Insecticide-treated cattle for controlling tsetse flies (Diptera: Glossinidae): some questions answered, many posed

G.A. Vale[1]*, G. Mutika[2] and D.F. Lovemore[1]

[1]Regional Tsetse and Trypanosomosis Control Programme, PO Box A560, Avondale, Harare, Zimbabwe: [2]Tsetse and Trypanosomosis Control Branch, Department of Veterinary Services, PO Box CY52, Zimbabwe

Abstract

Bioassays in Zimbabwe with wild-caught *Glossina pallidipes* Austen and *G. morsitans morsitans* Westwood showed that formulations of deltamethrin (Decatix, SpotOn and an experimental variant of SpotOn), alphacypermethrin (Renegade) and cyfluthrin (Cylence) applied to oxen at the manufacturers' recommended doses gave knockdowns above 50% for 5–24 days in hot months and 24–55 days at cooler seasons. Within these periods, the average knockdowns were 77–86% with deltamethrin, 74% with alphacypermethrin and 59% with cyfluthrin. None of the insecticides affected the numbers of tsetse attracted to oxen from a distance, the proportion of tsetse that engorged, and the alighting responses on cloth screens. In the hot season most tsetse engorged on the belly. At other times the front legs were preferred, especially in the wet season and for a few months after. Chemical assays indicated that insecticide persisted at greatest concentration on the backs of oxen and least on the legs. Modelling the experimental data suggested that 4–21 annual applications of insecticide in areas >1000 km^2 would give good control at least 10 km from the invasion source if the treated cattle contributed at least 50% of tsetse diet. No treatment regime under any diet conditions would give good control near an invasion front. Insecticide at concentrations up to 0.15 ppm occurred in dung from treated oxen for up 12 days post-treatment. Dead beetles occurred in and near fresh dung.

Introduction

The ability to control tsetse flies (*Glossina* spp.) (Diptera: Glossinidae) by applying deltamethrin to cattle was demonstrated in southern Africa in the mid-1980s (Thomson, 1987; Thomson *et al*., 1991). However, the technique seemed of limited use then because government agencies in the region intended to remove tsetse from vast invasion sources where cattle were absent and could not be introduced. Hence, most research in the region continued to be directed towards artificial baits (Vale, 1993a), with much of the interest in cattle treatments passing to other parts of Africa (Bauer *et al*., 1992; Fox *et al*., 1993; Leak *et al*., 1995). More recently, the strategy in southern Africa has moved towards local control of tsetse in farming districts, leaving invasion sources largely untouched and encouraging the farmers themselves to fund and perform the work. The strategic switch makes the insecticide-treatment of cattle the most appealing method of control, and demands that our understanding of the use of cattle catches up quickly with our knowledge about artificial baits.

Many questions relating to cattle treatment need fuller answers. For example, what are the suitable insecticides and treatment strategies? Does repellence modify the performance of the insecticides? What are the effects on creatures other than tsetse? Perhaps most important of all: why are cattle treatments highly successful against tsetse in some places and virtually ineffective in others (Baylis & Stevenson, 1998)? The present article uses a combination of field work and modelling that addresses these questions and raises others.

*Address for correspondence: 93 The Chase, Mount Pleasant, Harare, Zimbabwe
E-mail: gvale@healthnet.zw

Experimental work

General methods

Bioassays and behavioural studies were performed at Rekomitjie Research Station in the Zambezi Valley of Zimbabwe where *Glossina pallidipes* Austen and *G. morsitans morsitans* Westwood occur. Test cattle were brown or black oxen with a high proportion of indigenous blood, and weighed an average of 420 kg (range 345–561).

Toxicity and persistence

Each of the test oxen was treated separately with one of the following proprietary insecticides, at doses recommended by the manufacturers.

1. Decatix – a 50 g l^{-1} suspension concentrate of deltamethrin that was diluted with water to a concentration of 0.05 g of active ingredient (ai) per litre. Fifteen litres of the diluted preparation were applied by a pressurized knapsack sprayer to the whole surface of the ox, to simulate dipping (approximate dose of 0.04 g of ai per 100 kg of body weight).
2. SpotOn – a 10 g l^{-1} pour-on formulation of deltamethrin applied at the rate of 0.1 ml of formulation per kilogram of body weight (0.10 g of ai per 100 kg).
3. Experimental variant of SpotOn (called SpotOn-E, henceforth) – as for the regular SpotOn (above), but formulated with a cheaper oil, allowing the estimated supply cost of the formulated insecticide to be reduced by a quarter.
4. Renegade – a 15 g l^{-1} pour-formulation of alphacypermethrin, applied at 0.15 ml kg^{-1} (0.23 g of ai per 100 kg).
5. Cylence – a 10 g l^{-1} pour-on formulation of cyfluthrin, applied at 0.15 ml kg^{-1} (0.15 g of ai per 100 kg).

Decatix, SpotOn and SpotOn-E were supplied by Cooper Ltd. Renegade and Cylence were supplied by Fort Dodge Ltd and Bayer Ltd, respectively. The pour-ons were deposited in lines extending from the base of the skull to the root of the tail, about 5 cm either side of the spine. All treatments were applied at about 0900 h. From about 1500 h on the day of treatment, (day 0) and on subsequent days, each ox was sited separately in woodland within 1 km of Rekomitjie. Tsetse that engorged on the ox were caught by hand-nets and transferred to glass tubes, 2.5 cm in diameter and 7.5 cm long, with netting sealing one end and a cork at the other. To minimize contamination, new hand-nets were used each day. Tubes at the site were shaded by storage in a polystyrene box. Catching ceased when 30 flies had been caught, or at dusk, whichever was the sooner. The tubed flies were then taken to the insectary and held at 23–25°C and 60–70% relative humidity for 72 h. Flies which were unable to stand or fly when disturbed were classed as knocked-down – a condition assumed to cause death under field conditions (Laveissiere *et al.*, 1985). The percentage of knockdowns was scored at its peak, i.e. 2 h after entering the insectary and about 3.5 h after exposure to insecticide. Mortality, covering dead and moribund flies, was scored at 72 h. When not involved in catching, each ox was stationed in a separate pen that was exposed to wind and rain, but with 50% shade to simulate the shade of the open woodland in which the cattle would normally have grazed.

Four main trials were performed between April 9, 1997 and August 26, 1998 and involved six oxen at any one time – an untreated control and one for each of the five insecticides. Each of these trials lasted 10–17 weeks and each involved a distinctive allocation of insecticides, so that during the whole group of trials each insecticide was used on four different oxen. In each trial there was an initial treatment with insecticide, followed by one or two re-treatments when the knockdown produced by all treated oxen had declined consistently below 50%. The next trial started 3–15 weeks later when bioassays, sometimes supplemented by chemical assays of hair (see below), had confirmed that the insecticide had gone. It was impossible to give each insecticide a turn on each individual ox because some of the oxen died (of causes unrelated to insecticide) and were replaced with others. A supplementary trial involved only three oxen, two of which were treated with SpotOn on November 10, 1997, and one of which was a control.

Behavioural studies

Studies of the parts of the oxen on which tsetse engorged were made during the bioassays, by recording the capture positions of most (87%) of the flies taken from the treated and non-treated oxen. The positions were classified as: front legs, hind legs, belly (trunk below centre of flank) or back (including upper flank, neck and head). In addition, two other behavioural studies were performed separately from the bioassays.

The first study investigated the extent to which insecticide altered the numbers of flies attracted to an ox and the proportion that engorged. From 1500 h to 1800 h on various days after insecticide application the oxen were placed individually in a pen, 3 m in diameter, within an incomplete ring of electrocuting nets (Vale, 1977), consisting of three individual nets, 1.5 m square, placed 2.5 m from the centre of the pen. The total catch of the inside and outside faces of the nets was taken as an index of the number of flies attracted to the ox, and the proportion of recently engorged flies in the total catch was adopted as an index of the proportion of flies that fed.

The second study elucidated whether insecticides affected the numbers of tsetse alighting on baits. This work required the use of electrocuting grids (Vale, 1974) on or immediately beside the baits and so the baits could not be oxen. Hence, an artificial bait was employed. This consisted of a 1 × 1 m screen of black cotton cloth with a surface grid to catch alighting flies. The screen was used with and without insecticide and with and without an electrocuting net, 1 m tall and 0.5 m wide, on each side, to catch tsetse flying near the screen (Vale, 1993b). All screens were operated from 1430 h to 1800 h and used with odour attractants consisting of 150 mg h^{-1} of butanone and 1 mg h^{-1} of a 1:4:8 mixture of 3-*n*-propyl phenol, 1-octen-3-ol and 4-methyl phenol (Torr *et al.*, 1997). For the pour-on treatments the screen was given the dose for an animal of 100 kg, distributed evenly over the two sides of the screen. For the Decatix treatment the spray was applied to run-off. All insecticide applications were made once, a few hours before the first catches. The insecticide deposits were exposed to the sun, but not to rain. No insecticide was put on the electrocuting nets.

Although the ring of nets is a proven means of detecting the inhibition of feeding (Vale, 1977), it was not clear how readily the screen technique could detect the inhibition of alighting responses. Hence, the screen was used with and without a known repellent, 2-methoxy phenol (Vale *et al.*,

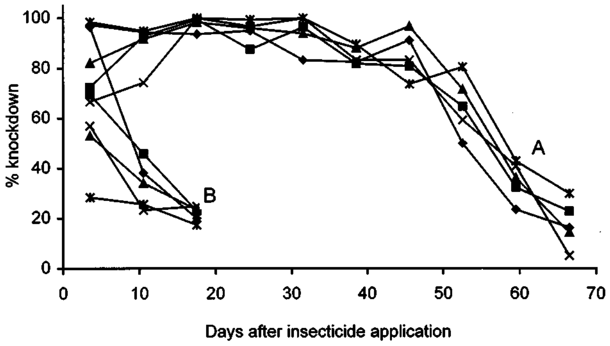

Fig. 1. Weekly averages of the knockdown of tsetse produced by each insecticide (◆, Decatix; ■, SpotOn; ▲, SpotOn-E; ×, Renegrade; *, Cyclence) in the periods when the apparent persistence of insecticide was longest (A, second treatment of first trial) and shortest (B, second treatment of third trial).

1988b), released at 1 mg h^{-1} beside the attractants. The tests of 2-methoxy phenol and each insecticide were made separately, with the four treatments, i.e. +/- nets and +/- chemical, arranged in one or a series of Latin squares of treatments × sites × periods. In the study with phenol, each period was a day, but with the insecticides each period was 3–5 days because the work was performed at seasons when the one-day catch was too small for analysis.

In all behaviour studies the catches of tabanids (mostly Tabaninae) and muscoids (mostly Stomoxyinae) were also recorded. Catches were transformed to log (n + 1) for analysis of variance and were detransformed for reporting.

Chemical assays

A dung pat was homogenized in the field prior to taking samples for chemical assays. Hair samples were taken from various parts of the body, with some pooling, so that the assays referred to: (i) legs, consisting of the front and hind legs, 10–30 cm above the hoof; (ii) flank, comprising two points midway up the flank on each of the left and right sides; and (iii) back, i.e. four points along the spine. Assays were performed by the Tobacco Research Board of Zimbabwe and the Natural Resources Institute, UK. The samples were macerated and extracted to give a hexane solution that was injected at 270°C into a GLC column fitted with an electron capture detector. Reference standards were prepared from insecticides of analytical grade.

Experiments and results

Test insects

A total of 51,896 tsetse were used in the bioassays of the main and supplementary trials. This total consisted of 64.9% female *G. pallidipes*, 32.4% male *G. pallidipes*, 2.3% female *G. m. morsitans* and 0.4% male *G. m. morsitans*, so that the average number of tsetse for each of the 2297 ox/days was 22.6. Of the total tsetse, 12,582 were controls which showed average knockdowns and mortalities of 2.8% and 3.3% respectively. Since these percentages were low, no control correction was made to the knockdowns and mortalities associated with treatment. Female *G. pallidipes* seemed the least susceptible to insecticides. For example, the average knockdown for all insecticides at all times after treatment was 46.4% (n = 24,974) for these flies, as against 63.4% (14,340) for the other tsetse ($P < 0.001$, by chi-squared). Nevertheless, the bioassay data for all tsetse were usually pooled because it made no material difference to the conclusions. For example, if only the data for female *G. pallidipes* were used, the periods for which knockdown remained above 50% would have been reduced by an average of only three days (range 0–8).

Persistence and toxicity

Figure 1 exemplifies the decline in knockdowns with increasing time after insecticide application in the main trials. Mortalities (not shown in fig. 1) were low with all insecticides, averaging 45% immediately after treatment, and declining to 12% when knockdown had fallen to 50%. The numbers of insects in bioassays with individual insecticides were too few to assess accurately the period of each insecticide's persistence after each application. Hence, a general indication of persistence at various seasons was obtained by pooling the data for all insecticides. The persistence period was taken to be the time required for the running seven-day average of knockdown to drop below

Table 1. Start date of each treatment in the main trials, the persistence period (days in which the daily knockdown of tsetse for all insecticides pooled remained at or above 50%) and the mean knockdown with each insecticide during the persistence period.

Trial	Treatment	Start date	Persistence (days)	Decatix	SpotOn	SpotOn-E	Renegade	Cylence
1	1st	9 Apr 97	36	83.8^{2}	73.2^{5}	67.4^{4}	61.1^{1}	83.8^{6}
	2nd	28 May 97	55	81.7^{2}	85.2^{5}	88.1^{4}	83.6^{1}	90.4^{6}
2	1st	23 Aug 97	9	98.0^{5}	80.9^{4}	81.5^{3}	80.2^{6}	50.0^{1}
	2nd	24 Sep 97	24	81.9^{5}	68.7^{4}	91.0^{3}	82.9^{6}	48.0^{1}
3	1st	15 Jan 98	5	98.8^{6}	69.2^{1}	55.2^{7}	53.7^{4}	31.7^{8}
	2nd	5 Feb 98	8	86.7^{6}	74.4^{1}	76.2^{7}	76.1^{4}	70.2^{8}
	3rd	12 Mar 98	12	91.5^{6}	90.4^{1}	62.3^{7}	76.2^{4}	59.2^{8}
4	1st	14 May 98	24	73.2^{1}	80.5^{8}	85.9^{9}	71.5^{7}	38.9^{4}
	2nd	16 Jul 98	26	80.61	75.6^{8}	82.5^{9}	77.2^{7}	57.3^{4}
Overall average for all persistence periods				86.2	77.6	76.7	73.6	58.8

Superscripts are the code nos. of the oxen used.

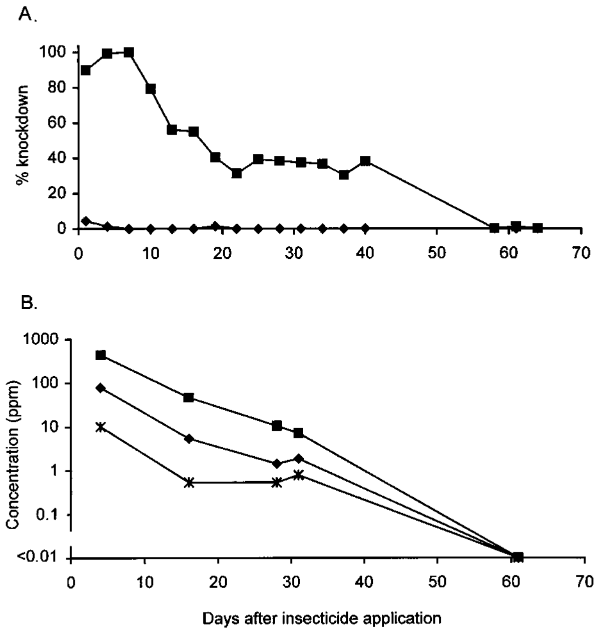

Fig. 2. Three-day averages for (A) the knockdown of tsetse feeding on treated (■) and control (◆) oxen, and (B) the concentration of deltamethrin on hair from different parts of the treated oxen (■, back; ◆, flank; ✱, legs), at various times after application of SpotOn in the supplementary trial.

50%, and to stay below for the remaining 9–38 days (average 19) before the trial ended or re-treatment occurred. The results (table 1) indicate that persistence ranged widely, from five to 55 days. With the three deltamethrin products (Decatix, SpotOn and SpotOn-E) the average knockdown within the persistence periods was 3–27% better than for the other two insecticides. However, since each insecticide gave a variable performance and each could not be tested on the same set of oxen, it was impossible to make confident comparisons between insecticides. For example, although cyfluthrin (Cylence) gave the poorest performance overall, it performed better than any other insecticide in the first trial.

In the supplementary trial, involving bioassays and chemical assays of two oxen treated with SpotOn, the period for which the pooled knockdowns on both animals remained above 50% was 16 days. Within this period, the mean knockdowns were 88% on treated ox X and 80% on treated ox Y. The geometric means of deltamethrin concentration on hair from all body regions at intervals from two to 32 days after treatment were 6.2 ppm (range 0.54–441 ppm) for X and 5.4 ppm (0.32–442) for Y. No insecticide (<0.01 ppm) was detected on the back, flank and legs of the control ox. The general pattern of insecticide persistence was studied by pooling the data for both treated animals. The results (fig. 2) show a marked decline in concentration with time after treatment. In the period when insecticide could be detected (>0.01 ppm), the concentration on the back was on average six times greater than on the belly and 39 times greater than on the legs, consistent with the findings of Stendel *et al.* (1992) for flumethrin. The decline in knockdown followed most closely the insecticide concentration on the legs, with knockdowns reaching 50% when the concentration of deltamethrin there was about 1 ppm.

Temperature and rain

Although it was surprising that the set of persistence periods evident in the main and supplementary trials varied so widely, it was less surprising that the mean knockdown within the persistence period was more constant, averaging around 80% for most insecticides. This implies that the knockdown in control campaigns could be predicted well if it were possible to forecast the persistence period under various conditions and to assume that insecticide would always be reapplied at the end of the period. It is encouraging, therefore, that linear regression analysis indicated that the length of the persistence periods in the main and supplementary trials was significantly ($P < 0.01$) correlated with the mean of daily maximum temperatures, measured in a Stevenson screen (fig. 3). For every 1°C increase in temperature the period declined by 4.9 days, with a 95% confidence range of 1.9–7.9 days. Before or after removing the effect of temperature, there was no significant effect of mean daily rain ($P > 0.1$), although most of the short periods of persistence were in the wet season when temperatures were high. Given that seasonally temperatures can be forecast to within a few degrees, it seems that the persistence periods can be predicted with a precision of plus or minus a week or so.

Distribution of engorging tsetse

There were no clear effects of individual oxen and the presence or absence of the various insecticides on the distribution of engorging flies and so the data for each of these factors were pooled. The results (table 2) showed that *G. m. morsitans* fed mainly on the belly whereas *G. pallidipes* fed mostly on the legs. With both species, the engorgements on the legs were concentrated mainly on the front legs. Too few *G. m. morsitans* were sampled to show any seasonal effect on the distribution of engorgements with this species, but the much larger catches of *G. pallidipes* exhibited a seasonal pattern, as illustrated by the data for females (fig. 4). In the hot months of January–March and September–October a relatively large proportion of the

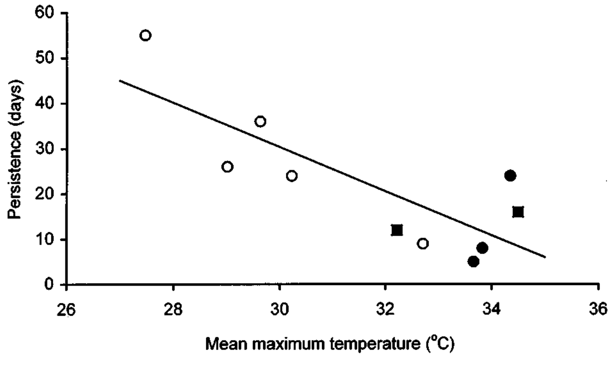

Fig. 3. Effect of temperature on the period for which the knockdown of tsetse remained at or above 50%. Plots distinguish periods with different amounts of average daily rain (○, none; ●, 0.1–0.9 mm; ■, 2.4–3.6 mm), but the regression line (slope significant at $P < 0.01$) is fitted to the pooled data. Details of the regression are given in the text.

Table 2. Percent distribution of the various species and sexes of tsetse caught by hand-nets when engorged on oxen.

Species and sex	Sample size	Percent distribution			
		Front legs	Hind legs	Belly	Back
Glossina pallidipes, males	11,482	63.0	13.1	23.5	0.4
G. pallidipes, females	33,591	50.2	13.7	35.8	0.3
G. m. morsitans, both sexes	149	25.5	4.0	65.8	4.7

engorgements were on the belly. However, temperature alone cannot explain the whole of the pattern since the percentage of flies engorging on the hind legs rose steadily from January to October, despite the cool weather in mid-year. Presumably, the abundance of tabanids and other insects in the rains and shortly after caused the ox to flick its tail more often, so disturbing tsetse on the hind legs. The fact that most test insects engorged on the legs accords with the previous indication that knockdown related most closely to the insecticide concentration there (fig. 2).

Ring of nets

Since the treated oxen were put in the pen at various times after insecticide application they would have had varying amounts of insecticide remaining on them when tested for repellence. The concentration remaining on each ox at each time was judged from the average of knockdowns produced by that ox on the three days before and after the day on which it was in the ring. High, medium and low concentrations were taken to be associated with knockdowns that were 90–100% (mean 96.4), 50–89% (75.4) and 10–49% (25.8), respectively. Control oxen, which were regarded as having a nil concentration of insecticide, gave an average knockdown of 3.2 %. The catches of tsetse, muscoids and tabanids, and the proportions of fed tsetse showed no significant ($P > 0.1$) correlation with insecticide concentration. This is illustrated in table 3 by the tsetse data. For the pooled data for muscoids and tabanids, the mean catches with high, medium, low and nil insecticide were 358, 469, 210 and 337, respectively.

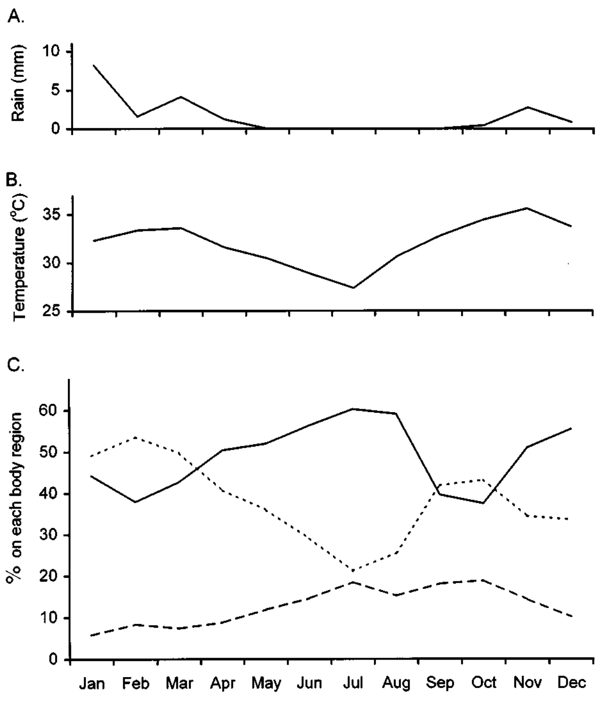

Fig. 4. Monthly means of daily rain (A) and daily maximum temperature (B), and the percent distribution of female *Glossina pallidipes* (C) caught by hand-nets while engorging on various parts of oxen (..., belly; –, front legs; – –, hind legs). Pooled data for 1987 and 1988. Monthly catches: 956–5138 (mean 2799).

Table 3. Detransformed mean catches of tsetse in a number of daily replicates in which oxen with various concentrations of insecticide were placed singly in the incomplete ring of nets.

Insecticide concentration	Replicates	*Glossina m. morsitans*	*G. pallidipes*
High	21	1.3 (40.0)	9.0 (43.4)
Medium	24	1.5 (24.0)	5.5 (33.7)
Low	19	1.0 (25.8)	4.6 (36.1)
Nil	10	1.8 (49.4)	7.0 (39.2)

Insecticide concentration was assessed from the knockdown in bioassays, as discussed in the text. Figures in parentheses indicate the percentage of fed flies in the pooled catches of the inside and outside faces of the nets.

Screens

Few tabanids were caught at any of the screens because the screens were used outside the flight season of these insects. The greater catches of tsetse and muscoids showed that with and without nets at the screens, the mean daily catches were not affected significantly ($P > 0.05$) by the presence of either of the pyrethroids, but the 2-methoxy phenol reduced catches substantially (table 4). The effect was greatest when the nets were absent. These results indicate that 2-methoxy phenol prevented many flies from flying close to the screen, and also inhibited the alighting responses of those flies that did fly close. The effect on alighting behaviour is evidenced further by the distribution of total catches at the screen with nets. In the absence of 2-methoxy phenol, 45.6% (n = 660) of tsetse and 61.2% (317) of the muscoids were caught alighting on the screen, as against only 34.1% (164) and 47.4% (116), respectively, in the presence of the phenol. For each group of insect, the effect of the phenol was significant at $P < 0.05$ (by chi-squared). Hence, the screen technique was sensitive to the inhibition of alighting responses, so that the failure to show any effects with the insecticides suggests that the insecticides did not interfere with such responses.

Contamination of dung

On the day after the first treatments of the third main trial, about 500 dung beetles (mostly species of *Onthophagus*, *Copris* and *Onitis*) were found dead or dying in and beside the dung dropped the previous afternoon by the Renegade-treated ox. This acute toxicity was evident in the dung dropped during four more days. It seemed that the toxicity was due to insecticide since alphacypermethrin was detected at 0.10 ppm in the wet weight of the dung and 1.85 ppm in the dry weight of the beetles.

Table 4. Detransformed mean catches of tsetse and muscoids at screens treated with pyrethroids or 2-methoxy phenol, as percentages of the control catches with untreated screens, in 20 replicates with pyrethroids and 12 replicates with the phenol, with and without electrocuting nets beside the screens.

Treatment	Nets	*Glossina m. morsitans*	*G. pallidipes*	Muscoids
Pyrethroids	Present	80.2 (12.2)	84.4 (70.5)	117.4 (239.8)
	Absent	98.6 (8.1)	78.8 (51.8)	61.8 (211.5)
Phenol	Present	53.1 (1.7)	25.7 (43.6)***	47.5 (15.0)***
	Absent	35.5 (2.0)*	13.0 (37.5)***	21.7 (8.4)***

Control catches are shown in parentheses

*, *** indicate that catches with the treated screens differ significantly from catches with untreated screens at the 0.05 and 0.001 level of P, respectively.

Chemical studies with dung continued on October 7, 1998. In the afternoon, the animals treated with SpotOn and Decatix in the fourth of the main trials were retreated with these insecticides, that is 12 weeks after the last insecticide application. The animal that had been used as the control in the fourth of the main trials was the control in the current study. On the morning of October 7, just before insecticide treatment, and on the next 12 mornings each ox was taken from its pen and tethered at a separate site where no animal had been stationed previously. As soon as each animal had defacated, a dung sample was taken and the animal was returned to its pen.

The analyses showed that the dung contained no deltamethrin (< 0.005 ppm) before treatment. After the treatments the control dung remained free of insecticide. However, insecticide was found in the dung from the animal treated with Decatix (table 5). About ten times as much insecticide occurred in the dung from the animal treated with SpotOn.

Modelling

The most notable indication of the experiments was that the persistence of all insecticides was substantially less than the three months indicated for SpotOn by Bauer *et al.* (1992) and Mangwiro & Wilson (1993). This suggests that if knockdown is not to fall below 50%, the recommended frequency of treatment must be increased about five times. It is necessary to see what the different frequencies of treatment imply about efficacy of control campaigns. This and other matters relating to field performance were addressed by a deterministic model employing present experimental data.

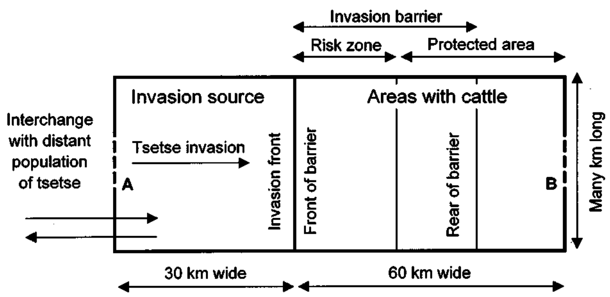

Fig. 5. Diagram (not to scale) showing the relative positions of the areas recognized in the modelled use of insecticide-treated cattle for controlling *Glossina pallidipes* and *G. m. morsitans*. Lines under the headings for the risk zone and invasion barrier indicate the width of these areas. Points A and B indicate the ends of the transect along which tsetse densities were modelled.

Modelled situation and required outputs

The type of output that the model was required to produce can be appreciated by reference to fig. 5, which illustrates a simple situation in which the area with cattle is subject to tsetse invasion from only one side. This is typical of the areas with insecticide-treated cattle in Zimbabwe (Warnes *et al.*, 1998). It is pertinent to consider two scenarios in the mapped area.

In the first scenario, tsetse are initially present only in the invasion source. The task is to treat the cattle near the front to provide an invasion barrier that is wide enough to prevent the flies occupying the whole of the area with cattle. Given that tsetse must enter the barrier to be killed, those cattle within the barrier and near the invasion front will be in a risk zone, i.e. where they remain exposed to the threat of trypanosomosis.

In the second scenario, tsetse are initially present in the whole of the mapped area, i.e. in the invasion source and the cattle area. The prime task is to tackle the flies in the whole of the cattle area. Then, when the distribution of tsetse has stabilized, the cattle treatments far from the front can be withdrawn, leaving only the treated cattle within an invasion barrier. This barrier has an easier task than in the first scenario because, as illustrated later, the abundance of flies at the invasion front will be depleted by the time the barrier is required to stand alone. However, it would be safest to take the width of this barrier as being the same as in the first scenario, allowing that at some stage in field work the barrier might have to withstand a restoration of the initial density of tsetse in the invasion source. The stabilized risk zone will be the same width in both scenarios.

There are several questions for the model to answer. How wide must the invasion barrier be? How wide will be the risk zone? How long will it take for the distribution of tsetse to stabilize, and hence, when will it be possible to withdraw the cattle treatments behind the barrier? How do these matters change with the initial density of tsetse and the abundance of treated cattle? How are the answers to all of these questions affected by the frequency of insecticide application?

Table 5. Concentration of deltamethrin (ppm) in dung produced at various days after treating oxen with Decatix and SpotOn.

	Concentration	
Days	Decatix	SpotOn
1	0.020	<0.005
2	<0.005	0.150
3	0.005	0.150
4	0.005	0.120
5	0.010	0.110
6	0.010	0.100
7	0.010	0.140
8	0.010	0.090
9	<0.005	0.080
10	0.010	<0.005
11	<0.005	0.010
12	0.010	0.060

The model

The modelled area (fig. 5) was produced as a block of cells in an Excel spreadsheet, with each cell representing a square kilometre. Since the area was assumed to be homogenous in matters such as vegetation and topography, and since the cattle were considered to be evenly distributed where they occurred, it was permissible to model the abundance of tsetse in a single line of cells, from A to B in fig. 5. Female tsetse were assumed to move randomly (Hargrove & Lange, 1989) at rates reflecting age-dependent activity (Hargrove, 1991). The daily displacement was taken as 200 m on emergence, rising linearly to a plateau of 600 m on day 30, and then declining linearly after day 50 to become 400 m on day 184. Such rates of movement are compatible with field data for females of *G. pallidipes* and *G. m. morsitans* (Vale *et al.*, 1984). Density dependent growth of the tsetse population was incorporated by allowing that the natural daily death rate was 1.33% at minimal population density, rising linearly to 2.33% at carrying capacity. Flies were considered to feed every three days and to visit an ox twice before feeding (Vale, 1977). Parameters for larval and pupal periods, adult life span and fecundity were as in Glasgow (1963). It was taken that the population in any square kilometre was unsustainable in any year if the computed abundance was less than one adult female for the whole year. Hence, if the computed population stayed below one female per square kilometre for a year the model started the next year with no adults or pupae in the square. A computed population could be established again only by invading flies and their breeding, before the annual criterion for sustainability was re-applied. This sort of modelling covered ten years from the start of cattle treatment.

Two types of treatment regime were modelled. First, it was imagined that there were four insecticide applications per year, evenly spaced so that two occurred in cool months and two in hotter seasons, to give an average daily knockdown of 25% for the whole year. Second, it was considered that the insecticide was always re-applied when daily knockdown approached 50%, so that the average knockdown for the year was 85%, based on the rounded average performance of Decatix in the experimental work (table 1). This regime would require about 21 applications per year. Each regime was envisaged to be applied under circumstances in which cattle formed either 10%, 50% or 90% of tsetse diet. The initial abundance of tsetse was allowed to be 100 or 10,000 adult females per square kilometre to represent, respectively, the densest populations likely to be experienced, and the densities more typical of most settled areas prior to the application of control measures. When interpreting the data, it was taken that the risk zone was the area where at stability the cattle would be exposed to a tsetse density that was at or above one adult female per square kilometre for at least part of the year. The protected area was regarded as the area where at stability tsetse densities did not rise to one adult female per square kilometre in any part of the year.

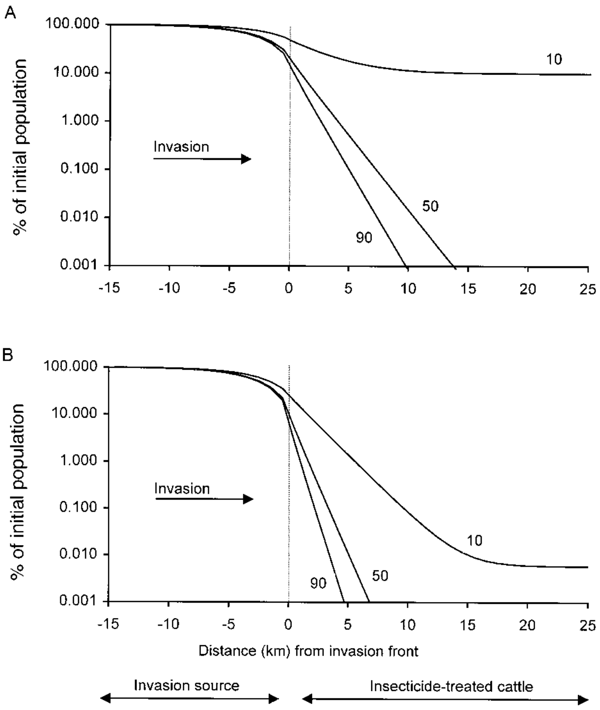

Fig. 6. Modelled population density of tsetse at various distances from the edge of an area with insecticide-treated cattle, after a year in which four (A) or 21 (B) treatments were given, under conditions in which cattle contributed various percentages of tsetse diet (percentages shown near each plotted line). The model covered −30 to +60 km, with tsetse initially distributed evenly throughout. The annual criterion for self-sustaining population densities is not applied.

Results of model

The workings of the model can be illustrated by interrupting them to examine the population calculated to remain after a year of treatment. Figure 6 shows the population remaining in a situation where tsetse were initially present in the invasion source and in the treated area. An important feature of the results is that the density of tsetse was reduced for several kilometres inside the invasion source. To validate the output, it is pertinent to focus on the modelled level of control on both sides of the front when well maintained deposits of insecticide were on cattle providing 10% diet (fig. 6B). This output accords with the actual results of a year of field trials that used such deposits on artificial baits for *G. m. morsitans* and *G. pallidipes* (Vale *et al.*, 1988a). The attractiveness of the 'population' of artificial

Table 6. Estimates (in km) of the width of the risk zone and minimum width of an invasion barrier, when cattle are given various numbers of insecticide treatments per year, under conditions in which the cattle provide various percentages of tsetse diet, with initial densities (D) of tsetse of 10,000 km^{-2} or 100 km^{-2}.

Treatments per year	Diet %	Risk zone, width (km)		Invasion barrier, width (km)	
		D = 10,000 km^{-2}	D = 100 km^{-2}	D = 10,000 km^{-2}	D = 100 km^{-2}
4	10	35^{7}	15^{5}	39	19
	50	10^{2}	4^{1}	13	6
	90	7^{1}	3^{1}	9	5
21	10	13^{2}	5^{2}	16	8
	50	5^{1}	3^{1}	7	3
	90	3^{1}	1^{1}	5	2

Superscripts against the widths of the risk zone indicate the number of years (rounded up) required for the zone to stabilize.

baits was roughly as expected for a host population contributing around 10% of tsetse diet.

The model's indications for the stabilized width of the risk zone and the invasion barrier (table 6) were produced by allowing the model to complete its 10-year run. Since the results are determined primarily by the dynamics within the invasion barrier and invasion source, the results are applicable to any situations where the width of the area with cattle exceeds the indicated width of the barrier, i.e. not only the modelled width of 60 km for the cattle area. With all variations to the diet conditions and the initial density of tsetse, the reduction in annual treatments, from 21 to four, increased the widths 2–3 times, emphasizing that confusion over persistence periods and optimal treatment frequency could be disastrous. Reducing the contribution of the cattle to tsetse diet, from 90% to 10%, increased the widths 4–5 times. Reducing the density of tsetse by two orders of magnitude reduced the widths by a little more than half. The invasion barrier was usually a few kilometres wider than the risk zone. With four applications and 10% diet, the risk zone stabilized after 5–7 years. In other cases stability occurred in 1–2 years.

Credible changes to the model's parameters did not affect much the indications for the widths of the invasion barrier and risk zone, and the times required for stability. For example, when the modelled rate of daily movement was halved the widths of the risk zone with four annual treatments and 50% diet was 8 km for an initial fly density of 10,000 km^{-2} and 3 km for 100 km^{-2}. These widths compare with the 10 km and 4 km using the normally modelled rate of movement (table 6).

Other modelled results showed that any self-sustaining population which breaks through the invasion barrier starts to establish itself most readily at 2–3 km behind the barrier. Hence, surveys to monitor the effectiveness of the barrier should give attention to this location, not just to the immediate rear of the barrier.

Discussion

Comparison with other results

The extent to which the present work can help to answer the questions raised in the Introduction depends on the degree to which the results accord with existing information. Work in Burkina Faso (Bauer *et al.*, 1992), indicated that pyrethroids do not affect the alighting responses of tsetse but that they do inhibit feeding responses. Present work confirms the absence of effects on alighting responses but contradicts the Burkina Faso findings in that no inhibition of feeding was evident. Studies in Kenya (Baylis *et al.*, 1994) agree with the present work in showing no feeding inhibition. Presumably, the distinctions between the findings in west Africa and those in Zimbabwe and Kenya relate to variations in test conditions. The west African insects were taken from a laboratory colony and enclosed with stabled oxen for two hours, whereas in the present work and in the Kenyan studies the test insects came to the ox at their own 'volition' and attempted to feed soon after. The persistence and pick-up of insecticide may have been enhanced in the stable – by the time the stabled flies attempted to feed they may have already been exposed long enough to impair feeding responses. Hence, it seems that insecticide treatment does not inhibit the feeding of wild flies, and so the risk of trypanosomosis will not be reduced as soon as insecticide is applied. The upshot is that the modelled abundance of tsetse offers acceptable indications for the probability of cattle being bitten.

Following the previously published work in Burkina Faso (Bauer *et al.*, 1992) and Zimbabwe (Mangwiro & Wilson, 1993) it has commonly been accepted that SpotOn persists for about 100 days. Present work emphasizes that the persistence can often be much less, in accord with the findings of Thomson *et al*. (1991), and with the unpublished results of Mangwiro (personal communication) which showed that SpotOn persisted for only about 40 days at Rekomitjie. The present demonstration that persistence is affected by temperature offers a means of reconciling the different indications for persistence. Thus, despite the contrast with some of the earlier findings on persistence and repellence, the combination of present results and modelling offers preliminary answers to several outstanding questions, as below.

Questions answered

What is the best insecticide? In keeping with the results of Bauer *et al*. (1993), present results suggest that deltamethrin gives the best overall performance. However, the present performances of the insecticides were so variable as to indicate that there is unlikely to be a gross and consistent difference between their efficacies in the field. Hence, the choice of insecticide seems governed largely by the convenience and the cost of providing the recommended dose. Pour-ons may be more convenient where dip tanks or spray races would have to be specially built, but insecticides formulated as dips are usually about a quarter of the cost.

What are the ecological risks? The threat to dung fauna could be serious, reducing the incorporation of manure into the soil and so decreasing the agricultural benefit of cattle. After South African farmers complained that dung beetles were killed by a flumethrin pour-on for tick control, Kruger *et al.* (1998) conducted bioassays which failed to confirm the effects. Hence, the researchers wondered whether the farmers' observations were due to overdosing. Present results show variations in contamination of dung but indicate that pyrethroid applications at recommended dose can sometimes have the effect that the farmers claimed. The importance of contamination of dung seems as variable and controversial with pyrethoids as it is with ivermectin (Dadour *et al.*, 1999).

Why do cattle treatments give variable success against tsetse? Part of the variability must be due to differences in the weather and the species and abundance of tsetse in various situations. Perhaps more importantly, the present model and experiments suggest that the risk zone and the required width of invasion barrier can vary by many kilometres with only a few-fold change to treatment frequency and to the percentage of cattle in tsetse diet. With such a pool of critical variables, it is hardly surprising that cattle treatment gives variable results.

Despite the variability, some generalizations can be made. First, if the treated area is so large that most of it is at least 10 km from the invasion source, then good control will occur within a year or two provided there are at least four treatments per year, with the treated animals forming at least 50% of tsetse diet. Second, whatever the diet and initial density of tsetse, and whatever the treatment regime, good control is impossible if most of the treated area is no more than a few kilometres from the invasion source. This means that tsetse cannot be removed by using cattle treatments alone in non-isolated areas of much less than 1000 km^2 even when, as in the model, the invasion comes only from one side. These modelled indications for the importance of invasion in small plots accord with field results (Baylis & Stevenson, 1998). The invasion problem would be more serious, and hence the minimum feasible size of the treated area would be greater, if the invasion were from several sides. Invasion could be even more serious if the cattle are grazed in only those vegetation types where tsetse are least abundant, leaving large blocks of heavily infested vegetation to produce 'invasion from within'. Such a problem seems to have been important in the imperfect control achieved by Fox *et al.* (1993). Isolation could be improved by using artificial baits in the invasion source (Bauer *et al.*, 1992; Warnes *et al.*, 1999).

Questions raised

Predicting the success of various tactical options for each field campaign requires surveys of the density and distribution of tsetse, cattle and other hosts, and then demands the application of many scientific principles. To what extent can the surveys and science be left to farmers? Even if it is recognized that practical and scientific assistance is required in most cases, there remain many questions that the scientists themselves must answer before being able to assist confidently. Some of these questions refer to tsetse biology. For example, now that control operations are expected to deal with relatively small areas, the significance of tsetse invasion is much greater than before, so we need to know more about the routes and rates of tsetse movement under various circumstances (Vale, 1998). What scope is there for improving the cost-effectiveness and convenience of the relatively cheap dips? Given that many tsetse feed on the lower legs, would a weekly foot-bath give good control?

Other questions are veterinary. For example, why does the incidence of trypanosomosis decline when there is sometimes only a slight reduction in tsetse abundance (Bauer *et al.*, 1992; Fox *et al.*, 1993; Baylis & Stevenson, 1998)? How can we be sure that the insecticide treatment for tsetse control will not aggravate tick resistance to acaricides or upset the natural immunity to tick-borne diseases (Norval *et al.*, 1992; Van den Bossche & Mudenge, 1999)?

In the spheres of sociology: how can a farmer be convinced to take his herd into vegetation types where tsetse are most abundant, i.e. the places hitherto avoided? How is cattle distribution governed by the school calendar, i.e. the availability of children to graze herds widely?

Compared to artificial baits, cattle have the advantage of being closely guarded against theft, and of not having to be specially purchased for tsetse control. Nevertheless, as the unanswered questions illustrate, the use of insecticide-treated cattle on a relatively small scale by individual farmers can be more complex than a government's extensive, standardized and even deployment of artificial baits that suffer no diseases and attract no ticks or dung beetles. The complexities of the insecticide-treatment of cattle do not mean that the technique should be scorned for application now, especially not in those areas where the natural abundance of tsetse is so low that even a small reduction in fly density could have a significant impact on the incidence of trypanosomosis. However, the complexities do emphasize that scientific advice should be taken before starting the treatment in any area, and that urgent research is required on a wide range of topics.

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