of sterile males. Eradication was achieved but the authors admit that the result was confused by the unknown effect of 'a natural decline in the population of [wild] host animals'.

Williamson *et al.* (1983) used the method against the same species in Mkwaja Ranch, Tanzania. The area targeted was small, however, and was quickly invaded. Similar campaigns were carried out against four species in Burkina Faso (Politzar and Cuisance, 1984) and Nigeria (Oladunmade *et al.*, 1990). In both cases it was claimed that tsetse had been eradicated, but little was ever published on sampling methods and intensity, and results in the published reports make it impossible to judge whether eradication was actually achieved.

Whether or not the species involved had been eradicated, tsetse flies were later caught in both areas. The tsetse populations were then suppressed using other means (targets or spraying) and it is unclear whether the alleged eradication could actually have been achieved by the alternate methods used alone. In a nutshell: was SIT necessary or sufficient to effect eradication?

2.6.2   Eradication of *G. austeni* on Unguja Island

In the case of the population of *G. austeni* on Unguja Island, Zanzibar, however, there is virtually no doubt that eradication was achieved following the release of sterile male tsetse (Vreysen *et al.*, 2000). The tsetse population had first been suppressed – by how much is not stated – by deployment of insecticide-treated cattle and screens. Thereafter, increasingly large numbers of sterile male *G. austeni* were released on the island. The numbers released in each four-week period are shown in Fig. 29. The original data are from Vreysen *et al.* (2000) who provide only a qualitative analysis of the valuable data, and no estimates of the absolute sterile and wild populations. Nonetheless, it is

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Figure 29. **Numbers of sterile male *G. austeni*, Zanzibar**
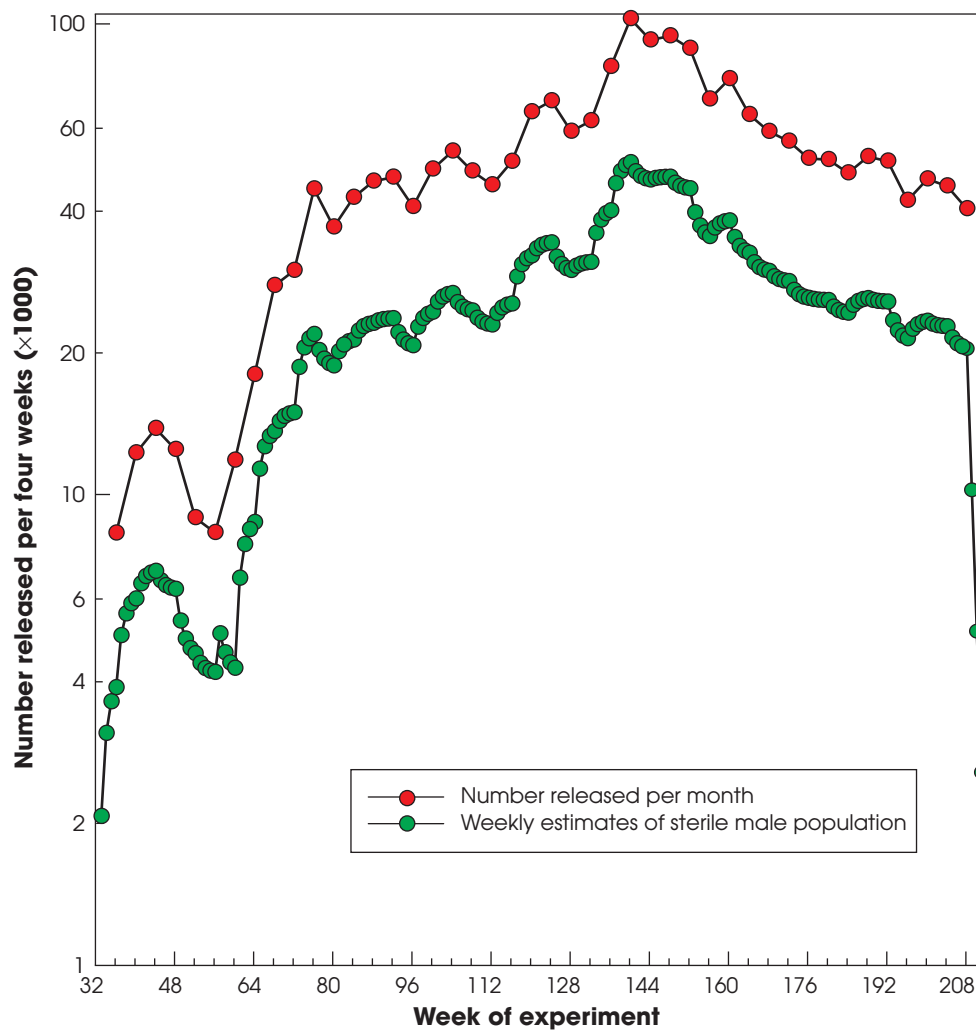
Numbers of sterile male *G. austeni*, Zanzibar released per four-week period on Unguja Island, Zanzibar and estimates of the number surviving at the end of each week.

possible to make population estimates from their published data and these provide interesting insights.

Assuming, as a first approximation, that the stated number of four-weekly releases were distributed uniformly across weeks, it is possible to estimate the decline in numbers from each

week's releases – if, as stated by Vreysen *et al.* (2000), the half-life of the average male on Unguja was around one week. These estimates of the total surviving sterile male population (N_s) can then be used in conjunction with the given estimates of the ratio (α) of sterile:wild flies in the main population in and around the Jozani Forest (Fig. 30, estimated from Fig. 4 of Vreysen *et al.*, 2000) to indicate the total number of male *G. austeni* surviving in that area (Fig. 30). As a first approximation, the population in the Jozani Forest is simply estimated by $N_w = N_s / \alpha$. Figure 30 shows how this estimated wild population declines with time. Since the estimate N_s refers to the whole island, whereas estimates of α are only available for Jozani, N_w tends to over-estimate the forest population. As long as the degree of over-estimation is approximately constant across time, however, the estimated rate of decline will be independent of the level of the absolute population. The regression for changes in population levels between weeks 60 and 115 shows that this rate of decline is a surprisingly low 1% per day (Fig. 30).

Whereas this estimate of the rate of change in *absolute* tsetse populations on Unguja is derived rather indirectly and approximately, it is entirely in accord with the observed changes in *apparent* density, as judged by catches of male and female *G. austeni* on sticky panels in the Jozani area (Fig. 7 of Vreysen *et al.*, 2000). These data are plotted here in Fig. 31, which shows that the rate of decline estimated from these data is also of the order of 1% per day for both sexes. This is markedly slower than the rate of decline of the *G. pallidipes* population in the Rifa Triangle of Zimbabwe when just odour-baited targets at four per km² were deployed (Figs 15, 30 and 31).

It is noteworthy, moreover, that while the sterile:wild male ratio on the island increased by more than an order of magnitude (from *c.* 40 to >400) between weeks 72 and 110, there was little change in the rate at which the population decreased over this period (Fig. 30). Why was the rate of decline so low and why was it so insensitive to gross changes in the flooding ratio?

These problems were investigated using the following equation (Williams *et al.*, 1990; their Equation 11) relating growth rates to various parameters of tsetse populations:

$$\beta \exp[(\sigma_a - r)\tau_a + (\sigma_b - r)\tau_b + (\sigma_c - r)\tau_c] = 1 - \exp[(\sigma_c - r)\tau_c] \qquad (2)$$

where r is the growth rate, β is the fecundity, counting female larvae only, τ_a, τ_b and τ_c are the durations of the pupal period, the nulliparous stage and the inter-larval period respectively, σ_a, σ_b and σ_c are the survivorships during these periods. For the present purpose it was assumed that $\tau_a = 29$, $\tau_b = 7$ and $\tau_c = 9$ days respectively, that there was a constant pupal mortality of 1% per day (Rogers and Randolph, 1990) and that adult mortality was independent of age, so that $\sigma_b = \sigma_c$.

Equation (2) was solved for various values of β and σ_c and a selection of results is shown in Fig. 32. The horizontal line just below a growth rate of –1% per day marks the observed decline of the Zanzibar population. Solving Equation (2) for varying levels of β, and a constant level for σ_c,

Figure 30. **Zanzibar SIT experiment**
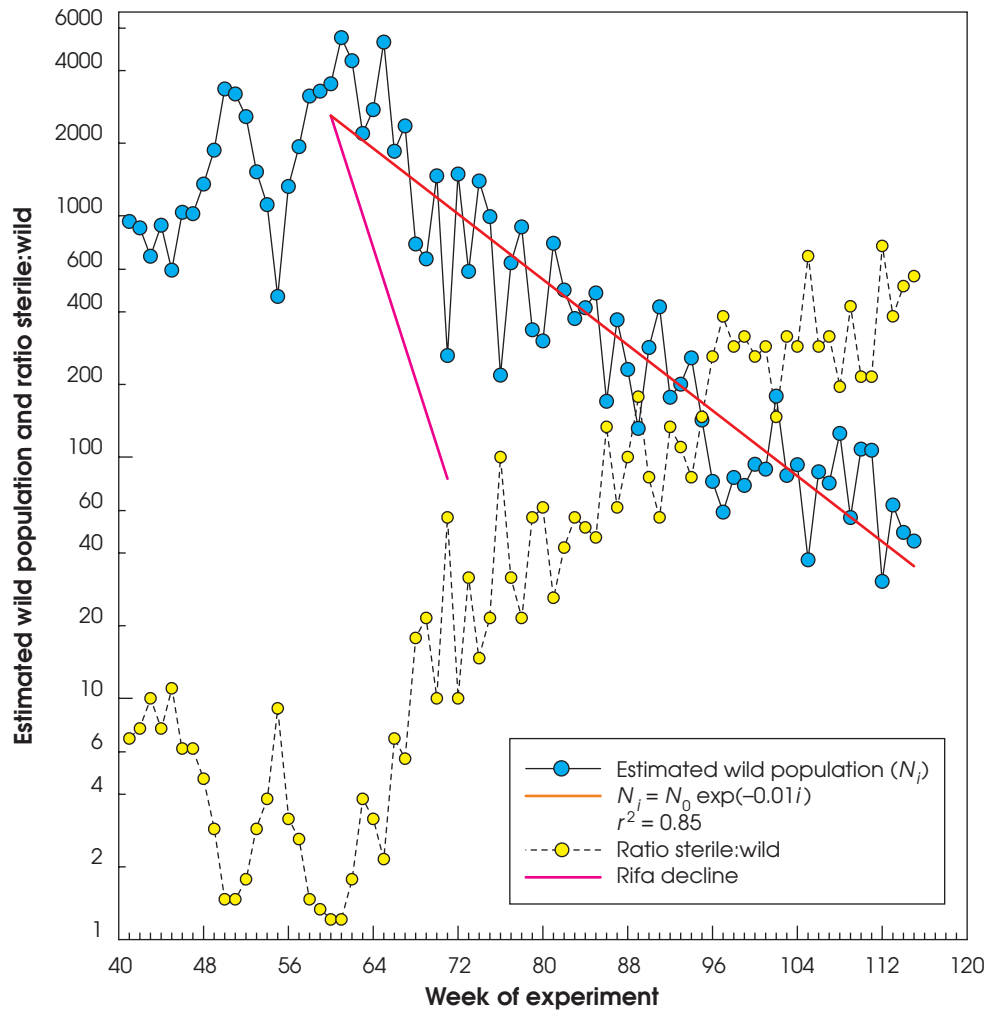
Ratio of sterile:wild male *G. austeni* as estimated from catches of flies at fixed monitoring sites 1–6 in the Jozani Forest ecosystem and the estimated population of wild flies. See text for details of calculations.

produces plots that cut this horizontal line at the point defining the fecundity of the Zanzibar population. The imposed decline resulting from the release of the sterile males on Zanzibar can then be estimated for known background adult mortality.

In a normal wild population, $\beta = 0.5$, as long as the abortion rate is small enough to be ignored (Hargrove, 1999c). That is to say the female produces a viable female larva with probability

Figure 31. **Decline in catches of wild *G. austeni*, Zanzibar**

a) Apparent density of males

- ● Wild males
- ○ Sterile/wild males
- — $N_t = N_0 \exp(-0.012i)$
  $r^2 = 0.84$

b) Apparent density of females

- ● Wild females
- ○ Sterile/wild males
- — $N_t = N_0 \exp(-0.009i)$
  $r^2 = 0.62$

Flies per panel per week

Week of experiment
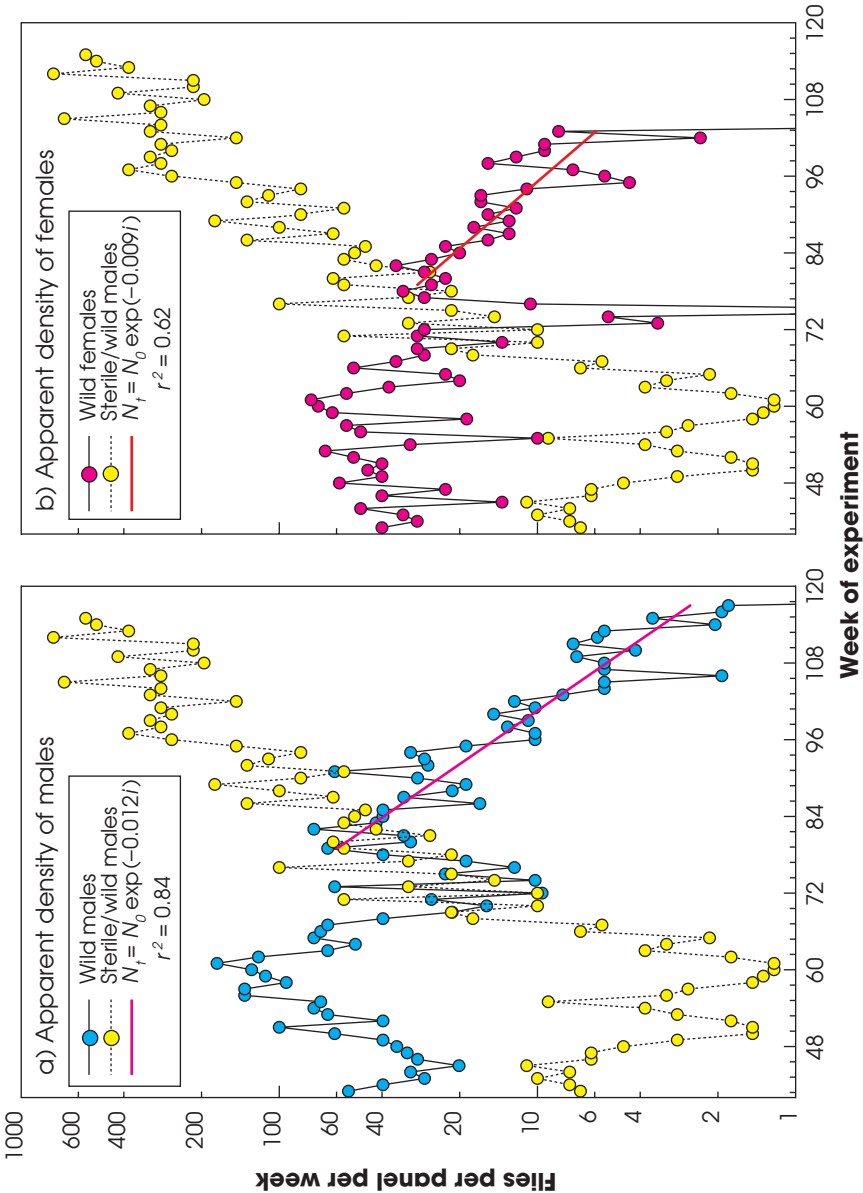
Catches of male and female *G. austeni* from sticky panels deployed at monitoring sites 1–6 in the Jozani Forest of Unguja Island, Zanzibar. Redrawn from Fig. 7 of Vreysen *et al.* (2000).

Figure 32.   **Growth rate and fecundity**
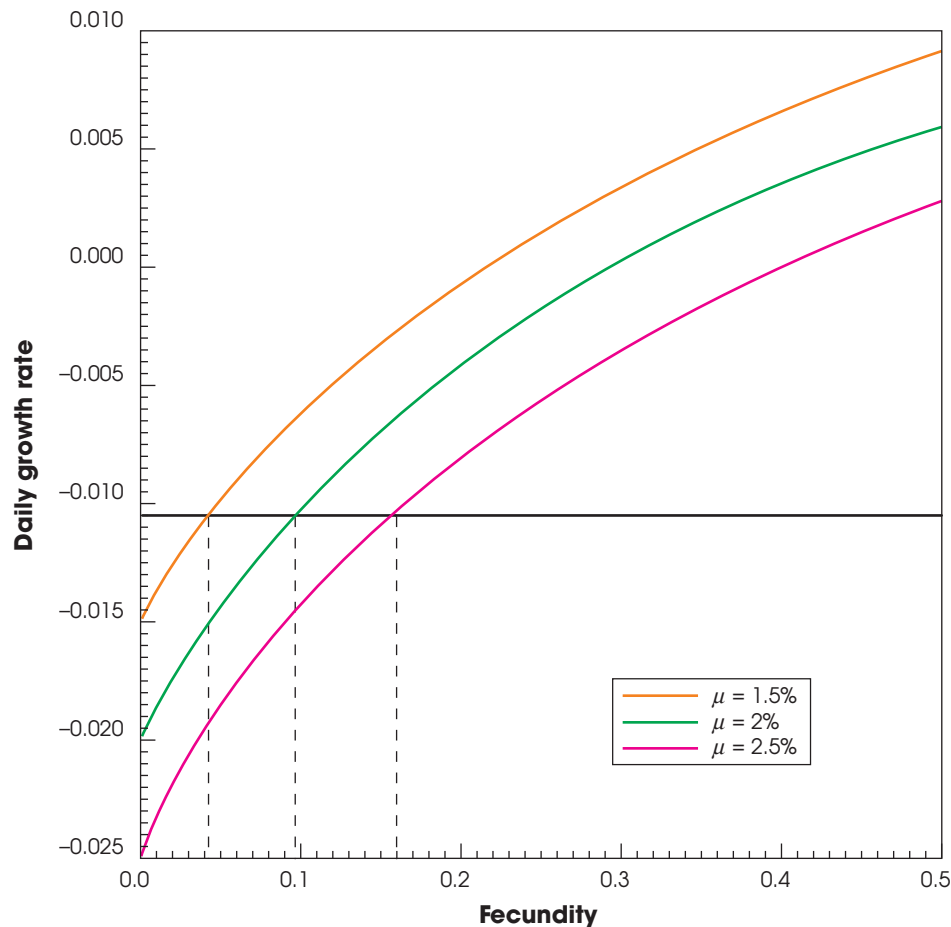
Relationship between growth rate, adult mortality and fecundity in tsetse populations. Values of other vital parameters are defined in the text. The horizontal line in the body of the graph indicates the apparent rate of decline of the female *G. austeni* population in the Jozani Forest area of Zanzibar. The intersection of each graph with this line provides an estimate of the fecundity of the population under the assumed level of adult mortality.

0.5 at the end of each pregnancy. With $\beta = 0.5$, and the remaining vital parameters defined as above, Equation (2) was solved for an adult mortality of between 1.5 and 2.5% per day for a stable population. With this background level of adult female mortality, Fig. 32 implies that female fecundity was reduced to 0.17 in the case of the Zanzibar population during weeks 79–103 of the control operation. This means that fecundity has been reduced by a factor of only three, which

also defines the *effective* ratio of sterile:wild males. So, even though the ratio of sterile to wild males was more than 100:1 for most of the period in question, the very slow decline in the population suggests that the probability of a wild female mating with a wild male was still of the order of 0.3.

This estimate is, of course, particularly dependent on the assumed value of the background adult mortality. When populations are small, it may well be that density-dependent effects mean that adult mortality is lower than the assumed values of 2.5% per day and that the population would be expanding were it not for the control programme. Figure 32 shows, however, that even when the mortality is reduced to 1.5% per day (giving an exceptionally long mean life of 67 days) the estimated value of β was still approximately 0.4, implying an *effective* flooding ratio of just over 10:1 as opposed to an observed sterile:wild ratio of greater than 100:1.

This massive discrepancy, which seems to have been ignored, should cause some alarm amongst proponents of SIT. If, in truth, at least 90% of the sterile male *G. austeni* were not sexually competitive in the field, or died before becoming so, large amounts of money are being wasted on releasing poorly competitive males.

Consideration of Fig. 32 and Equation (2) suggests, in fact, that the release of such massive numbers of tsetse in Zanzibar was counter-productive. It will be seen from Fig. 32 that as the fecundity tends towards zero – i. e. as the flooding ratio tends to infinity – the rate of population decline tends towards the assumed natural death rate. This is clear from Equation (2). When $\beta = 0$ this becomes:

$$\exp\left[(\sigma_c - r)\tau_c\right] = 1 \qquad (3)$$

which reduces to $r = \sigma_c$ on taking logs. This simple fact, not remarked upon in the published analysis of the Zanzibar data, may partly explain why the rate of population decline was so insensitive to increases in the apparent flooding ratio.

2.6.3   Feasibility of large-scale use of SIT

The above analysis raises serious questions about the feasibility of using SIT against large, potentially open populations such as those on the African mainland. It is sobering that it took more than two years and the release of more than 8.5 million sterile males to complete the eradication of a population whose male component comprised only 1000 flies at the start of the release program (Fig. 30). Moreover, the vast majority of the population was restricted to the Jozani Forest, an area rather smaller than the 5 km^2 of Antelope Island where targets, even in their early stages of development and used only with acetone as an attractant, removed *two* tsetse species simultaneously and at relatively little cost. If two species had existed on Zanzibar, there would have been substantial additional cost to rear the second species – a problem that would occur in many mainland areas, where several species can occur together.

The calculations summarised in Table 6 indicate the high level of expense required. In making the calculations for this table, it is assumed that, as in Zanzibar, in order to achieve eradication, a total of 8500 (= 8.5 million/1000) sterile males need to be released for each wild male *of each species* present in the target population.

On Unguja Island, with an area of 1650 km^2 (Vreysen *et al.*, 2000), the overall mean density of male *G. austeni* at the onset of sterile male releases was only 0.6 per km^2 (= 1000/1650). If one assumes a cost of just US$0.1 per sterile male produced and released then the estimated cost of production is around US$500 per km^2 (Table 6). This is somewhat lower than, but in the same neighbourhood as, the figure of US$626 per km^2 quoted by Leak (1998; Table 19.2) for the total cost of SIT campaigns.

SIT can thus appear to be a moderately attractive economic proposition if used against a single species at, and presumably suppressed to, a level of less than one wild male tsetse per km^2. Costs rise to much less attractive levels if more than one species need to be removed from an area (Table 6). It needs to be clear, moreover, what is implied by the requirement of such a low starting density of the wild male population. In particular, it is necessary to use (and fund) some other technique to reduce the tsetse population to such low levels and this may be no mean undertaking. In the case of the 600 km^2 Rifa Triangle, for instance, it may be inferred from the work by Vale *et al.* (1988) that, before odour-baited targets were deployed, there were at least 3 million males in the area, giving a density of around 5000 per km^2. To reduce this population to a density of 0.6 per km^2 means that a control level of 99.99% has already been achieved.

It seems intuitively obvious that any method that can produce this level of control in a reasonable time period (say one to two years) can surely also be used to effect eradication. SIT is thus not only unnecessary under such circumstances, but also undesirable, since its use will only add to the total cost of the operation. Conversely, if the alternative technique is, or can, only be used to reduce the male population to a density of perhaps 10 males per km^2, the cost of the SIT part of the operation will then balloon by more than an order of magnitude and SIT will not be a reasonable economic proposition, even against a single species.

These estimates are subject to many sources of error and opinion will differ as to the values used. It seems unlikely, however, that the cost of production and release of sterile male tsetse can be reduced much below the figure of US$0.1 used in Table 6. In support of this, note that economists advised the Tsetse Research Laboratory in Bristol to charge £1 as a realistic price for each tsetse fly they provided for research and development purposes.

Regardless of the true cost of SIT, however, the fact remains that this will always be in addition to the costs of the complementary technique(s) used. Moreover, because of the time-scales involved, much of the SIT programme costs, such as those for the materials and labour involved in

Original density (per species) of wild males	Number of species present in target area		
	1	2	3
0.6	0.5	1.0	1.5
1	0.85	1.8	2.55
10	8.5	17	25.5
100	85	170	255

Estimates for the cost of the eradication of tsetse per km^2 using SIT. With reference to the Zanzibar results (see text) it is assumed that, in order to achieve eradication, 8500 sterile males must be released for each wild male originally present in the target population. Figures in the body of the table give the cost per km^2 in thousands of US dollars.

building and running breeding facilities, will have to be incurred *before* the other technique is used and, critically, before it is known whether or not the other technique is capable of achieving eradication by itself.

2.6.4   The future for SIT in tsetse eradication campaigns

The major argument for the use of SIT in Zanzibar was that, whereas aerial spraying could undoubtedly have been used to eradicate the very small population of *G. austeni* left after the use of baits, there were fears about the simultaneous destruction of endemic animal species (Vreysen *et al.*, 2000). It is hard to fault this ecological argument and there may be areas on mainland Africa where similar problems need to be considered.

Where there are no such ecological considerations, the results in the previous section suggest that there may be limited scope for the use of SIT against tsetse. In every eradication campaign, regardless of ecological considerations and prior to the use of SIT, some other technique will have to be used to suppress tsetse populations. That being the case, the issue is simply whether that technique, or some other simple, cheap, acceptable method, can also be used to eradicate the target tsetse population. SIT will only have a role if this proves to be impossible – and the preceding analysis shows this role will be economically justifiable only if the remnant male population density is *sufficiently small*.

The problem is that we don't know what is meant by *sufficiently small* and it must surely be a major research priority to determine this for a given species under a given situation. An important part of this process would be an independent and realistic assessment of the true overall cost of

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producing sterile male tsetse. Obviously, the more cheaply flies can be produced, the greater is the size of the population that could be eradicated using SIT. Regardless of the cost, however, the Zanzibar data suggest that the greatest room for improvement lies in identifying the reasons behind the massive gulf between the real and the apparent flooding ratio (see above). If this order of magnitude difference could be removed, there would be a massive reduction in the number of released sterile males needed to eradicate a given population. Alternatively, the same number of releases could be used to eradicate a larger population. Either way, SIT would become a more attractive option.

The discussion of the use of sterile tsetse has so far concerned their part in *effecting* eradication. An alternative use, which has not so far been given prominence, is as an *index* of the probability that eradication has been achieved. As a preliminary to the discussion of this new idea it is necessary first to consider the conditions under which control becomes eradication.

2.7   When does control become eradication?

Regardless of the method chosen for an eradication campaign, there will come a point at which it must be decided whether this objective has been achieved – or even whether it is achievable with the method being used. There is a world of difference between a successful control operation, in which so many flies are killed that there *appear* to be none left, and one where the population actually does become extinct. As is clear from the Botswana experience of the early 1990s, the former situation can deteriorate rapidly – despite the low reproductive rate characteristic of all *Glossina* species.

Eradication does not necessarily mean killing every single fly. If a control operation is so successful that the only remaining flies are all of one sex, or if numbers are so small that surviving males and females never meet, then the population will become extinct without further effort on the part of tsetse control agencies. Even if males and females do survive and mate, the numbers may be so small that the pioneer population becomes extinct by chance. The probability with which such an event occurs depends on the numbers of survivors and the rates of reproduction, death and development. The precise dependence is developed in Appendix 5. Figure 33 shows the estimated probability of extinction for the case in which varying numbers of females survive the control operation and are subsequently inseminated.

When only one inseminated female survives, even if natural daily mortality rates in females are quite low (say 1% in adults and 0.5% in pupae) there is still a greater than 20% chance that the

Figure 33. **Extinction probabilities for tsetse populations**
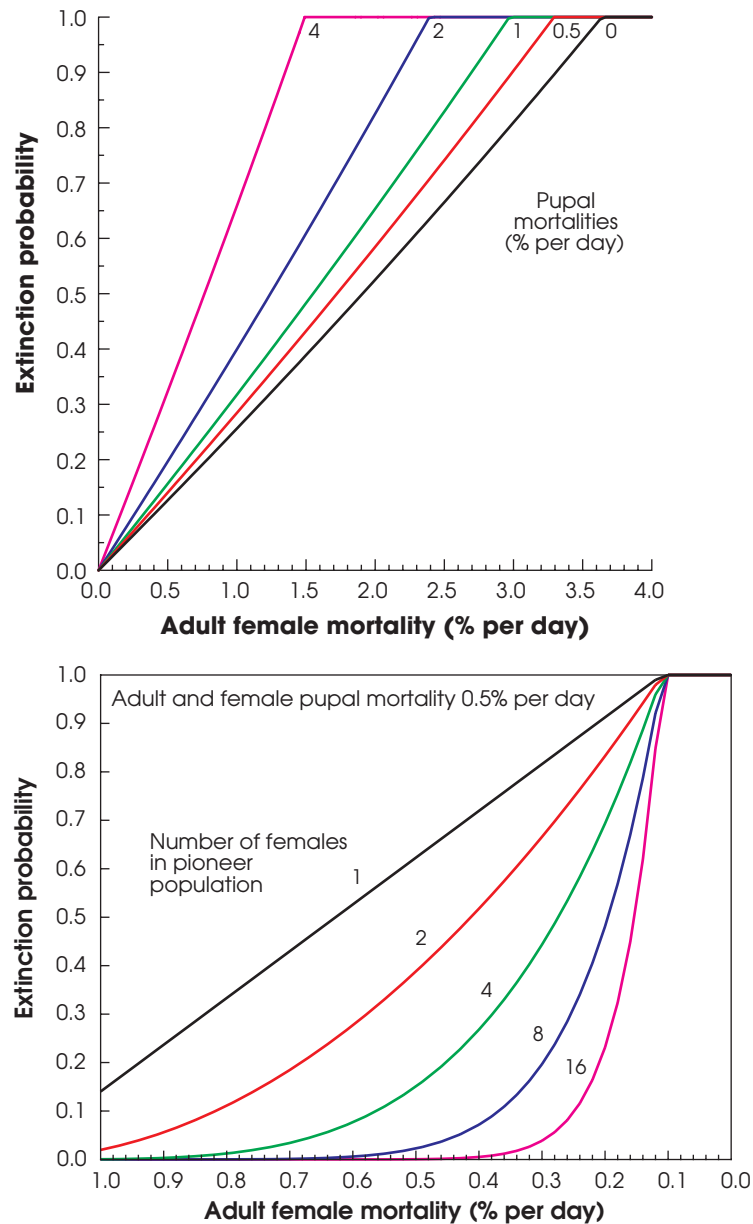
Upper graph: pioneer population is a single inseminated female. Extinction probabilities calculated for varying levels of adult female mortality (abscissa) and female pupal mortality (see body of the graph). Lower graph: various sizes of pioneer population and constant pupal mortality. Time to first ovulation is 7 days; inter-larval period 9 days; pupal duration 27 days.

population will become extinct. Regardless of the pupal mortality, however, the population will become extinct with a probability of 1.0 if the adult mortality is greater than 3.5% per day. When larger numbers of females survive the control operation, the probability of extinction declines to the point that when there are just 16 survivors, and with a pupal mortality of 0.5% per day, there is zero chance that the population will become extinct as long as adult female mortality is less than 2.5% per day. This analysis suggests that the auto-extinction of a tsetse population can seldom be relied on. Either all of the flies must be killed in the initial onslaught using something like an aerial spraying operation, or an imposed adult mortality of at least 3.5% per day must be maintained using techniques such as odour-baited targets or insecticide-treated cattle, until intense sampling indicates eradication has been achieved.

The predictions in Fig. 33 are all made under the assumption that surviving females are inseminated. As noted earlier, insemination may not occur if surviving flies are so sparsely distributed that males and females have a low probability of meeting. Equally, the probability of effective mating can be reduced by, for instance, releasing sterile males into the population. The techniques developed in Appendix 5 to calculate the extinction probability of a tsetse population as a function of the mortality can equally be used to calculate the effects of reduced fecundity.

The results in Fig. 34 show the relationship between the extinction probability and the probability (ι) that a fly is inseminated for various numbers of surviving flies in the target population. Obviously, the higher the natural or imposed mortality in the wild adult female population, the smaller the required reduction in ι that will ensure that the population becomes extinct (left graph). As previously shown, the population would go extinct even if $\iota = 0.9$ as long as this mortality is more than 3% per day (Fig. 33, left graph). If the adult and pupal mortalities are both as low as 0.5% per day, however, ι must be reduced to 0.1 before the population goes extinct with a probability of 1.0. In the event that a wild virgin female has an equal probability of mating with all sterile and wild males in the population, this is the equivalent of saying that we require a sterile:wild ratio of 10:1 among males. This 10:1 ratio is approached when the starting wild population is larger (Fig. 34, right graph) but the probability of extinction falls more rapidly with decreasing values of ι, as the size of the starting population increases.

Notice that the results in Fig. 34 are based on the assumptions that the viability and sexual competitiveness of wild and sterile males is the same and that females mate only once. If either assumption is violated then the flooding ratio required to achieve eradication will need to be higher than that indicated in Fig. 34.

These results agree with the analysis of the Zanzibar data (see above and Vreysen *et al.*, 2000) where it was found that there was little or no decline in the *G. austeni* population until flooding ratios exceeded 10:1. Similar findings were noted by Politzar and Cuisance (1984) and

Figure 34.   **Extinction probabilities for tsetse populations**
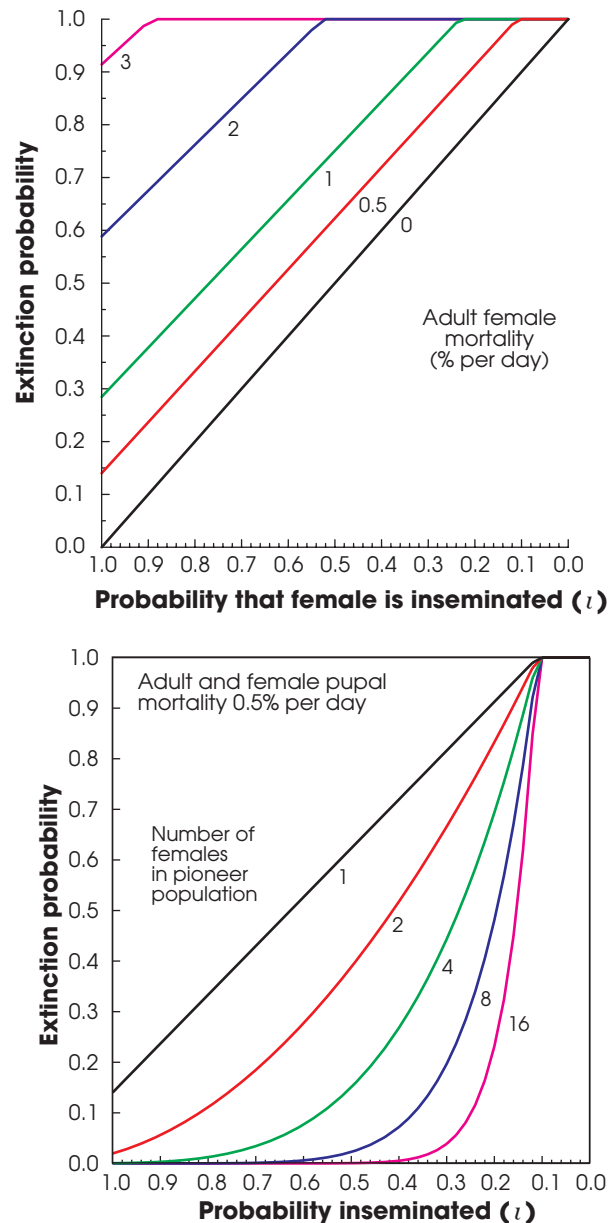
Upper graph: pioneer population is a single inseminated female. Extinction probabilities calculated for varying probabilities of insemination (abscissa) and adult mortality (body of the graph). Lower graph: various sizes of pioneer population with constant pupal and adult mortality. Time to first ovulation 7 days; inter-larval period 9 days; pupal duration 27 days.

Takken *et al*. (1986) in operations against riverine tsetse species in West Africa. Knipling (1963), in contrast, predicted that a flooding ratio of 3:1 would be sufficient to eradicate a stable tsetse population in one year. The present model is more in keeping with the observed results.

2.8   Indicators of eradication

2.8.1   Direct detection of survivors using traps

The previous section produced *theoretical* results indicating the conditions under which we can expect eradication to be achieved. In the real world, even if the eradication campaign goes according to plan, we will be faced at some point with the problem of deciding whether we have succeeded *in practice* in eradicating a tsetse population. A minimum requirement for making such a decision will be that we are unable to catch any tsetse despite intensive sampling over a long period. This rather loose statement is made concrete in the theoretical development in Appendix 6. There it is shown that, if we sample an area A for t days using S traps (or other sampling devices) each of efficiency σ, then the probability ($C'(N,S,\sigma,t)$) that *none* of the traps catches any of N surviving flies is:

$$C'\,(N,S,\sigma,t) = \exp(-\,St\sigma\lambda) \qquad (4)$$

$$= \exp(-\frac{St\sigma N}{A})$$

An approximation to the probability (C) that we capture *at least* one fly is given by:

$$C\,(N,S,\sigma,t) \;\; = 1 - C'\,(N,S,\sigma,t) \cup = \frac{St\sigma N}{A} \qquad (5)$$

The approximation works well when, as in the situations that interest us, the population density and the overall capture probability are both low. The relationship between C and the various parameters in Equation (4) are shown in Fig. 35 for two different levels of sampling efficiency.

As a simple example of the application of Equation (5), if there are 100 flies surviving in 16,000 km^2, about the area of the Okavango Delta that could support tsetse and that was sprayed in 2001–2002, and if 10 traps are each deployed for about three months (90 days), and if $\sigma = 0.01$, then $C(N,S,\sigma,t) \approx 0.06$. That is to say, with this level of trapping, there is a 94% chance that we will fail to detect that there are flies present. In order to be 90% sure that we detected at least one fly, given that there were 100 present, application of Equation (3) suggests that over 400 traps would

Figure 35. **Probability of catching a tsetse fly in a low density population**
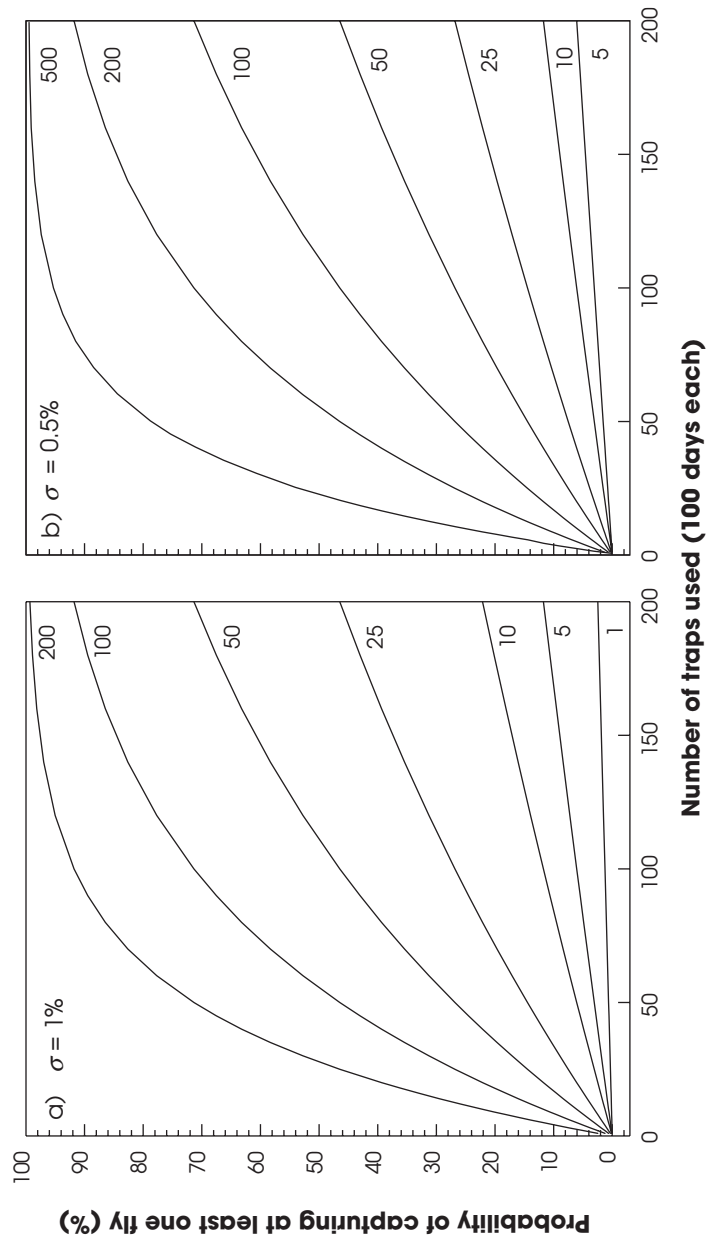
The probability of catching a tsetse fly in a low density population in an area of 8000 km² as a function of the number of traps deployed, each for 100 days, and the population size, denoted by the numbers in the body of the graphs. The results are calculated for two levels of σ, the probability that a single trap catches a single fly in one day, given that the fly is present in a 1 km² neighbourhood of that trap.

need to be run for three months. To be 99% certain, the figure rises to over 800 traps. These figures are based on the assumption that the traps are distributed fairly evenly. It is important to bear in mind that the flies might exist in places the sampling teams decide to avoid or ignore – and this would substantially reduce the chances of detecting a residual population.

In view of these considerations and the likely levels of sampling used in the Okavango, it seems at least possible that the tsetse detected by Wooff in 1992 were not new immigrants but had been there all along, having survived the aerial spraying campaigns of the 1970s and 1980s. Tsetse had gone undetected previously because the population was even lower and because previous sampling had been less intense.

With regard to the present aerial campaign in Botswana, the results suggest that a very much more aggressive sampling campaign is required before we can have any confidence that tsetse have indeed been eradicated from the area. The serious consequences of failing to detect small remnant populations are indicated in Fig. 36. Even if 0.1% of the initial tsetse population survives in only 1% of the area sprayed in the Okavango, modelling of the expected population growth suggests that the whole area will have been re-infested within three years. The rapid deterioration in the tsetse situation here in the early 1990s, following a period when the population was so low that it was considered to be extinct or nearly so, shows that the concern is not simply theoretical.

The need for intensive surveys is not just to allow researchers to claim with confidence that flies have been eradicated. It is just as important to know where any sparse but potentially invasive populations occur *prior* to planning a control campaign. Populations of flies in the area do not even have to be self-sustaining, as they can easily become so when they invade the treated area after control measures have ceased.

2.8.2 Indirect detection: using SIT to detect and estimate surviving populations

As is evident from the previous section, it will often take a great deal of effort to detect the presence of surviving tsetse populations, particularly if the population is small and the search area large. In practice, tsetse control authorities have instead used the indirect approach of introducing test herds of cattle into areas where tsetse are supposed to be eradicated. Potts and Jackson (1952) and Vale *et al.* (1984), among the studies included in this review, used this technique (see also Section 3.1).

The method may not always be practicable, however. In the Okavango Delta and within other wildlife areas, it may be hazardous and also undesirable to introduce herds of cattle. In such circumstances the use of sterile insects provides an alternative and indirect means of detecting the presence of tsetse. If sterile virgin *female* tsetse were to be released into the environment and then

Figure 36. **Predicted growth of a tsetse population**
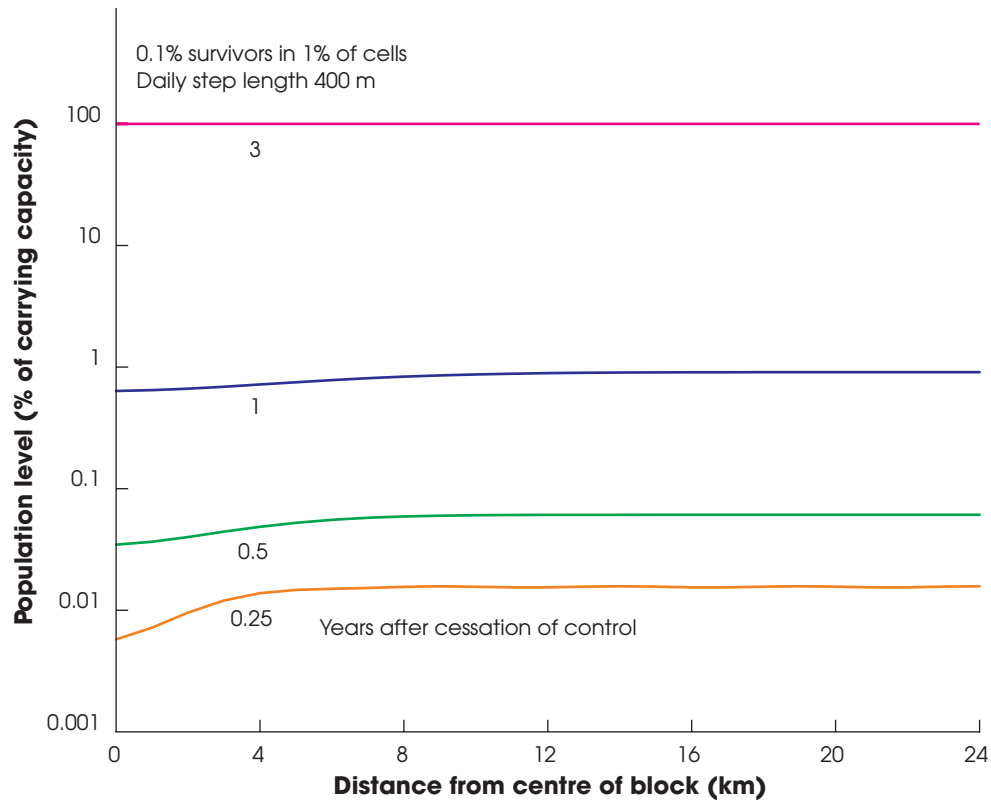
The predicted growth of a tsetse population in an area of 10,000 km² following a control campaign in which 0.1% of the female flies have survived in 1% of the cells. (Redrawn from Hargrove, 2000).

recaptured and subjected to ovarian dissection, the presence of inseminated flies would show that eradication had not been achieved.

Mark–release–recapture efforts with known numbers of sterile *male* tsetse could similarly be used to estimate an upper limit to the surviving wild population. Such estimates are of interest given the relationship between population size and extinction probability (Section 2.7). They can, of course, be produced as a by-product of any eradication campaign using SIT (Vreysen *et al.* 2000). The present suggestion is that the detection/estimation technique could be used even when SIT is not involved in the eradication programme.

2.9 Tsetse control and eradication in Zimbabwe

The preceding consideration of tsetse control and eradication campaigns involving a variety of methods is usefully concluded by looking at the way many of them have been used to remove tsetse from large areas in Zimbabwe. Figure 37 shows areas in the Sebungwe region of northwest Zimbabwe that have been subjected to ground and aerial spraying and where targets have been deployed.

Note that many of the areas, particularly those to the south of the operational regions of the 1980s and 1990s, had previously been subjected to ground spraying and hunting campaigns. Early trials with hunting at Nagupande and ground spraying at Kariangwe, for example, were both carried out in this region. Moreover, Antelope Island in Lake Kariba saw not only the first use of odour-baited targets in the field but also the first trial of SIT against tsetse.

Ground spraying and hunting were largely responsible for the removal of tsetse from large areas of the Sebungwe prior to 1980. Thereafter, aerial spraying was used successfully (Hursey and Allsopp, 1983, 1984) and the combined use of this technique with ground spraying and odour-baited targets resulted in the eradication of tsetse from the vast majority of the Sebungwe (see below). A combination of aerial spraying, odour-baited targets and insecticide-treated cattle

Figure 37.   **Tsetse control in Sebungwe, Zimbabwe, 1982–1999**
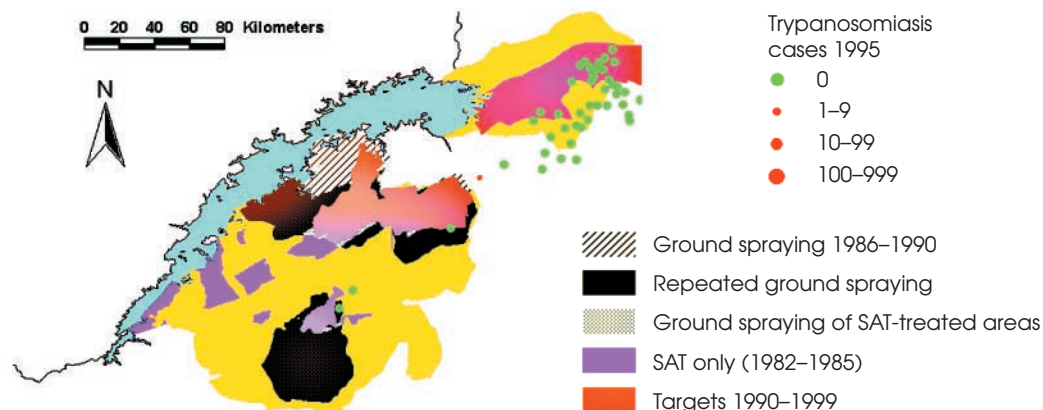
Areas in yellow indicate previous ground spraying operations. Map by kind courtesy of Dr S. J. Torr.

was similarly used to remove tsetse from a large proportion of the area to the east of the Sebungwe (Fig. 38).

A measure of the success of these enterprises is given by the reduction in trypanosomiasis cases in northern Zimbabwe between 1984 and 1987. The situation in 1984 was serious with nearly

Figure 38.   **Tsetse control in northern Zimbabwe, 1980s and 1990s**
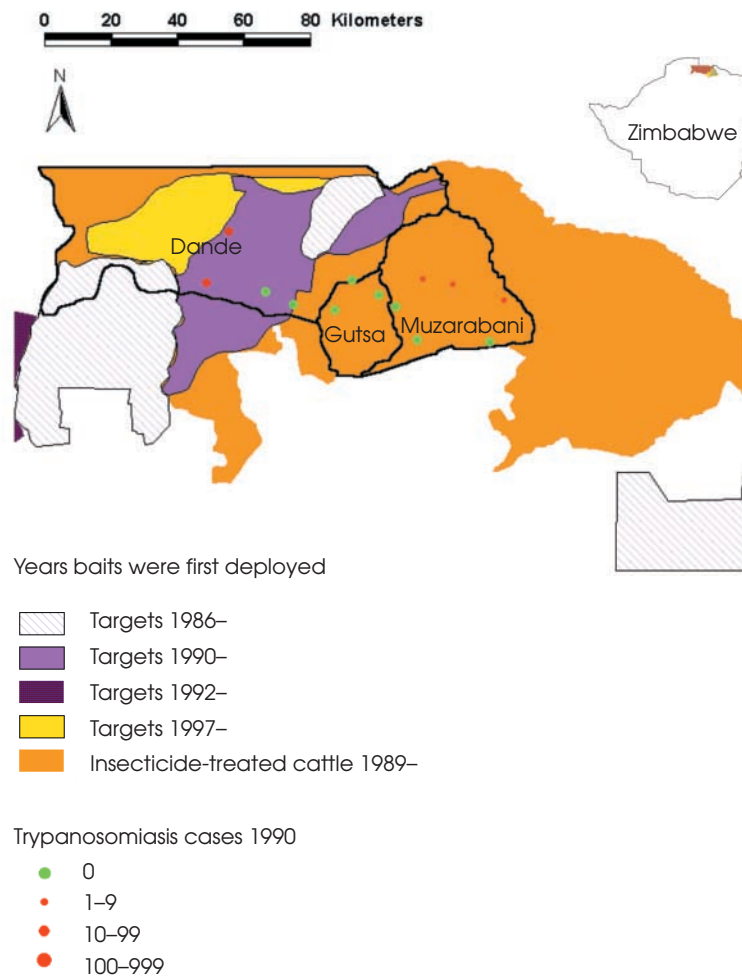
10,000 cases detected across a broad front (Fig. 39, upper map). By 1997, despite vigorous sampling efforts, as indicated by the numbers of sites involved, no cases of trypanosomiasis were detected and it may be concluded that the disease has been entirely eliminated from the area (Fig. 39, lower map). The actual change in numbers of cases annually is shown in Fig. 40.

Figure 39.   **Decline in trypanosomiasis cases, northern Zimbabwe,1984–1997**
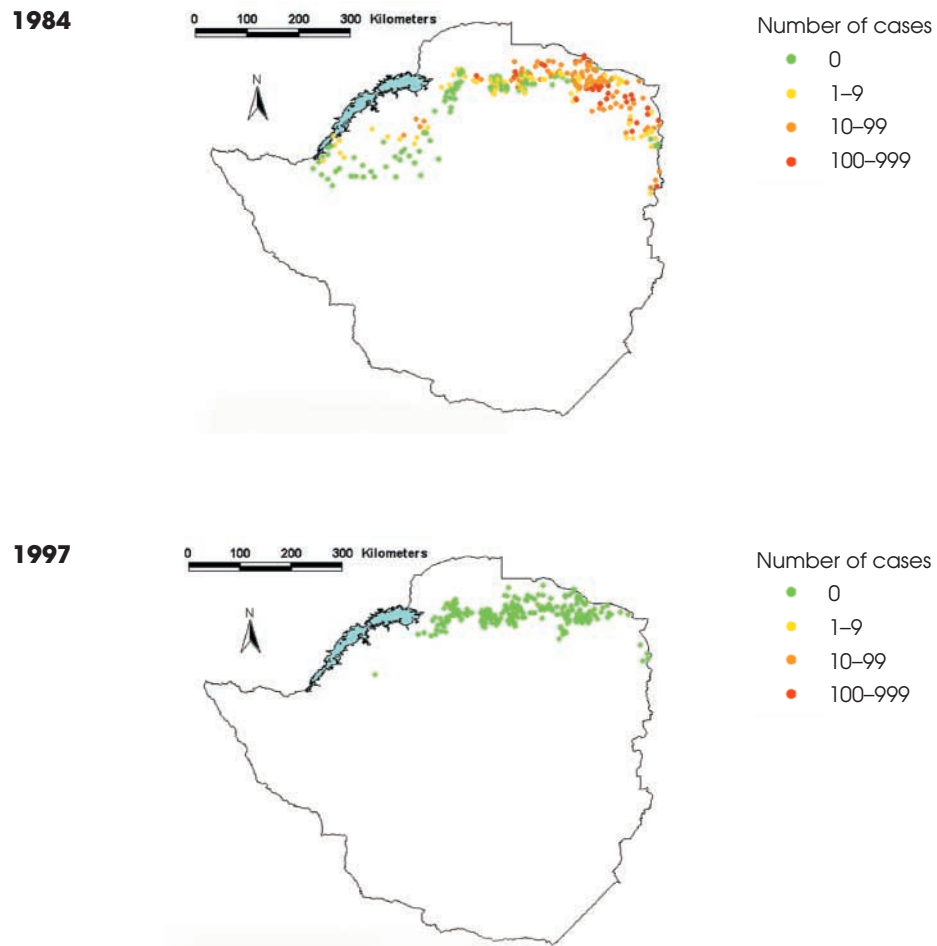
Each dot on the map indicates a dip tank where cattle were tested for trypanosomiasis. Maps by kind courtesy of Dr. S. J. Torr.

Figure 40. **Trypanosomiasis cases in Zimbabwe, 1970–1997**
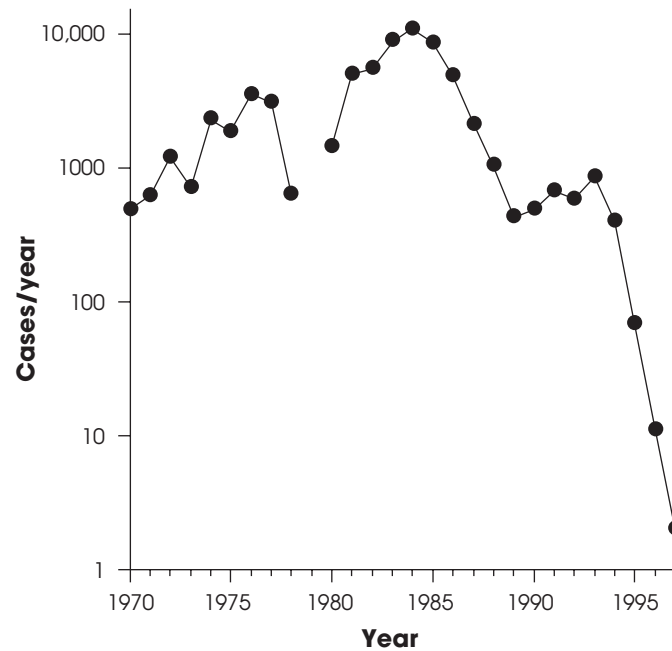
The discontinuity in the graph marks a point during the war in Zimbabwe where trypanosomiasis data could not be collected.

In the 1960s and early 1970s, a combination of bush clearing, hunting and ground-spraying was used to eradicate tsetse from the southeast of the country and, indeed, to push the front 50 km into neighbouring Mozambique.

3. Discussion

3.1 Large-scale tsetse control and eradication

The take-home message arising from Section 2.9 is simply that several techniques, used alone or in combination, have been shown to provide large-scale eradication of tsetse in Zimbabwe. These successes are by no means limited to Zimbabwe, as the body of the report makes clear. On the other hand, closer scrutiny of the various operations reveals that success was often not sustained. Despite the eradication of *G. pallidipes* in Zululand, trypanosomiasis returned to the area, as it has in the recent past to the southeast and to the Urungwe area of Zimbabwe. Tsetse even returned to the island of Principe.

So, while massive reductions in tsetse populations and disease can clearly be achieved, 'once and for all' eradication is deceptively elusive. The current review indicates that there are two elements to this. First, tsetse populations can be reduced to extremely low densities, but still recover. And second, detecting these surviving populations is very difficult and time consuming – to the extent that levels of sampling in most control operations are insufficient to provide compelling evidence that eradication has been achieved. This situation was even worse in the past, before the advent of efficient sampling tools.

In some operations where 'eradication' was achieved, it is quite possible that tsetse numbers were reduced to below the level of detection – but that this only reflected the facts that sampling was ineffective even while the control measures were in place, and that sampling efforts declined soon after the operation ceased. In other cases, local and even extensive eradication may well have been achieved – only to be thwarted eventually by re-invasion. Again, without effective sampling, it is impossible to separate the two causes of eventual failure.

More compelling demonstrations of eradication are provided by operations conducted in areas where cattle are abundant. In these situations, the cattle themselves provide a food source that allows surviving populations to recover rapidly. Recovery of the tsetse population soon becomes

apparent as cases of trypanosomiasis. For this reason, tsetse departments have long understood that the prolonged absence of trypanosomiasis in a cattle population is the 'gold standard' of effective tsetse eradication. On this basis, tsetse control operations in Nigeria, South Africa and Zimbabwe have been profoundly successful.

These successful operations were the consequence of large, intensive and repeated operations by well-funded and well-organised government departments. They were achieved with a variety of techniques, but the common denominator was institutional strength and a national policy aimed at eradication and supported by the government at the highest level. With such an enabling policy environment, it was necessary only for the circumstances to be right for the particular technique, and for it to be planned and executed with understanding and determination.

The institutions and policies concerned have now largely disappeared, and it is difficult to see how the large-scale successes of the past could be repeated in the modern setting. Large-scale efforts against trypanosomiasis currently involve livestock owners using large quantities of drugs. It is noteworthy that this was a government activity in the past, but is now funded mostly by the livestock keepers. Farmers and individuals are able to, and do, take on the activities of government – in keeping with modern philosophies of 'privatisation'. The problem is that drugs are often not used properly, resistance is developing and there are no second-line drugs in prospect. It is therefore likely that some manner of vector control is not only necessary and desirable but also unavoidable. The question is what form should that control take?

3.2   *Laissez faire*

Bourne *et al.* (2001) provide one answer, pointing out that the greatest changes in tsetse distribution have resulted simply from the expansion of human populations into tsetse habitat. The consequent reduction in game numbers and habitat, and the increase in roads, crops and settlements, all result in effective tsetse control – if not actual eradication. Tsetse control thus occurs by a combination of game destruction and bush clearing, which we have seen can be extremely effective when used purposively.

In spite of this fact, many thousands of people and millions of cattle suffer, and have suffered for decades, from the effects of trypanosomiasis, and the problem shows little sign of disappearing of its own accord. What should be done about such a situation? Is it best to 'take no purposive action whatsoever, and to rely on the autonomous control of the disease through agricultural expansion and hunting' (Bourne *et al.*, 2001)? They regard this *laissez faire* approach as the 'simplest and arguably most appropriate and sustainable way of dealing with tsetse and trypanosomiasis in Africa'.

In fairness to them, their view rather accurately reflects the practical reaction, if not the stated attitude, of most African governments towards tsetse control. Government spending, particularly on the operations side of tsetse control, has declined dramatically during the past 40 years, and most tsetse control departments have effectively collapsed. International donor funding in this area has also declined substantially in the last decade, partly as a reaction to this declining priority, and there is particularly little donor interest in large-scale control or eradication campaigns.

3.3　Small-scale projects

There has been rather more interest in community-based and other small-scale, self-help control projects. These became particularly fashionable following the demonstration that odour-baited targets were apparently simple to use, relatively inexpensive and ecologically clean, and after they had been used to such good effect in early trials in southern Africa. The technique appeared to offer a perfect opportunity for livestock owners to carry out tsetse control on their own account.

Unhappily, there was often little thought given to the transference of target technology, from the large-scale eradication operations for which it was originally designed, to its use on a local scale. Moreover, wherever there was a choice, there appeared to be an unfortunate tendency to opt for the least effective set of options available. In the Nguruman operation, for instance, catch-and-kill traps were used instead of insecticide-treated targets, and acetone and octenol were not used as attractants, despite their demonstrated effect on *G. pallidipes*. These problems were compounded by the fact that the operation was carried out on a small scale, in an area particularly vulnerable to re-invasion. Not surprisingly, the rate of population decline was very much lower than the target-based operations in Zimbabwe and Zambia (Fig. 17) and the effort ultimately failed.

This failure of traps to eradicate tsetse at Nguruman, or even to control them in the long term, has been blamed on factors of a quasi-political nature (Brightwell *et al.*, 1997). Barrett and Okali (1999) have been more generally sceptical on socio-economic grounds that communities will effectively participate in meaningful tsetse control and eradication efforts. Both viewpoints are quite probably valid but miss the most important point that, *even if optimally managed*, tsetse efforts will fail on purely technical grounds when they are applied in too restricted an area. By their very nature, community-based projects tend to be carried out in small areas and are therefore subject to invasion pressures that frustrate the control efforts. Under these circumstances, it is hardly surprising that there are problems in maintaining long-term local enthusiasm.

Similar comments apply to the use of insecticide-treated cattle for tsetse control. Whereas this approach has allowed a degree of private 'spontaneous' use by livestock owners, the Mkwaja

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Ranch experience shows that, even when well managed and effectively applied by a commercial organisation, insecticide-treated cattle may fail to achieve the desired results and may, in the end, fail to be cost-effective.

The generic problem in the above misadventures is the mistaken idea that because the actual implementation of bait technology is as simple as pouring insecticide on cattle, or erecting a few simple screens, then planning the implementation must also be easy. Expert knowledge and predictive modelling are still required, however, to assess strategic matters such as the appropriate size and shape of operational area that will deal with the operational objectives, tsetse species and invasion pressures that occur in different situations. Even when the strategy is optimised, there is still a need to make tactical decisions such as exactly what type of baits to use, at what density, under what management regime and for how long. While a number of handbooks and training courses have helped with the implementation of bait technology, they have been poor substitutes for expert assistance at the strategic and tactical levels. Unfortunately, the number of experts available to help at these levels is not only small but is also declining. Moreover, when experts can be found there is often expense and delay in getting their on-site assistance.

A solution to the problem may be to offer on CD an interactive computer-based programme that provides a 'virtual expert' to conduct the necessary question-and-answer sessions and 'what-if' modelling. The modelling required is essentially the same as that performed in the present report, but needs to be made executable by anybody with basic keyboard skills. Such a facility, called *Tsetse Plan*, is currently being produced by way of a DFID-funded project (Vale and Torr, in preparation) and will soon be ready for free distribution. In addition to advising on strategy and tactics, the programme will also offer help with the design and interpretation of surveys of pre-treatment populations, monitoring, budgeting, shopping lists, accounting and experiments in support of planning, together with notes on technical details and implementation.

3.4 Can there be no joy in Mudville tonight?

Taken together, the first three sections of this discussion may seem to provide a somewhat gloomy picture of the prospects for tsetse control. Whereas the review has shown that large-scale tsetse control and eradication is a technical feasibility, neither African governments nor international donors display much real commitment to this approach. On the other hand, technical and socio-logical considerations suggest that small-scale community-based projects are unlikely to succeed in the long-term. Add to that the threat of increasing drug resistance, and, in the end, perhaps all we will have left is *laissez faire*, *à la* Bourne *et al.* (2001).

The July 2000 declaration by OAU Heads of State in Lomé and the suggestion of a New Economic Plan for African Development (NEPAD) has re-kindled interest and a resurgence of donor support for Africa in general – and, as a part of this, African government interest in tsetse control. These initiatives prompted the present review and led to a re-thinking of the principles of tsetse control based on a more thorough approach to planning campaigns. This planning would consider a wider range of options including different methods and scales of operation and, whenever possible, would consider carefully whether or not it is necessary or desirable to choose eradication over control.

However, it has become clear in the last year that donors and African governments have stepped back from the more extreme statements of the Lomé declaration. That being the case, there is a less urgent need to make immediate practical decisions of the sort referred to in the last paragraph. Nonetheless, it seems likely that at some point in the future there will be a resurgence of interest in vector control, and the remainder of this discussion is based on the assumption that this is the case.

3.5 Technical advances

In contrast to the rather negative feel of the previous sections, it should be noted that there have been recent technical advances in the field of tsetse control and these should result in more effective programmes in the future. The aerial spraying operations in Botswana have benefited greatly from the advent of Global Positioning System (GPS) technology, which enables computers to guide aircraft to within a few metres of their target area. At the same time, the computer keeps track of exactly where the aircraft has flown and precisely when and where the insecticide has been delivered. This advance, in conjunction with careful attention to the specific rates of tsetse development in the area, to their rate of movement and hence the scale of operation required, should result in further improvements to the outcome of future aerial spraying operations.

In the field of bait technology, recent work has shown that the application of insecticide to the legs of cattle can kill tsetse just as effectively as spraying the whole animal (Vale, 2002). This reduces the amount of insecticide used, and therefore, the cost of control. Vale's study also suggests that this practice reduces the risk of destroying the host animal's natural resistance to tick-borne infections and the risk of killing dung fauna (Vale *et al.,* 1999; Vale and Grant, 2002), which are so important in the process of recycling dung and enriching the soil. There is much scope for further work aimed at reducing the costs of tsetse control. Ideally, if the cost of tsetse control could be reduced to the level of trypanocidal drug treatment, livestock owners would be in a position to implement control operations themselves, thereby reducing their reliance on drugs that are rapidly losing their efficacy due to resistance. As argued above, however, effective tsetse control will also depend on the scale of the operation, and will require the co-operation of people over a large area.

3.6 Selecting the most suitable options

3.6.1 Bush clearing and game destruction

Given the foregoing discussion we are now in a position to discuss the necessity, sufficiency and desirability of the various methods of vector control available. Game destruction and bush clearing as *purposive* methods of tsetse control are likely to be rejected on ecological grounds, but, as argued by Bourne *et al.* (2001), these will in reality be an inevitable, integral part of agricultural development. The difference is one of degree; early use of these two techniques was often carried out in a ruthless fashion with the prime purpose of eradicating tsetse, without regard to the particular needs of agriculture or to wider ecological issues.

Where fields are cleared for agricultural purposes and where game is hunted for meat, tsetse numbers are certainly reduced. The fly may even be eradicated as a consequence, although there are many areas of Africa that are long-settled and farmed by humans and where flies continue to be a major problem. Often this may be as a result of invasion from adjacent unsettled areas where game still exist in sufficient numbers to provide a host for tsetse. In this event, it will be necessary to look to alternative methods of vector control if the stockowners are not to rely entirely on chemotherapy. Alternatively, flies may persist in the absence of wild life hosts, feeding entirely on domestic livestock. This is the case in western Kenya and southeast Uganda, where there are almost no wild animals left.

3.6.2 Insecticide-treated cattle

Where the area under threat is well stocked with cattle, and these areas are likely to be the ones requiring the most urgent attention, the most credible technical option for tsetse control will be to apply insecticide to the cattle. Where the cattle numbers are sufficiently large, and where there is no more than modest invasion pressure, this intervention may be sufficient to maintain adequate disease control – either by itself or with occasional drug treatment of infected cattle. Given recent advances in the use of insecticide on cattle, this approach may soon be as affordable as the use of chemoprophylaxis. If this becomes the case, it is reasonable to expect that the stockowners will be able to carry out the tsetse control process themselves.

3.6.3 Odour-baited targets

As the Mkwaja Ranch experience suggests, however, if the area grazed by the cattle is small and subject to invasion, it may be necessary to supplement the use of insecticide-treated cattle with targets. In order to ensure maximum effect per unit of effort, all effective odour attractants should be used with the targets, and targets should always be used instead of the less efficient traps.

The type of model developed and described in this review can be used before the start of the programme to indicate whether either intervention will be sufficient to provide adequate relief.

The unfortunate problem of theft of targets remains, however, and this is hard to include in predictive models. This occurred in Somalia when target operations were carried out in support of an aerial spraying programme (Wooff, 1989). Thefts were so severe that the target operation rapidly collapsed.

3.6.4   Ground and aerial spraying

Ground spraying and aerial spraying with *residual* insecticides are, on ecological grounds, the least desirable options, even where they are sufficient means for achieving eradication. By contrast, aerial spraying with non-residual insecticides can be sufficient to provide highly effective control or even eradication without causing undue damage to the environment. An exception to this rule may be small islands or similarly restricted habitats, where the spraying process could endanger endemic animal species susceptible to the insecticide used to kill tsetse. The degree of this danger will increase as aerial spraying is carried out over larger and larger areas in single operations.

3.6.5   Sterile insect technique

The techniques discussed above have all been used in campaigns where tsetse have been eradicated for long periods of time over extended areas in mainland Africa. They can also be used if the intention is just to provide local relief from trypanosomiasis. In contrast, SIT has always been regarded in the tsetse world as a method to be used as the *finale*, or *coup de grace*, to eradicate a tsetse population that cannot be eradicated using other means.

Considering that the other means can be quite sufficient between them to effect eradication under a variety of circumstances, the question arises as to whether SIT is in fact necessary and hence desirable. Cost will remain a major issue until there is a more transparent and independent review of the true cost of previous SIT programmes. Until this is carried out a suspicion will remain that using SIT alongside another suppression technique will seriously, and quite un-necessarily, inflate the cost of eradication. In addition to financial concerns, it is not clear that SIT, as currently practised, is technically sufficient to eradicate tsetse on the African mainland (see Section 2.6.3).

3.6.6   Which?

Which of the three basic methods of tsetse *control* (aerial spraying, targets or insecticide-treated cattle) or which combination to use is determined in part by their technical feasibility in any particular operational area. For example, aerial spraying cannot be used on mountainous terrain,

cattle cannot be insecticide-treated if they are not present, and targets cannot be used if they are likely to be stolen.

In addition, the relative costs, convenience and suitability of community participation should be considered. Aerial spraying can be performed only by a wealthy organisation, while treating cattle with insecticide is the most suitable option for poor farmers. Targets are suitable at a number of different levels. As is clear from work in Zimbabwe and Zambia, they can be used in large-scale eradication exercises organised at the national level. They can also be used on a smaller scale by local organisations and stockowners, as long as due consideration is taken of the effects of scale. Targets can be used in stand-alone control exercises but are also particularly useful in preventing invasion into blocks that have been subjected to aerial spraying or where cattle have been treated with insecticide.

3.6.7   Combinations

In some cases it has proved effective to use two or more techniques in combination, usually in adjacent areas. Examples include the use of odour-baited targets in the Rifa and ground spraying in the nearby escarpment, the use of targets in the Umfurudzi immediately to the south of an aerial spraying exercise, and the use of insecticide-treated cattle on some parts of Mkwaja and insecticide-treated targets on others. This 'mosaic' of control measures is a form of integrated control, but should be distinguished from the type of integration commonly used against mosquitoes, where the various control measures are 'layered' on top of each other.

The practice of 'layering' seems acceptable against mosquitoes since the methods are not particularly expensive, for example draining cans that hold water, cutting grass near huts and putting insectivorous fish in ponds. Moreover, it is generally only necessary to control mosquitoes close to human habitation. With the more mobile tsetse fly, however, control must usually be performed over a minimum of hundreds, and sometimes thousands, of square kilometres. The various methods of tsetse control are too expensive for layering, especially over vast areas. Hence, for tsetse, the preferred philosophy is to use only one method in any single area or any one part of a mosaic. It is principally reasons of cost that discourage the layering of a SIT programme on top of another campaign.

Although it is generally undesirable, the use of more than one technique in the same area does occur – sometimes unintentionally, as in the case of bush clearing and its consequent destruction of game. More commonly, the layering is sequential; for example when a technique fails to achieve eradication, or when re-invasion follows a successful campaign.

Mkwaja Ranch provides an extreme example. It has been used over the years for major trials of trypanocidal drugs and has been subjected to bush clearing, game destruction, ground and aerial

spraying, insecticide-treated targets, insecticide-treated cattle and even SIT – all over an area of less than 200 km². In short, every control technique studied in this review has been used there – but sadly, all to little avail. At the time of writing, at least two species of tsetse are still happily ensconced on the property and the ranch owners, deciding that the battle is too unequal, have abandoned the attempt to keep cattle in the area.

On a more positive note, tsetse control using a combination of methods has sometimes had a much more successful outcome. Thus, many areas of Zimbabwe (see Figs 37 and 38) have been subjected over the past 30 years to ground and aerial spraying, game destruction (both purposive and as a result of human population movements) and to the use of insecticide-treated targets and cattle. In others, a subset of the control techniques listed above have been used. As a consequence, tsetse has been eradicated from a large proportion of the country. Moreover, once control techniques became more effective (in the 1980s) it was possible to restrict the layering so that fewer methods were used. Thus, the aerial spraying operations described by Hursey and Allsopp (1984) failed to achieve eradication over the treated area, but deployment of odour-baited targets in a relatively small area thereafter was sufficient to remove the remaining flies.

The important point arising from the present review is that knowledge of tsetse population dynamics and movement, and improved understanding of the mechanics of tsetse control, coupled with our ability to model these processes, make it possible to understand what happened in many past control campaigns and to deduce why they succeeded or failed. The hope, as discussed more fully in the following sections, is that this improved understanding of tsetse population dynamics should, in the future, allow us to suggest ways in which tsetse control and eradication can be carried out to best advantage.

3.7 Planning the use of the chosen methods

3.7.1 Usefulness of models

By and large, the present modelling of the successes and failures of classical control campaigns produces a good fit to the actual data in a wide range of conditions. The models and their basic parameters, as they now stand, should therefore produce passable predictions for the effects of classical tsetse control in most circumstances. Indeed, to avoid the worst types of past failures, the modelling should be routinely used in 'what-if' analyses to assist the selection of the most appropriate strategy and tactics for control.

There are some provisos, however. First, the modeller must have comprehensive maps of the abundance of tsetse in and around the proposed operational area before control begins, and the maps must be produced using the information from widespread sampling at a suitable intensity with appropriate sampling methods. Second, the predictions of the models should be regularly updated in the light of measured progress of the control campaign, so producing suggestions for improving cost-effectiveness of the fieldwork. Third, modelling of sampling efficacy would be helpful in designing the survey programme before, during and after the control effort.

3.7.2   Partnership between scientists and implementers

While modelling is desirable to enhance the cost-effectiveness of a control plan, it is not the kind of exercise that can be performed readily by the majority of control personnel, and certainly cannot be undertaken by the local communities that have been forced to take the initiative in control measures. Moreover, although not considered in this review, there appears to be a problem in getting the implementers of a control programme to abide by technical recommendations. For example, getting them to use the correct dose of odour and type of odour dispenser to employ with artificial baits, the right frequency of treating cattle with insecticide, and suitable survey procedures to monitor aerial spraying.

The implication is that there must be a close and continuing partnership between modellers, technologists and implementers, even when the technology seems as easy as treating cattle with insecticide or deploying simple cloth screens. The actual work involved in the use of bait technologies might be far simpler than flying and maintaining aerial spraying planes, but its planning and design are certainly not.

3.7.3   Research on models: universal problems

Certain modelling problems have appeared repeatedly, whatever the control method. For example, with the exception of a few campaigns, poor surveying before, during and after the control/eradication programme is the norm rather than the exception. In the context of PATTEC, it is essential that any given campaign be closely monitored, providing the data necessary for modelling aimed at refining the predictions of the likely outcome of future campaigns. Sophisticated survey technologies do exist, and must be applied rigorously.

3.7.4   The problem of movement and invasion

The major problem of all tsetse eradication campaigns is to stop the flies re-invading, even in island situations. The invasion problem is not confined to the re-occupation of a single treated block – the

flies can 'dodge' to and fro between blocks treated in different years, as in the Okavango Delta aerial spraying campaign.

The dodging problem can also occur between adjacent areas where a mosaic of control techniques is being used. A concrete example of this problem was evident around the southern edge of the Umfurudzi area in Zimbabwe, where an area of target use (the Safari Area) adjoined a ground spraying area. Target deployment in the Safari Area started in June 1996, at the same time as the ground spraying began. By the end of the year, when the ground spraying campaign had removed the flies in that block, there were still flies present in the Safari Area, and these were free to invade the ground sprayed block once the spray had been washed away by the rains. In the next few months, the targets removed all tsetse from the main body of the Safari Area, but the flies that had invaded the ground sprayed block could re-invade the first few kilometres of the Safari Area before being killed by the targets there. The problem was tackled promptly and effectively by extending the target placements into the adjacent parts of the ground sprayed block.

This problem would probably not have occurred if, as in the Rifa, target deployment had started in March, several months before the ground spraying began. Then both control measures would have produced eradication in their separate areas at about the same time, at the end of 1996.

3.7.5   Movement model

Since the movement problem is so important, designing a model of movement might be regarded as the most pressing concern. However, interpreting the consequences of movement demands more detailed knowledge of natural rates of birth and death and rates of imposed mortality. It is also important to recognise that the movement problem is not always exactly the same in all circum-stances. For example, with evenly placed targets, there is the problem of diffusion of the flies over a broad front. With treated cattle, which are usually not uniformly distributed between vegetation types, there is a more acute concern with the role of different vegetation as invasion routes. SIT raises the additional concern of how far the sterilised and un-sterilised flies can travel, and how well they can become infected with, and transmit, trypanosomiasis as they go.

While the modelling of movement has given a good fit to data for *G. m. morsitans* and *G. pallidipes*, and must be approximately right for other species, more information is needed for these other species, especially regarding their mean rates of daily displacement in various seasons and environmental situations. This is perhaps a matter of extending mark–recapture work to other species, as has been recently done with *G. austeni* and *G. brevipalpis* in South Africa (Kappmeier, in preparation). Far better information would be obtained if harmonic radar tracking, already developed in the UK, could be applied in the field in Africa.

3.8 The way forward: have we answered Harris and Ormerod?

If Harris were able to read this review he might gain some satisfaction from the progress that has been made toward identifying 'the most scientific and economical means by which to overcome the pest'. If the focus is to be on simplicity, convenience and low cost, then the use of insecticide-treated cattle should be the first choice in areas that have already been developed for agriculture and where there are reasonable numbers of cattle. This choice is particularly consistent with current political pressure on stakeholders to bear the main economic responsibility for the costs of treating the diseases of their own livestock. Given the potential importance of this approach, further research and development to improve its cost-efficiency would certainly be worthy of investment. The cost savings and improvements already achieved as a consequence of Vale's recent work (see Section 3.5), more than adequately justify the modest costs of that particular piece of research.

Where cattle densities are relatively low and there is a serious threat of invasion, as in northeast Zimbabwe, the simplest, cheapest and most effective solution may be to supplement insecticide-treated cattle with odour-baited targets. With this approach, socio-economic factors become significant, as target deployment and maintenance is unlikely to be paid for and carried out effectively by livestock owners.

The question then arises whether national governments and/or donors should pay for tsetse control initiatives that livestock owners cannot, or will not, pay for themselves. Stockowners are clearly willing to invest a great deal of money in trypanosomiasis control, as evidenced by widespread investment in trypanocides and an increasing use of insecticide applied to cattle. However, the models developed above indicate that, under many situations, the scale required for control operations to succeed is beyond the financial and organisational means of individuals or even co-operative groups of livestock owners. African governments therefore have a clear choice between abandoning livestock owners to a peasant existence, where disease control is limited by the amount individuals can afford to spend on drugs to keep their animals alive, and the alternative of once again investing centralised resources in tsetse control. Based on the arguments developed here, it is both necessary and desirable for national governments and/or donors to be involved in target-based tsetse control operations and the more extensive and costly alternatives such as ground/aerial spraying and especially SIT. These large-scale operations cannot possibly be funded and managed by livestock owners alone. In particular, the resources required by SIT for the rearing and sterilisation of enormous numbers of flies are far beyond the means of livestock-owning communities and probably of most African governments.

Aerial spraying is the obvious choice where tsetse control is deemed necessary over large, particularly flat areas, such as the Okavango Delta, or when a rapid reduction in the tsetse

population is required to combat an epidemic of human sleeping sickness. In the latter case particularly there is certainly a moral imperative for involvement at the national level.

The answer to Harris' question therefore lies only in a small part within the technical domain and in a much larger part with politicians inside and outside Africa. Political will and good governance are as closely linked to effective tsetse control as they are to every other problem of life in Africa today.

Ormerod's question similarly does not find a ready answer in the technical domain. We have certainly developed methods of tsetse control that do less direct harm than previously to the environment, but the essential part of his question still remains: is tsetse control a 'good thing'? Where there is a direct threat to human life or livestock the answer must clearly be in the affirmative. Given that some species of tsetse can, and often do, cause severe disease, the wider issue is whether all species of tsetse should be eradicated across the whole of Africa, as suggested in the original OAU Declaration (Appendix 1).

Authors frequently state that 'tsetse flies constitute a barrier/restraint to sustainable rural development'. But it is becoming apparent that they do not mean 'sustainable rural development' at all; they mean the 'development of herds of livestock'. This is most evident when cost: benefit analyses of tsetse control generally include only the effects of increased/improved livestock productivity on the benefit side. Due consideration is rarely given to the inevitable changes in land use and whether the consequences of such changes are likely to be found on the 'cost' or 'benefit' side of the balance sheet.

Land in Africa is valuable, not just for livestock production, but for arable crops, for tourism, for industry and as a reservoir of wildlife. It is beyond the scope of this review to fully explore Ormerod's query as to whether or not tsetse control is justifiable in all situations.

For too long tsetse workers have perpetrated the attitude that their job is to kill flies and that they should leave all other consequent issues to a higher authority. If only one message emerges from this review, I would like it to be that we have the technical ability and the knowledge required to eradicate tsetse throughout Africa, but this ability and knowledge carry with them a terrible responsibility to see that they are used wisely and to best long-term advantage for the continent.

Appendices

1. Declaration by OAU Heads of State, Lomé, July 2000

- DECLARES the year 2001 as the year of the control of tsetse fly, to mark the beginning of renewed efforts in the campaign for the eradication of tsetse flies in Africa.

- REQUESTS the Secretary-General to undertake all necessary consultations with a view to initiating the campaign from all possible partners and seeking their support and cooperation in the implementation of the Pan-African Tsetse and Trypanosomiasis Eradication Campaign.

- WELCOMES the establishment of the Pan-African SIT Forum as a mechanism through which sustainable area-wide tsetse eradication can be achieved and CALLS UPON the Secretary-General to provide support to the Pan African SIT Forum.

2. Statement by the PAAT community

This statement reflects the consensus reached at the 8th Meeting of the Panel of PAAT Advisory Group (PAG) Coordinators, 24–25 September, 2002, Nairobi, Kenya, which included members from the mandated international organisations (AU/IBAR, FAO, IAEA, WHO)[1], tsetse-affected countries, national agricultural research systems, international research institutes and relevant international institutes (ILRI, ICIPE, CIRAD, IFAD)[2].

Following the decision of African Heads of State and Government, the broad Tsetse and Trypanosomiasis (T&T) community as represented by the Programme Against African Trypanosomiasis (PAAT) is united in its resolve to reduce and ultimately eliminate the constraint of tsetse-transmitted trypanosomiasis in man and animals.

The PAAT community believes that progress towards the final objective is best achieved through concerted efforts towards intervention, in a sequential fashion, with the focus on those areas where the disease impact is most severe and where control provides the greatest benefits to human health, well-being and sustainable agriculture and rural development (SARD).

It is recognized that the scale and impact of trypanosomiasis in man and animals varies between African countries and progress towards the ultimate objective will also vary.

It is also recognized that in the case of human trypanosomiasis, disease management will continue to depend on disease surveillance, detection and treatment as the principal priority for the foreseeable future, with tsetse suppression as a complementary tool. Tsetse intervention strategies need to be developed as a component of longer-term human trypanosomiasis prevention measures.

In animal trypanosomiasis, tsetse intervention has a key role to play in the effective control and eventual elimination of the disease. A significant stage in achieving this objective is the creation of tsetse-free zones through the integration of appropriate and environmentally acceptable technologies, including SAT and SIT, as economically justified. In this context, the PAAT community supports the outcome and the associated joint press release resulting from the PAAT–PATTEC

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[1] AfricanUnion/International Bureau for Animal Resources (AU/IBAR), Food and Agriculture Organization of the United Nations, (FAO), International Atomic Energy Agency (IAEA) and World Health Organization (WHO).

[2] International Livestock Research Institute (ILRI), International Centre for Insect Physiology and Ecology (ICIPE), Centre de cooperation internationale en récherche agronomique pour le développement (CIRAD) and International Fund for Agricultural Development (IFAD).

harmonization workshop, Rome, 2–3 May 2002. The workshop identified criteria for selecting priority areas for joint international action. Governments, international and funding agencies are encouraged to also apply these criteria.

The PAAT community also recognizes the need to continue encouraging livestock producer-based practices against T&T wherever the diseases present themselves as a problem.

In order to more effectively combat the diseases, both in man and animals and their vectors, further concerted efforts are needed with a view to develop and implement joint field programmes for sleeping sickness and animal trypanosomiasis interventions.

In this regard, it is opportune to consider refinement of T&T intervention policies, and enhance synergies and complementarities among all concerned international agencies and governments.

3. Modelling tsetse population dynamics

Population growth in time and space

Williams *et al.* (1992) suggested that the Fisher equation:

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

provides a suitable model of spatio-temporal changes in tsetse populations. The model describes a population which grows logistically in time with growth rate r and carrying capacity K, and for which movement is approximated by a diffusion process.

The operator $\nabla^2 \int \delta^2/\delta x^2 + \delta^2/\delta y^2$, $\rho(x, t)$ defines the population density at position $\mathbf{x}$ in the x, y plane at time $t \geq 0$, and α is the diffusion coefficient. If a mortality rate (μ) is imposed, this results in new growth rates and carrying capacities, defined by:

$$r^* = r\,(1 - \mu/r) \tag{2}$$

$$K^* = K\,(1 - \mu/r) \tag{3}$$

and the Fisher equation is as above with r^* and K^* substituted for r and K respectively.

Except in special cases the Fisher equation cannot be solved analytically. Here, as previously (Hargrove, 2000), the population changes were approximated using a numerical procedure in an Excel spreadsheet.

Numerical solutions of the Fisher equation using a spreadsheet

A block X of land is defined by an $n \times n$ lattice where each cell $X(i,j)$ $(i = 1,n; j = 1,n)$ is equivalent to a 1×1 km piece of land. For any cell $X(i,j)$ located in the interior of the block let the population at time t be $N_t(i,j)$. One unit of time later this population will have grown, due to the birth and death processes only, according to the logistic equation such that:

$$N_{t+1}(i,j) = N_{t+1}(i,j) + N_t(i,j).r.(1 - (N_t(i,j)/K)) \tag{4}$$

There will also have been movement into and out of the cell – defined in the instantaneous case by the operator ∇. In the finite approximation the change in $X(i,j)$, due to movement only, is defined by:

$$N_{t+1}(i,j) = N_t(i,j) + \alpha C \tag{5}$$

where

$$C = N_t(i,j-1) + N_t(i-1,j) + N_t(i,j+1) + N_t(i+1,j) - 4.N_t(i,j)$$

This equation is simply explained in heuristic terms. For each interior cell, at each step, the number of flies immigrating from each of the four laterally adjacent cells is α multiplied by the number of flies in that cell. Equally, flies *emigrate* from a given cell into four adjacent cells; the total number leaving is thus $4 \times \alpha \times$ the number of flies present.

The total change is obtained by adding the components in Equations (4) and (5). For cells on the edge of the modelled area, Equation (5) is not defined. At each update, the value of each edge cell was set equal to the value of the cell immediately to its interior. For modelling purposes, Equations (4) and (5) were translated in Excel using a programme written in Visual Basic. Each cell was assigned values of α, μ, r and K appropriate to the tsetse population in that cell at a given time. It was recognised that growth rates and carrying capacities might vary with season and between different areas, but movement rates for a given species were assumed constant in this study.

For each cell it is necessary to define the additional mortality at the time of each step. The mortality depends on the particular situation being modelled and each case is dealt with separately in the main body of the text. Similarly, for each study, initial modelling was carried out in Excel. This provided a good visual indication of changes in fly numbers in time and space and ballpark estimates of the parameters. In each case, however, it was found that improvements to the fit could only be made by trial and error, and it was never clear whether any particular fit was in any way optimal. Accordingly, the simulation routine was also written in FORTRAN and linked to a non-linear least-squares optimisation routine. In this way it was possible to improve the model in a systematic fashion and to move towards an optimal, parsimonious model for the population changes. This process, described in detail by Hargrove and Williams (1998), is outlined here for reference purposes.

Optimised simulation

The minimisation routine used here, SEARCH (©Kenneth Lange, 1985–1991), is a FORTRAN 77 subprogram which requires the following input: i) a set of observed data, ii) a parametric model to describe the data, iii) a loss function to measure the difference between the observed and predicted data, iv) starting values for each parameter in the model.

Using the initial parameter values as inputs, the minimisation starts by producing a set of predicted population levels for each cell of the study area and for each time during the experiment. The present simulation used six-hour time steps. Since the observed data consisted of monthly mean trap catches, however, it was only necessary to store the predicted population levels every 120 time steps, and then only in the cells corresponding to the trap sites. Note that time steps of the order of one day led to problems because the degree of emigration from a given cell, per single step, could be big enough to cause the value of that cell to go negative and the programme to fail. This was particularly a problem when populations had been much reduced due to the control measure.

The difference between the observed and predicted data was used to calculate a value for a loss function, in this case the residual sums of squares (RSS). Each parameter for the model was then, in turn, perturbed slightly (positively then negatively, with all other parameters kept at their initial values) and the predicted data and RSS recalculated via simulation. This allowed the programme to identify the change in RSS, and its first and second derivatives, with respect to each parameter. The information was used to select a new set of parameter values which, when used again to recalculate the predicted data, resulted in a reduction in the loss function. This procedure was iterated automatically until no perturbation could be found which resulted in a decrease in the RSS.

Initially only one parameter was varied at a time, with the other parameters held constant at the starting values suggested by the Excel modelling. Once this procedure had been used to get improved estimates for all parameters, further runs were carried out where all of the important parameters were allowed to vary in the same run so that they were all optimised simultaneously. This procedure can, of course, only be used to improve models by comparing the best fits achieved with different formulations of that model; the onus is on the modeller to select appropriate candidate variables.

4. Nagupande selective game elimination: theory

Estimating the host population

The numbers of animals killed each month were taken from an unpublished report of the Tsetse and Trypanosomiasis Control Branch, Government of Zimbabwe. Given the approximately constant hunting effort, and that the area was fenced and hence (largely) closed to emigration and immigration, a removal method of population estimation akin to Zippin's (1958) method is indicated. Since the study lasted more than three years, however, there were clearly births and deaths from causes other than hunting.

It is possible to allow for these factors if we assume that the births and deaths occur at constant rates B and D respectively. If, in addition, animals were killed by the hunters at rate K then the number, $N(t)$, of animals remaining at time t is defined by:

$$\frac{dN(t)}{dt} = (B - D - K)N(t)$$

$$= (r - K)N(t)$$

with solution

$$N(t) = N(0)\exp((r - K)t) \tag{1}$$

where $r = B - D$ is the growth rate and $N(0)$ is the population just before hunting started. Here and elsewhere notation of the form $\exp(x)$ denotes the exponential function e^x.

Animals are killed at the rate of $KN(t)$ so in any month (i) the number killed is:

$$N_K(i) = \int_{i-1}^{i} KN(0)\exp((r - K)t)$$

$$= k_1[\exp(k_2(i - 1) - \exp(k_2 i)] \tag{2}$$

where $$k_1 = \frac{-KN(0)}{k_2} \text{ and } k_2 = r - K$$

Equation (2) was fitted to the data on numbers of animals killed per month using the non-linear least squares regression programme PAR in the BMDP statistical package (Dixon, 1992). If we assume a value for the growth rate (r), then K and $N(0)$ can be estimated from k_1 and k_2 and used to estimate the numbers of animals remaining in the Nagupande area at any time during the experiment. Thus:

$$\hat{K} = B - D - k_2 \tag{3}$$

and $$\hat{N(0)} = \frac{-k_1 k_2}{\hat{K}} \tag{4}$$

Estimating the increase in tsetse mortality due to host elimination

Bursell (1970b) estimated the relationship between host encounter and tsetse longevity but did not consider the problem of how host encounter was related to host density. The latter problem is addressed here as part of a more rigorous quantitative development.

In order that a fly feeds on a given day the following conditions must be met:

1) There must be a host in its vicinity.
2) The fly must 'attempt to feed'; we denote this by saying that the fly is 'active'.
3) Given that there are hosts present, and the fly is active, the fly must succeed in finding a host and feeding from it.

Accordingly, we define:

A Total area (km²), assumed closed to host immigration and emigration.

N Total hosts, assumed randomly distributed in area A.

P_k Probability there are k hosts resident, on a given day, in a given 'neighbourhood' (defined as 1 km² of country surrounding the fly).

i Number of days since the fly last fed.

η_i Probability fly is active on day i.

σ Conditional probability that a fly finds a host and feeds on a given day, given that it is the only host resident in a 1 km² neighbourhood containing the fly, and given that the fly is active.

f_i Probability that a fly succeeds in feeding on day i after its last blood-meal.

F_{NA} Probability that a fly succeeds in feeding at some point in a given hunger cycle, given a host density of N/A.

The complement of any of the above probabilities is denoted by a 'prime' suffix; *e. g.* $f_i' = 1 - f_i$.

S Maximum number of days fly can survive without feeding.

I Inter-larval period.

On any particular day, the probability (ρ) that a given animal is present in a given neighbourhood is $\rho = 1/A$. If, as in the Nagupande experiment, the area is large, then ρ is small. Assuming, for the moment, independence between the hosts in their movement the probability (P_k) that there are k animals present in this neighbourhood can then be defined approximately by a Poisson distribution with parameter $\lambda = \rho N$. That is:

$$P_k = \frac{\lambda^k}{k!} \exp(-\lambda) \tag{5}$$

Figure A1 shows how P_k changes with the total number of animals present in the study area. If there is only one host in the fly's neighbourhood the probability that the fly fails to feed from it on a given day, given that the fly is active, is σ'. If there are k hosts in the neighbourhood and we

assume independence among the hosts, then the fly fails to feed from any of them with probability $(\sigma')^k$. The probability that it *does* feed, given that there are k hosts present and given that the fly is active, is thus $1 - (\sigma')^k$.

With the above definitions, the probability (f_i) that a fly succeeds in feeding on day i of its hunger cycle is:

$$
\begin{aligned}
f_i &= \eta_i \sum_{k=1}^{\infty}(1-(\sigma')^k)P_k \\
&= \eta_i \exp(-\lambda)\sum_{k=1}^{\infty}(1-(\sigma')^k)\frac{\lambda^k}{k!} \\
&= \eta_i \exp(-\lambda)[\sum_{k=1}^{\infty}\frac{\lambda^k}{k!} - \sum_{k=1}^{\infty}\frac{(\sigma'\lambda)^k}{k!}] \\
&= \eta_i \exp(-\lambda)(\exp(\lambda) - \exp(\lambda\sigma')) \\
&= \eta_i (1 - \exp(-\lambda(1-\sigma'))) \\
&= \eta_i (1 - \exp(-\lambda\sigma))
\end{aligned}
$$

(6)

The probability (F'_{NA}) that, given a host density of N/A, the fly *fails to feed* on S consecutive days, and hence starves, is:

$$
\begin{aligned}
F'_{NA} &= \prod_{i=1}^{S}(1-f_i) \\
&= \prod_{i=1}^{I}(1- \eta_i(1 - \exp(-\lambda\sigma)))
\end{aligned}
$$

(7)

The probability that a fly starves is a function of its activity pattern (η_i), its search efficiency (σ), the host density (N/A) and the number (S) of days it can survive without feeding. Immediately after taking a blood-meal, tsetse show essentially zero feeding activity. Hargrove (1999a, 1999b) estimated that the feeding rate in *G. pallidipes* increases exponentially thereafter and, as a first approximation, one can infer from that work probabilities of activity of 0, 0.05, 0.3, 0.9, 1.0 and 1.0 respectively for the six days following a blood-meal.

With this selected activity pattern and with $S = 6$ days, the estimated starvation probability closely follows an exponential decline with host density, with the slope depending on the search efficiency (Fig. A2a). Alternatively, if the search efficiency is fixed, the slope depends on S (Fig. A2b). These relationships, not immediately evident from Equation (7), become clearer if we use the approximation suggested by Rogers (1984) and divide the hunger cycle into 'feeding' and 'non-feeding' phases.

Figure A1. **Probability of finding host animals**
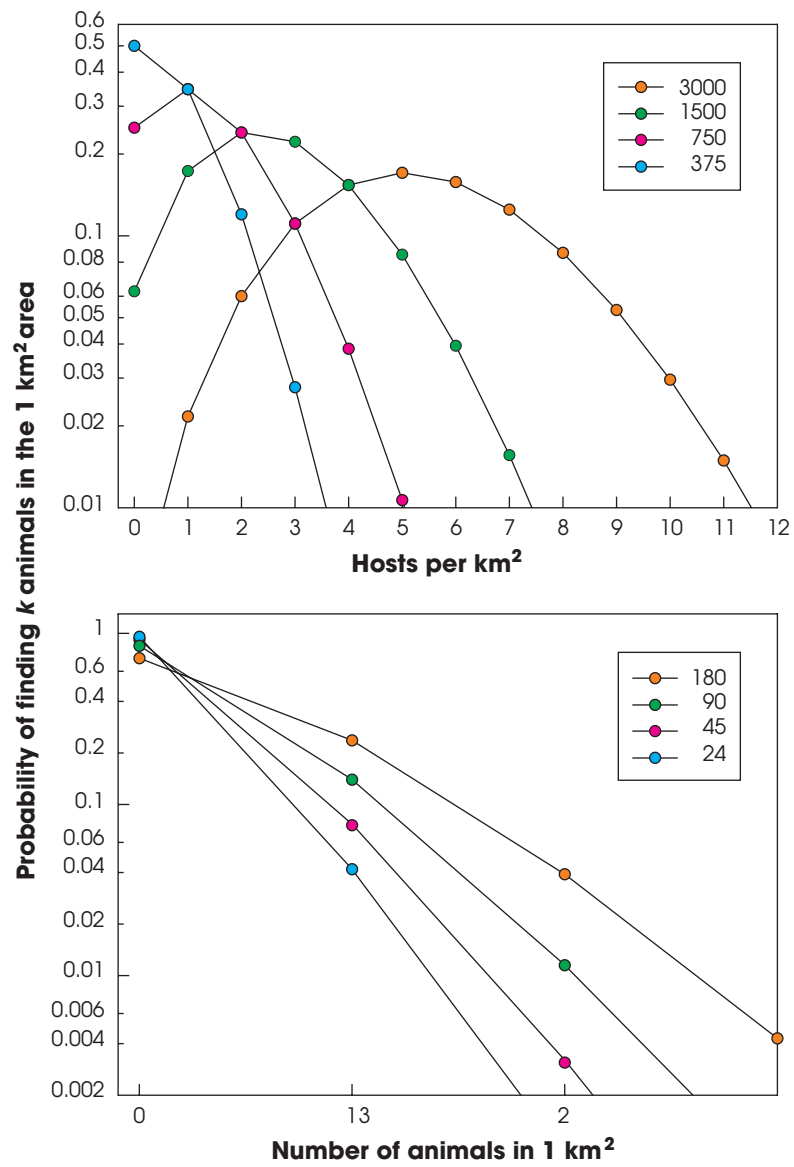
The probability of finding a given number of host animals in any 1 km² block of the Nagupande area, given the total number present in the whole 541 km² (as shown in the legend to each graph).

Figure A2.   **Starvation probability vs host density, search efficiency and days to starvation**
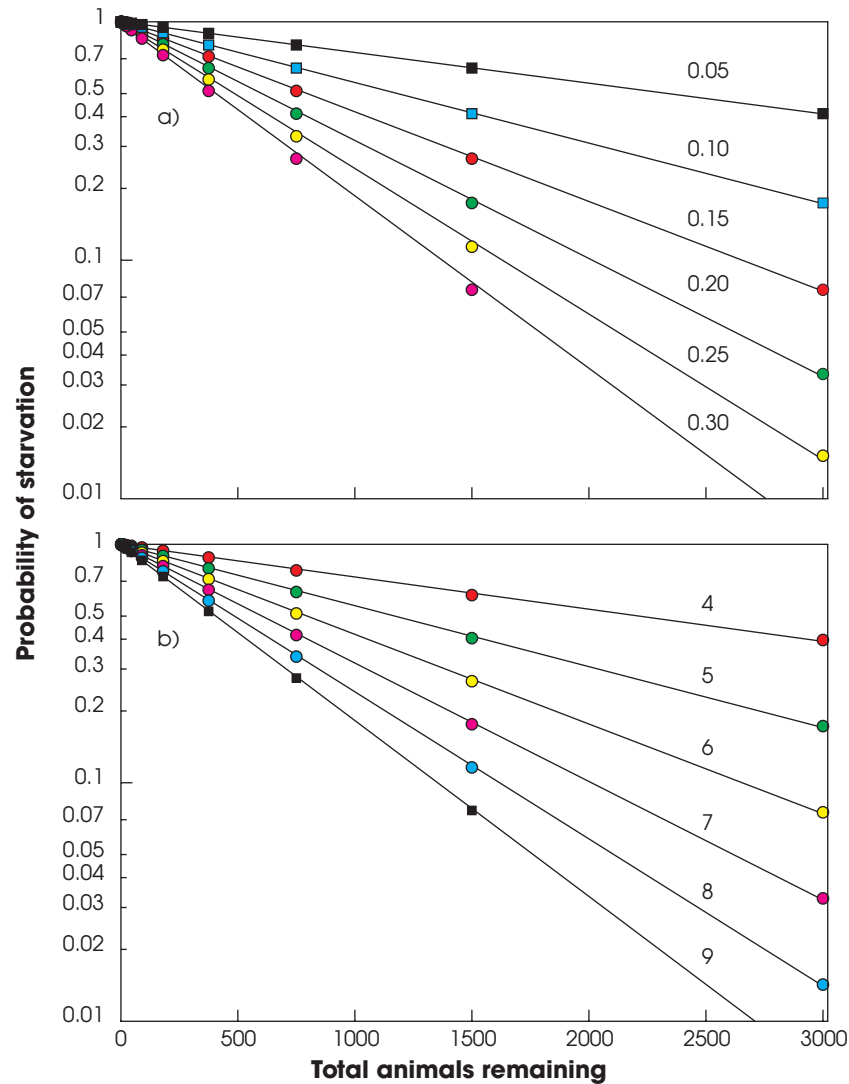
The probability that a tsetse fly starves, plotted as a function of the number of animals remaining in the Nagupande area and: a) the fly's search efficiency assuming that a fly can survive for six days without feeding before it starves; b) the number of days a fly can survive without feeding, assuming that its search efficiency is such that it has a 15% chance of finding a single host in 1 km^2 of habitat in one day.

Thus, if $\eta_i = 0$ for $i \leq s$ and $\eta_i = 1$ thereafter, Equation (3) simplifies to:

$$F'_{NA} = -\exp(-(S-s)\lambda\sigma)$$

$$= -\exp\left(-(S-s)\frac{\sigma}{A}N\right)$$

so that
$$\log_e(F'_{NA}) = -\frac{(S-s)}{A}\sigma N \tag{8}$$

Taking $s = 3$ in Equation (8) results in predicted starvation probabilities that are closely similar to those shown in Fig. A2a.

If, as in the Nagupande area, a constant hunting pressure is applied, the number of animals remaining at time t declines approximately exponentially such that:

$$N(t) = N(0)\exp((r-K)t) \tag{9}$$

where r is the population growth rate. Then, putting (9) into (8):

$$\log_e(F'_{NA}) = -\frac{(S-s)}{A}\sigma N(0)\exp((r-K)t) \tag{10}$$

For the purposes of modelling we need this expressed in terms of a daily mortality (μ). If Φ is the probability that a fly survives S days without starving then, using $\Phi = \exp(-\mu S)$,

$$\mu = -\frac{\log_e \Phi}{S} = \frac{-\log_e(1-F'_{NA})}{S} \tag{11}$$

Figure 5 in the main body of the text shows how starvation probability and daily mortality levels increase as host densities decrease.

Estimating the increase in tsetse abortions due to host elimination

The previous section provides estimates of the increase in mortality following a reduction in host density – and applies to male and female flies. Host density also affects the reproductive rate; at densities low enough to result in starvation, females will often be unable to feed sufficiently frequently to produce a viable offspring. Indeed, Hargrove (1999b) concluded that larval production, and not the avoidance of starvation, decides the pattern and frequency of feeding in female tsetse flies.

Thus, at 25°C, the inter-larval period (I) is $c.$ 9 days in the field (Hargrove, 1995). If the fly requires three meals to produce a larva in this time (Gaston and Randolph, 1993) then the fly must feed every three days on average. If four meals are required (Langley and Stafford, 1990) the interval period is reduced to $c.$ 2.5 days. Both estimates are shorter than the estimated times to starvation for field flies at similar temperatures (Vanderplank, 1947; Jackson, 1954; Glasgow, 1961).

Figure A3. **Estimated effect of mean temperature on inter-larval period and on the number of days a fly can survive without feeding**
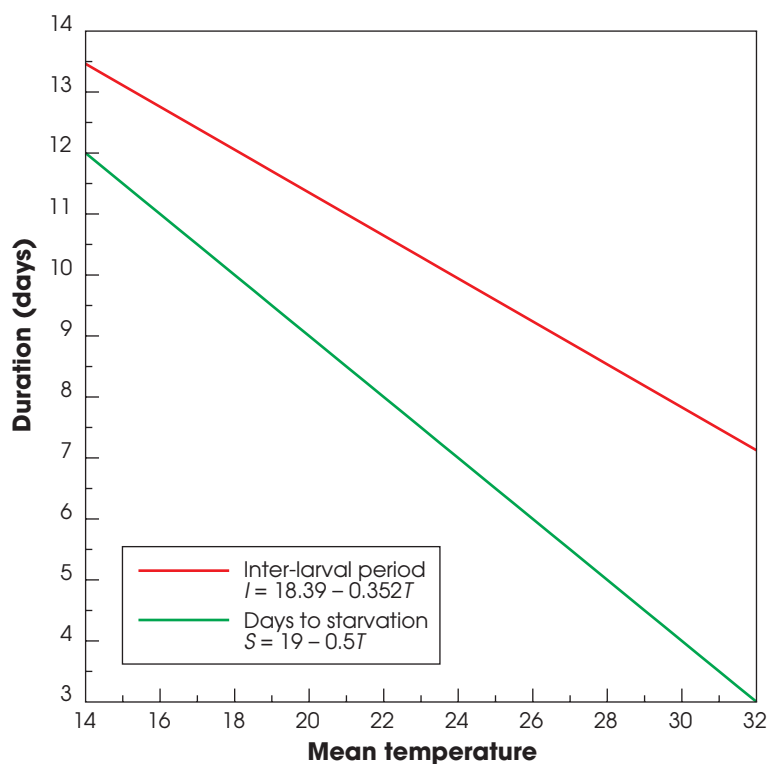
The only estimates for the effect of mean temperature on inter-larval period in the field are for *G. m. morsitans* and *G. pallidipes* in Zimbabwe (Hargrove, 1995). The given function:

$$I = 18.39 - 0.352T \qquad (12)$$

predicts that *I* declines linearly from 13.5 to 7 days as *T* increases from 14 to 32°C.

No quantitative relationship has been developed for the effect of *T* on *S* but, using the sources quoted above, it will be assumed here as a first approximation that *S* declines by 0.5 days per °C, from 12 to 3 days, as *T* increases from 14 to 32°C.

In estimating the effect of abortions on population growth, one needs to discount those flies which may abort but feed with such low frequency that they die anyway. From the graphs of *I* and *S* against *T* (Fig. A3) this is clearly the case for flies that take zero or one feed in a period of *I* days. Thus, if three meals are sufficient to produce a larva, then abortions will only occur in flies which have taken exactly two meals in *I* days.

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5. Estimation of extinction probabilities for tsetse populations

Growth in tsetse populations has been modelled hitherto as a deterministic process with population size considered as a continuous variable (Hargrove, 1988; Rogers, 1990; Williams *et al.*, 1990, 1992). For large, undisturbed populations this approach is adequate. When numbers are small, for instance following attempts to control or eradicate the fly, the approach is misleading, predicting as it does the existence of fractions of a fly and an infinite time until a population declines to zero.

In these circumstances a stochastic model is preferable and the simple life history of the tsetse fly makes it amenable to modelling as a branching process. This approach, followed in the present study, allows the estimation of realistic probabilities of extinction and expected time to eradication, plus the variances of these estimates, none of which have been estimated previously using the deterministic approach.

Methods

Tsetse life history

An adult tsetse fly emerges from its puparial case and, after less than an hour, its wings have hardened and it is ready to fly. Both sexes feed exclusively on blood and the first two or three meals are used largely to build the thoracic flight muscles. By this time, after six to eight days, the female fly in normal wild populations has almost always been inseminated.

The female ovulates for the first time about six to eight days after eclosion. Thereafter, at periods of around 7–12 days, depending largely on temperature, the female deposits a single larva, complete with all of the energy and raw material required to form the adult fly. The larva burrows rapidly into the substrate where it has been deposited, forms the hard puparial case around itself and emerges as the adult of the next generation in anything from 25–100 days, again depending on temperature. There is a slight bias in the gender of the pupae produced in the laboratory. The exact situation is not known in the field and we assume here that male and female pupae are produced in equal numbers.

In general, the female mates only once; the sperm from a single male is stored by the female and used to fertilise eggs throughout her life. This fact is of practical importance in terms of efforts to eradicate tsetse populations. If sterile males released into a population mate with virgin females, these females will not produce offspring and this effect is considered in the following model.

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Definitions

Φ	Daily survival probability for adult females
φ	Daily survival probability for immature female pupae
u	Days between female adult eclosion and first ovulation
η	Probability that the female is inseminated
I	Inter-larval period (days)
T	Pupal duration
$p_{n,k}$	Probability that a female tsetse dies between pregnancy n and $n+1$ and produces k 'surviving daughters', by which we mean daughters which survive until at least the first day of adult life
X_N	Size of the Nth generation, assuming $X_0 = 1$
$G_n(s)$	Probability generating function for the X_n

Results

Extinction probability

With the definitions given in the methods section we consider a population where the initial generation consists of one female fly. We assume that the probability generating function for the next generation is:

$$G_1(s) = G(s) = \sum_{k=0}^{\infty} p_k s^k \tag{1}$$

where p_k is the probability that the female produces k surviving daughters.

The probability $(p_{n,k})$ that a female tsetse dies between pregnancy n and $n+1$ and produces k surviving daughters is given by:

$$p_{n,k} = \eta \Phi^{u+nI} (1 - \Phi^I) {}_nC_k (0.5)^n \varphi^{kT} (1 + (1 - \varphi^T))^{n-k} \qquad n>0;\ 1{\leq}k{\leq}n \tag{2}$$

where ${}_nC_k$ denotes the binomial coefficient $\dfrac{n!}{(n-k)!k!}$. For $n = 1$ and $k = 1$ (i.e. the female survives one pregnancy and produces one surviving daughter) we have:

$$p_{1,1} = \eta \Phi^{u+I} (0.5) \varphi^T (1 - \Phi^I) \tag{3}$$

To see how this arises, note that the female is fertilised with probability η, survives with probability Φ^{u+I} until she produces her first pupa, which is female with probability 0.5 and survives with probability φ^T. The mother then dies during the next pregnancy with probability $(1 - \Phi^I)$.

The general result can be shown by induction. Heuristically it may be justified as follows. A female tsetse is fertilised and survives until pregnancy n, then dies before pregnancy $n+1$, with probability $\eta\Phi^{u+nI}(1-\Phi^I)$. During that time she can produce k surviving offspring in $_nC_k$ ways and each of the n pupae produced has probability 0.5 of being female. Each of the female pupae has probability φ^T of surviving the pupal period, so that k survive with probability φ^{kT}. Of the remaining $n-k$ pupae, the males fail to produce a surviving daughter (of course) with probability 1, and the females fail with probability $1-\varphi^T$. The probability for this group is thus $(1+(1-\varphi^T))^{n-k}$.

To find the probability (p_k) that a female produces exactly k surviving daughters during her life, regardless of the number of pregnancies she survives, we sum $p_{n,k}$ over all n and get:

$$p_k = \frac{\eta\Phi^{u+kI}(1-\Phi^I)(0.5)^k\varphi^{kT}}{(1-0.5\Phi^I(1+(1-\varphi^T)))^{k+1}} \qquad \text{for } k>0 \qquad (4)$$

Summing over all $k>0$ gives the probability that at least one surviving female is produced, and the complement of this probability is the probability that none is produced.

$$p_0 = 1 - \frac{\eta\Phi^{u+I}(0.5)\varphi^T}{1-0.5\Phi^I(1+(1-\varphi^T))} \qquad (5)$$

The mth moment (M_m) of p_k is found from:

$$M_m = \sum_{k=1}^{\infty} k^m p_k \qquad (6)$$

The first and second moments are:

$$M_1 = \frac{0.5\eta\Phi^{u+I}\varphi^T}{1-\Phi^I} \qquad (7)$$

and

$$M_2 = \frac{0.5\eta\Phi^{u+I}\varphi^T(1-\Phi^I(1-\varphi^T))}{(1-\Phi^I)^2} \qquad (8)$$

The first moment gives the mean, or expected, number $(m = M_1)$ of surviving daughters a female produces in her lifetime. The variance (σ) is estimated by $\sigma = M_2 - (M_1)^2$.
The expected number $E(X_n)$ in generation n is:

$$E(X_n) = m^n \qquad (9)$$

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with variance:

$$\sigma^2 m^{n-1} \frac{1-m^n}{1-m^I} \qquad m \neq 1$$

$$\mathrm{Var}\,(X_n) \;=\;$$

$$\sigma^2 n \qquad m = 1 \qquad (10)$$

Using Equation (4) to evaluate the probability generating function $G(s)$ we have:

$$G(s) = \sum_{k=0}^{\infty} p_k s^k \qquad (11)$$

$$= p_0 + \sum_{k=1}^{\infty} p_k s^k$$

$$= p_0 + \eta \Phi^u (1-\Phi^I) \sum_{k=1}^{\infty} \frac{(0.5)^k \varphi^{kT} \Phi^{kI} s^k}{(1-\Phi^I + 0.5\Phi^I \varphi^T)^{k+1}}$$

$$= p_0 + \frac{\eta \Phi^u (1-\Phi^I)}{1-\Phi^I + 0.5\Phi^I \varphi^T} \sum_{k=1}^{\infty} \left[\frac{(0.5)\Phi^I \varphi^T s}{1-\Phi^I + 0.5\Phi^I \varphi^T} \right]^k$$

$$= p_0 + \frac{\eta M \Phi^u}{M+B} \sum_{k=1}^{\infty} \left[\frac{Bs}{M+B} \right]^k$$

where $M = 1 - \Phi^I$ and $B = 0.5\Phi^I \varphi^T$

$$= p_0 + \frac{\eta M \Phi^u}{M+B} \left[\frac{\dfrac{Bs}{M+B}}{1 - \dfrac{Bs}{M+B}} \right]$$

$$= p_0 + \frac{\eta M \Phi^u}{M+B} \left[\frac{Bs}{M+B-Bs} \right]$$

And, since $p_0 = 1 - \dfrac{\eta 0.5 \Phi^u \Phi^I \varphi^T}{1 - \Phi^I + 0.5\,\Phi^I \varphi^T} = 1 - \dfrac{\eta B \Phi^u}{M+B}$

$$G(s) = 1 - \frac{\eta B \Phi^u}{M+B} + \frac{\eta M \Phi^u}{M+B} \left[\frac{Bs}{M+B-Bs} \right]$$

$$= \frac{(M+B)(M+B-Bs)-\eta B\Phi^u(M+B-Bs) + \eta MB\Phi^u s}{(M+B)\ (M+B-Bs)}$$

$$= \frac{(M+B)(M+B)-(M+B)Bs - (M+B)\eta B\Phi^u + (M+B)\eta B\Phi^u s}{(M+B)(M+B-Bs)}$$

$$= \frac{(M+B)-Bs -\eta B\Phi^u+\eta B\Phi^u s}{(M+B-Bs)}$$

$$= \frac{M+B(1-\eta\Phi^u)(1-s)}{(M+B(1-s))}$$

$$G(s) = \frac{M + B\gamma(1-s)}{M + B(1-s)} \tag{12}$$

where $\gamma= 1-\eta\Phi^u$

To find the extinction probability we need to solve:

$$G(s) = s \tag{13}$$

which is a quadratic in s with solution:

$$s = \frac{B\gamma + M + B \pm \sqrt{(B\gamma + M + B)^2 - 4B(M + B\gamma)}}{2B} \tag{14}$$

The extinction probability is the smaller of the two roots of Equation (14). This gives the probability that the line emanating from a single female fly goes extinct. If generation zero consists of N flies, all subject to the same survival probabilities and reproductive rates, then the whole population goes extinct with probability s^N. Figure 33 in the main body of the text shows the relationship between extinction probability and female mortality and Fig. 34 shows this relationship for varying probabilities that females are inseminated.

Time to extinction

For $m < 1$ the population goes extinct with probability 1. Suppose this occurs at generation T. Set t_K = probability $(T \leq K)$ and $t_0 = 0$. Then:

$$t_k = G(t_{k-1}) \tag{15}$$

$$E(T) = \sum_{k=0}^{\infty} (1-t_k) \tag{16}$$

and
$$E(T^2) = \sum_{k=0}^{\infty} (2k+1)(1-t_k) \tag{17}$$

The t_k can be computed by functional iteration. Thus, using Equation (15),

$$t_1 = G(t_0) = G(0) = \frac{M+B\gamma}{M+B} \tag{18}$$

$$t_2 = G(t_1) = G\left(\frac{M+B\gamma}{M+B}\right) = \frac{M+B\gamma\left(1-\dfrac{M+B\gamma}{M+B}\right)}{M+M\left(1-\dfrac{M+B\gamma}{M+B}\right)} \tag{19}$$

and so on. This process can easily be carried out numerically, using a spreadsheet for example, and for a sufficiently large number of iterations, this gives a good approximation to $E(t)$.

6. Probability of capturing a tsetse fly in a population that is close to extinction
The relationship between trap efficiency, catch effort and capture probability

Tsetse flies are sampled using various systems such as mechanical and electrical devices and artificial refuges (Vale, 1971, 1974a, 1974b) as well as the classical techniques of man or ox fly-rounds and hand-net catches from stationary baits. For simplicity, all of these sampling systems are referred to below as 'traps'.

We define:

A	Area sampled (km²), assumed closed to tsetse immigration and emigration
N	Total surviving tsetse, assumed randomly distributed in A
P_k	Probability there are k tsetse, on a given day, in a given 1 km² square of A
σ	Trap efficiency; *i.e.* the conditional probability that a fly is caught by a given trap, given that there is only one trap present in the 1 km² square containing the fly, and given that the fly is active
S	Number of traps present in all of A
t	Number of days for which trap is operated
$C(k,S,\sigma,t)$	Probability that *at least* one fly is captured – as a function of the number of flies in the given square, the number of traps used, the efficiency of each trap and the number of days on which sampling was carried out

The complement of any probability defined above is denoted by a 'prime' suffix; *e. g.* $\sigma' = 1 - \sigma$.

For a fly to be caught on a given day the following conditions must be met:

1) There must be a trap operative in its vicinity.
2) The fly must be active.
3) Given that there is a trap present, and the fly is active, the fly must succeed in finding it and be captured by it.

On any particular day, the probability (ρ) that a given fly, among the N survivors, is present in any given 1 km² square is $r = 1/A$. If the area treated (A) is large, then ρ is small; e.g. if $A > 1000$ km² then $\rho < 0.001$. If, too, N is small and the surviving flies are distributed randomly within A, then the probability (P_k) that there are k flies present in a given square is defined approximately by a Poisson distribution with parameter $\lambda = \rho N$. That is:

$$P_k = \frac{\lambda^k}{k!} \exp(-\lambda) \tag{1}$$

for a given square. The probability that there is one fly present in the square and that one trap fails to catch it in one day is thus $\lambda \exp(-\lambda)\sigma'$.

To find the probability $(C'(N,1,\sigma,1) = C'(k = N, S = 1, \sigma, t = 1))$ that a single trap fails to catch *any* of the surviving N flies on a given single day we sum over the probabilities that there are k flies present for $k = 1, \infty$.

$$
\begin{aligned}
C'(N,1,\sigma,1) &= \sum_{k=1}^{\infty} (\sigma')^k P_k \\
&= \exp(-\lambda) \sum_{k=1}^{\infty} (\sigma')^k \frac{\lambda^k}{k!} \\
&= \exp(-\lambda) \sum_{k=1}^{\infty} \frac{(\sigma'\lambda)^k}{k!} \\
&= \exp(-\lambda)\exp(\lambda\sigma') \\
&= \exp(-\lambda(1-\sigma')) \\
&= \exp(-\lambda\sigma)
\end{aligned}
\tag{2}
$$

If there are S traps in the square, run for t days, and if S is sufficiently small that the traps act independently of each other, then the probability $(C'(N,S,\sigma,t))$ that *none* of the traps catches any of the N surviving flies is:

$$
\begin{aligned}
C'(N,S,\sigma,t) &= \exp(-St\sigma\lambda) \\
&= \exp(-\frac{St\sigma N}{A})
\end{aligned}
\tag{3}
$$

assuming, for simplicity, that the capture probability is identical for all flies and is independent of time t. Putting $X = StN\sigma/A$ and expanding (3) as a Taylor series we have:

$$
\begin{aligned}
C'(N,S,\sigma,t) &= 1 - X + \frac{X^2}{2} + \ldots\ldots \\
&\approx 1 - X
\end{aligned}
\tag{4}
$$

when the value of the exponent is small. The approximation to the probability that we capture *at least* one fly is the complement of the probability in (4):

$$C(N,S,\sigma,t) \approx X = \frac{StN\sigma}{A} \tag{5}$$

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The approximation is intuitively reasonable. It increases linearly with the number of traps used, the period over which they are used, the efficiency of each trap and the number of surviving flies present; and it decreases as the area sampled increases.

As a simple example, if there are 10 flies surviving in 10,000 km² and we run 10 traps each for 100 days and if $\sigma = 0.01$ then $C(N,S,t) \approx 0.01$. The 'exact' value using (3) is 0.00995, differing only by 0.5% from the approximation. If there were 100 survivors in the same area and if each trap was 90% efficient the approximation is no longer valid, giving a value of 0.9, while (3) gives a value of only 0.59.

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About the author

John Hargrove was born in 1946, in Scotland, of English parents. At the age of three he was taken to Southern Rhodesia and was schooled in Matabeleland, where he developed a lasting love for the African bush.

In 1965 he returned to the UK to Pembroke College, Oxford, to read Zoology, with the initial intention of following a career in ornithology — but he was enticed away from this line by the intellectually more exciting advances in genetics, neuromuscular physiology and biophysics.

Returning to Rhodesia in 1969 he came under the tutelage of Professor Einar Bursell, who found funds for him to do a PhD on Tsetse Physiology, which he completed in 1973. He then joined the government services as a research worker under Dr Glyn Vale at Rekomitjie Research Station in the Zambezi Valley.

The research at Rekomitjie was always well funded and, with large numbers of able field assistants, it was possible to carry out the sorts of experiments that could not be contemplated anywhere else in the world. The basic thrust of the work was aimed at developing bait systems for tsetse control. In pursuit of this end John developed a variety of new traps, including one that captured more than 11,000 tsetse in a three-hour period, which is claimed to be a record. John also did the first experiment indicating that acetone was an attractant for *G. m. morsitans* and *G. pallidipes.*

Over time, however, John's interests strayed more in the direction of population dynamics and fly movement. Glyn took over the practical side of the further development of odour-baited trap and target technology and generously allowed John the luxury of indulging his more esoteric interests — in the knowledge, however, that these would be important in the long term in predicting the outcome of tsetse control operations.

John realised that his field of interest often involved mathematics and decided to further his schoolboy passion for that subject in the United States. In 1978 he departed for the University of California, Los Angeles and spent three years in the Biomathematics Department, returning to recently independent Zimbabwe at the end of 1981 with a Masters.

On John's return, Glyn immediately involved him in the running of the first field trial of odour-baited traps and targets, on Antelope Island, Lake Kariba. In particular he was tasked with the analysis of the vast dataset emanating from the detailed mark—release—recapture exercise carried out on the island. The practical and theoretical implications of this work continue to develop to the present day. Other experimental work in the field of fly development, movement and population dynamics followed over the next decade.

John left the government service in 1986 to take up a post under Dr Peter Langley with the Tsetse Research Laboratory, Langford, UK. He continued, however, to be based in the government offices in Zimbabwe and to work at Rekomitjie, developing the use of juvenile hormone analogues as agents for tsetse control. Whereas these had never been used on a large scale, field experiments at Rekomitjie showed that they could be used either with traps or with targets to effect major reductions in the birth rate.

As major funding for tsetse research dried up in the late 1990s it became apparent that a change of course was necessary. The simultaneous deterioration in the AIDS situation in Zimbabwe provided a ready avenue for further work and John has since been employed as a statistician in that field. Nonetheless, he maintains close communication with the tsetse world, carries out consultancy work in the field and acts as an adviser to the Zimbabwe Government tsetse research wing. He continues to publish papers on tsetse and estimates that he has sufficient unanalysed data to keep him busy well into his dotage.

John Hargrove and his wife Beverley have two children and live in Harare.