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Responses of *Glossina pallidipes* (Diptera: Glossinidae) to synthetic repellents in the field

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Abstract

In Zimbabwe, studies were made of the responses of *Glossina pallidipes* Austen to known and candidate repellents. Various chemicals, dispensed at *c.* 5–10 mg/h, were placed beside Epsilon traps already baited with a blend of acetone, octenol, 4-methylphenol and 3-*n*-propylphenol. Pentanoic or hexanoic acids or acetophenone halved the catch and 2-methoxyphenol reduced the catch by 90%. There were no consistent differences in the responses of males and females. Pentanoic acid or acetophenone or 2-methoxyphenol at an unbaited trap reduced the catch by 40%, 75% and 60%, respectively. Baiting traps with a combination of pentanoic acid, acetophenone and 2-methoxyphenol did not reduce the catch below that produced by 2-methoxyphenol alone. Pentanoic acid and 2-methoxyphenol reduced the efficiency of traps from *c.* 40% to 20% but acetophenone had no significant effect. Acetophenone and 2-methoxyphenol halved the numbers of tsetse attracted to a target baited with acetone, octenol and phenols but none had a significant effect on the proportion that landed. 2-Methoxyphenol significantly reduced the numbers of tsetse attracted to a source of natural ox odour but only pentanoic acid had a significant effect on feeding responses, reducing the proportion that fed on an ox from 59 to 45%. It is concluded that these repellents do not provide any useful degree of protection against trypanosomiasis. In areas where tsetse are abundant (500 bites/ox/day) and infection rates in tsetse are high (> 5%) it is highly unlikely that any repellents would be useful. However, in areas where tsetse are less abundant (1 bite/ox/day) and/or infection rates are low (*c.* 0.5%) the potent, unidentified repellents present in human odour might effectively complement the control of disease using trypanocidal drugs.

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Introduction

Currently, the most important methods of combatting human and animal trypanosomiasis rely on insecticide-treated baits to control tsetse (Green, 1994), or trypanocidal drugs to treat or prevent the disease (Jordan, 1986). The baits consist of either traps or insecticide-impregnated targets, sometimes baited with synthetic attractants (Vale *et al.*, 1986), or cattle treated with an insecticidal dip or 'pour-on' insecticide (Thomson *et al.*, 1991).

Early studies by Vale (1974a) showed that chemicals present in human odour reduce the numbers of tsetse attracted to a host and also the proportion that subsequently feed. Such chemicals could provide a useful tool in the integrated management of trypanosomiasis. For instance, in areas where cattle are protected from trypanosomiasis by the use of prophylactic drugs, disease challenge might be reduced by treating cattle with repellents. A large reduction in challenge would reduce drug costs and increase productivity (Barrett, 1994; Holmes & Torr, 1988). The same approach might be applied in areas where trypanotolerant breeds of cattle are used (Jordan, 1986). Repellents may also be useful in protecting people against sleeping sickness.

Although the identities of the repellents present in human odour remain unknown, a number of other potent repellents have been discovered in the course of identifying attractants. For instance, high doses of lactic acid (Vale, 1977b), acetophenone (Vale, 1980) and 2-methoxyphenol (Vale *et al.*, 1988) have been shown to reduce the catch of traps by 50–90%.

We report here investigations of the responses of tsetse to various known and candidate repellents dispensed at doses that might be practicably released from a dispenser attached to a host. The study assessed whether repellency could be enhanced by combining several repellents and estimated the level of protection that these chemicals might provide against trypanosomiasis. In addition to the chemicals previously reported to be repellent, studies were also made of N,N-diethyl-m-toluamide (DEET), a repellent for mosquitoes (Davis & Bowen, 1994), naphthalene, a commonly used repellent for insects (Den Ouden *et al.*, 1984) that is also known to be detected by tsetse (P. Beevor, personal communication), and various volatile carboxylic acids known to be present in human sweat (A. Cork, unpublished results).

Materials and methods

All experiments were carried out at Rekomitjie Research Station in the Zambesi Valley of Zimbabwe where *Glossina pallidipes* Austen and *G. morsitans morsitans* Westwood (Diptera: Glossinidae) are present.

Catching methods

Traps

All catches were made by Epsilon traps (Hargrove & Langley, 1990) supplied by Bonar Industries, Harare, Zimbabwe.

Targets

Targets consisted of a panel of black cloth (1 × 1 m) flanked with 0.5 × 1-m high panels of black mosquito netting. To estimate the number of tsetse that contacted target, an electrocuting grid (Vale, 1974b) covered all surfaces. The target was mounted on a corrugated t covered with polybutene. Tsetse that contacted the g were killed or stunned and fell onto the tray where th became stuck. Tsetse generally fall vertically (Vale, 197 and so, by recording the numbers of tsetse caught direc below the netting and cloth panels, it was possible to gau the proportion that was caught next to the netting or t cloth.

Odours

Synthetic attractants

Traps and targets were baited with a blend of acetor (500 mg/h), 1-octen-3-ol (0.4 mg/h), 4-methylphen (0.8 mg/h) and 3-*n*-propylphenol (0.1 mg/h) at rates know to increase the catch of tsetse in Zimbabwe (Vale & Hal 1985; Vale *et al.*, 1988) and henceforth this blend of odou is termed AOP. Acetone was dispensed from an open bottl and octenol and the phenols were dispensed from seale sachets of low density polyethylene, 0.15 mm thick with surface area of 50 cm^2 (Laveissière *et al.*, 1990).

Natural attractants

In some experiments, studies were made of the number of tsetse attracted to a source of natural ox odour with o without various repellents. Natural odour was obtained by placing an ox (*c.* 400 kg) in a roofed pit and exhausting the air from the pit at 2000 l/min via a ventilation shaft (25 cm dia.) fitted with a 12 V co-axial fan (Vale, 1974a). To gauge the numbers of tsetse attracted to the odour, an electric net (Vale, 1974b), 1.5 × 1.5 m, was placed 1 m downwind of the odour source. Tsetse orientate imprecisely to an odour source unless it is marked by a visual stimulus (Vale, 1974a and so a target, consisting of a panel of black cloth (75 × 75 cm), was sewn on to the centre of the electric net.

Repellents

Repellents were dispensed undiluted from either glass vials (1.7 cm wide and 4.3 cm deep) or from sealed polythene sachets. Unless reported otherwise, the odours were placed on the ground 30 cm downwind of the trap, targe or electric net.

Effect of odours on trap and feeding efficiency

To estimate the effect of repellents on trap efficiency, a trap baited with various odours was placed at the centre o an incomplete ring (8 m dia.) of six electric nets (1.5 × 1.5 m) The nets covered about 36% of the circumference of the ring and so the number of tsetse that approached the vicinity of the trap was taken to be the catch of the trap itself plus 2.78 times the catch from the inside surface of the ring of nets. Following Vale & Hargrove (1979), trap efficiency is defined as the catch of the trap expressed as the percentage of flies that approach the vicinity of a trap.

To assess the effects of repellents on feeding efficiency, an ox with or without various repellents was placed at the centre of the ring of nets. Flies were separated according to the side of the net on which they were caught and classed

Table 1. The catch index of *Glossina pallidipes* from traps baited with AOP plus various putative repellents.

Chemical			detrans-formed	transformed ±SE	Catch index	P
2-Methoxyphenol	10	12		2.093±0.0648	0.14	***
Acetophenone	5	12	123	2.093±0.0648	0.31	***
Hexanoic acid	5	12	33	1.530±0.0689	0.36	**
Pentanoic acid	10	12	61	1.792±0.0553	0.55	*
Lactic acid	100	8	107	2.034±0.053	0.56	***
	10	12	5	0.778±0.0738	0.70	ns
Acetic acid	10	12	5	0.778±0.0738	0.61	ns
	10	12	16	1.227±0.065	0.72	ns
Butanoic acid				1.342±0.0720	0.87	ns
	20	12	134	2.130±0.0807	0.80	ns
Propionic acid	5	16	15	1.208±0.0386	0.83	ns
Formic acid	10	8	107	2.034±0.053	0.91	ns
3-methyl butanoic acid	5	12	33	1.530±0.0689	0.98	ns
DEET	10	12	17	1.255±0.0833	1.29	ns
treated cloth (20×30 cm)		12	17	1.255±0.0833	0.91	ns
Naphthalene	10	6	128	2.111±0.0728	1.04	ns
	trace	6	43	1.643±0.0797	1.13	ns

The catch index is the detransformed mean catch of tsetse expressed as a proportion of that from a standard AOP-baited trap. n = number of replicates; P = probability that the catch index is significantly different from unity (F-test) at the $P < 0.05$ (*), $P < 0.05$ (**) or $P < 0.001$ (***) levels of probability. A=acetone (500 mg/h), O=1-octen-3-ol (0.4 mg/h), P=4-methylphenol (0.8 mg/h)+3-n-propylphenol (0.1 mg/h).

as fed or unfed based on the presence or absence of red blood being visible through the abdominal wall. Following Vale (1977a), feeding efficiency was estimated as the number of tsetse containing red blood caught on the inside of the ring nets expressed as a percentage of the total catch from the inside of the ring.

Experimental design and analysis

All field experiments were carried out in the 3 h before sunset when tsetse are most active (Hargrove & Brady, 1992). The various repellents were incorporated into a series of replicated Latin squares consisting of days×sites× treatments. For studies using the ring of nets, treatments were compared using a randomized block design; groups of adjacent days were regarded as different blocks and treatments were randomly allocated to days within these blocks. The catches (n) were normalized using a $\log_{10}(n+1)$ transformation and subjected to analysis of variance. The detransformed means are reported, accompanied by their transformed means and standard errors so that more detailed comparisons can be made. In studies of feeding and trap efficiency the results were analysed using GLIM4 (Francis *et al.*, 1993) which fits models using a maximum likelihood method. A binomial model with a logit link was used to control for non-normal and non-constant variance. The significance of changes in deviance were assessed by χ^2. The catches of *G. m. morsitans* were generally too low to analyse their responses to the various repellents. Consequently only the results for *G. pallidipes* are reported.

Experiments and results

Effects of repellents on trap catch

Traps with odour

Initial screening of various known and putative repellents were carried out using traps. Studies were made of the effect of adding candidate repellents to traps baited with AOP. The results (table 1) show that 2-methoxyphenol, acetophenone, pentanoic or hexanoic acid reduced the catches significantly. Lactic acid also produced a significant reduction in catch at 100 mg/h but not at 10 mg/h. Neither DEET nor naphthalene had a significant effect.

There was no significant difference in the responses of males and females. For instance, a trap baited with AOP had a detransformed mean catch of 42 male and 80 female *G. pallidipes*. Adding acetophenone reduced the catch of males and females by 71% and 68% respectively and adding 2-methoxyphenol reduced the catch by 84% and 87% respectively. The data for the sexes are therefore pooled henceforth.

The effects of adding several repellents to traps baited with AOP are shown in table 2. Adding pentanoic acid and/or acetophenone to 2-methoxyphenol did not reduce the catch further than the reduction produced by 2-methoxyphenol alone (Experiment 1). However, adding 2-methoxyphenol to either pentanoic acid (Experiment 2) or to acetophenone (Experiment 3) did reduce the catch further, suggesting that 2-methoxyphenol is a more potent repellent than either acetophenone or pentanoic acid. It is noteworthy that the repellents completely negated the effect of attractants. For instance, adding AOP increased the catch as expected but the catch with a combination of AOP and 2-methoxyphenol was either not significantly different (Experiment 1) or even significantly less (Experiment 3) than that with no odour.

Traps without odour

Adding repellents to otherwise unbaited traps also reduced the catch (table 3). The catches from traps baited with acetophenone or 2-methoxyphenol were significantly less than that from an unbaited trap (Experiments 1 and 2)

Table 2. The detransformed mean catch of *Glossina pallidipes* from traps baited with combinations of 2-methoxyphenol (2-ME), pentanoic acid (PEN) and acetophenone (ACETO).

Bait	Mean catch	
	Detransformed	Transformed
Experiment 1 (12 reps)		
AOP only	37.4	1.584a
AOP+2-ME	6.3	0.863b
AOP+2-ME+PEN	5.4	0.806b
AOP+2-ME+ACETO	8.5	0.978b
AOP+2-ME+PEN+ACETO	7.9	0.949b
None	5.2	0.792b
Transformed SE		0.0874
Experiment 2 (12 reps)		
AOP only	61.2	1.794a
AOP+PEN	33.6	1.539b
AOP+PEN+2-ME	6.5	0.875c
Transformed SE		0.0552
Experiment 3 (12 reps)		
AOP only	123.1	2.094a
AOP+ACETO	38.2	1.593b
AOP+ACETO+2-ME	19.6	1.314c
None	33.6	1.539b
Transformed SE		0.0622

For each experiment, transformed means followed by a different letter are different at the $P < 0.05$ level of probability (LSD-test). A=acetone (500 mg/h), O=1-octen-3-ol (0.4 mg/h), P=4-methylphenol (0.8 mg/h)+3-n-propylphenol (0.1 mg/h). For release rates of repellents see table 1.

but for pentanoic acid the effect was not significant (Experiment 2).

After this preliminary screening, more detailed studies were made of responses to 2-methoxyphenol, acetophenone and pentanoic acid to assess whether they might provide a useful degree of protection against trypanosomiasis.

Effects of repellents on attraction and landing

The effects of the various repellent blends on attraction were assessed by the reduction in total catch observed when they were added to an AOP-baited target, with effects on landing measured from the proportion of tsetse caught on the cloth section of the target. The results (table 4) show that 2-methoxyphenol and acetophenone reduced the total catch of tsetse but there was no significant effect produced by pentanoic acid. None of the treatments had a significant effect on the landing response.

To assess attraction to a natural host, targets w baited with natural ox odour. The results (table 5) w broadly in accord with those from the AOP-baited targ Addition of 2-methoxyphenol had a clear and signific effect, reducing the catch by *c.* 50%, while acetophenc also reduced the catch of tsetse but the effect was sma and only significant in one experiment. Pentanoic acid h no significant effect.

Effect of repellents on trap efficiency

The results from the traps and targets indicated tl pentanoic acid reduced the catch in traps but not at targ whereas 2-methoxyphenol and acetophenone reduced catch by both. This might be due to differential effects trap efficiency, so studies were made of the effect repellents on this variable. The results (table 6) show tl 2-methoxyphenol and pentanoic acid reduced the efficier

Table 3. The detransformed mean catch of *Glossina pallidipes* from traps baited with acetophenone, 2-methoxyphenol or pentanoic acid.

Bait	Mean catch	
	Detransformed	Transformed
Experiment 1 (14 reps)		
No odour	30.1	1.493
Acetophenone	4.0***	0.695
2-Methoxyphenol	12.4**	1.126
Transformed SE		0.0734
Experiment 2 (8 reps)		
No odour	9.7	1.029
Acetophenone	2.5*	0.544
2-Methoxyphenol	3.6*	0.667
Pentanoic acid	5.7	0.829
Transformed SE		0.0920

Asterisks indicate that the means are significantly different from no odour at the $P < 0.05$ (*), $P < 0.01$ (**) or $P < 0.001$ (***) level of probability. For release rates of repellents see table 1.

Table 4. The detransformed mean catch (transformed ± SE in brackets) of *Glossina pallidipes*, and mean percentage (± SE) alighting on the cloth panel, from targets baited with AOP with or without various repellents.

Bait	Mean catch	Percent landing
AOP		
AOP + 2-methoxyphenol		
AOP + pentanoic acid		
AOP + acetophenone		

Each treatment was repeated for 12 replicates. Asterisks indicate that the means are significantly different from AOP ($P < 0.05$, F-test). A=acetone (500 mg/h), O=1-octen-3-ol (0.4 mg/h), P=4-methylphenol (0.8 mg/h)+3-n-propylphenol (0.1 mg/h). For release rates of repellents see table 1.

of Epsilon traps significantly from 64 to 41–48% but acetophenone had no significant effect. Pentanoic acid appears to exert its repellent effect solely by reducing the tendency for tsetse to enter a trap. 2-Methoxyphenol, on the other hand, has this effect and also reduces the numbers of tsetse that are attracted to the vicinity of the bait.

Effect of repellents on feeding responses

The studies of feeding response (table 7) showed that neither 2-methoxyphenol nor acetophenone had a significant effect on the proportion of tsetse that fed on an ox, whereas pentanoic acid had a slight but significant effect, reducing the percentage feeding from 59 to 44%.

Discussion

The present results show that low doses (*c.* 10 mg/h) of 2-methoxyphenol, acetophenone, pentanoic and hexanoic acid reduce the catch of baited traps by 45–85%. These results confirm previous findings (Vale, 1980; Vale *et al.*, 1988) that baiting traps or targets with acetophenone (2000 mg/h) or hexanoic acid (100 mg/h) or 2-methoxyphenol (*c.* 2 mg/h) reduced the catch of tsetse significantly. Lactic acid was also repellent when dispensed at 100 mg/h but not at 10 mg/h, and was a potent repellent when dispensed by saturating a cloth (0.18 m^2) with 10% lactic acid or by treating an ox with 4.5 l of a 1% solution (Vale, 1977b). These latter treatments represent doses of 11 g/day and 49 g/day applied to the cloth or ox respectively for a 3-h experiment, so the release rates used by Vale were probably much greater than the 10 mg/h used here.

The results show that 2-methoxyphenol is the most potent repellent of those tested, reducing trap catches by *c.* 85%. However, its repellent effect was not enhanced by adding either pentanoic acid or acetophenone. The behavioural basis of this difference between 2-methoxyphenol and the other two seems to be due to pentanoic acid reducing trap entry but having no effect on attraction to an odour source, and to acetophenone having no effect on trap entry but reducing attraction. 2-Methoxyphenol, on the other hand, reduces both efficiency and attraction, hence its greater potency as a repellent and the absence of any enhanced effect when either acetophenone or pentanoic acid were added to it. Thus, from a practical viewpoint, combinations of these odours are no more effective than 2-methoxyphenol alone.

No behavioural activity was demonstrated for DEET which is a repellent for many insect species (Rutledge *et al.*, 1978), particularly mosquitoes (Davis & Bowen, 1994), or for naphthalene which has been used as a repellent against the cabbage root fly, *Delia radicum* Linnaeus (Diptera: Anthomyidae) (Den Ouden *et al.*, 1984). Vale (1977b) was also unable to show a response of tsetse to DEET.

It should be noted that adding 2-methoxyphenol, acetophenone and pentanoic acid to unbaited traps reduced the catch of tsetse, and thus these compounds qualify as true repellents as defined by Dethier *et al.* (1960). This is in contrast to most work on insect repellents which involves chemicals that reduce attraction to sources of attractive odours. As observed by Davis (1985), the term 'repellent' is more widely used for chemicals which elicit a combination of behavioural responses resulting in prevention of biting by an insect. Invariably, the specific behavioural patterns by which this result is attained are not determined, and there are even less data on the sensory mechanisms involved. Davis (1985) suggested at least five potential sensory mechanisms by which these 'attraction inhibitors' might act: (a) they may interact with and inhibit the response of a sensory neuron to a normally attractive signal; (b) they may interact with their own specific receptors and be attractants at low intensities but become repellent at higher levels; (c) they may activate a receptor system that mediates a competing or inappropriate behaviour pattern; (d) they may

Table 5. The detransformed mean catch (transformed mean in brackets) of *Glossina pallidipes* from a target at a source of natural ox odour with or without various repellents from *n* replicates and the probability (*P*) that the means are different (F-test).

Repellent	*n*	Ox odour only	Ox odour + repellent	Transformed SE	*P*
2-Methoxyphenol	12	63.4 (1.809)	37.1 (1.581)	0.0265	***
	6	53.6 (1.737)	15.9 (1.228)	0.0387	***
Acetophenone	12	107.9 (2.037)	87.0 (1.947)	0.0283	*(P = 0.0488)
	10	8.3 (0.968)	7.3 (0.919)	0.0694	ns
Pentanoic acid	12	79.3 (1.905)	68.4 (1.841)	0.0317	ns

For release rates of repellents see table 1

Table 6. Trap efficiency, sample size (n) and the efficiency index ($\pm$SE) for *G. pallidipes* from an Epsilon trap baited with AOP $\pm$ various repellents from six replicates.

Odour	Percent efficiency	n	Efficiency index
AOP	64.0		
AOP+2-ME	41.1		
AOP+ACETO	66.6		
AOP+VAL	48.3		

Asterisks indicate that the addition of a repellent to AOP has reduced efficiency index at the $P < 0.001$ level of probability (F-test). Efficiency index is the catch from the trap expressed as a proportion of the total (trap+inside of the ring of nets) catch. For release rates of repellents see table 1.

activate specific 'noxious odour' repellent receptors, or (e) they may simultaneously activate several different receptor types that mediate various behaviour patterns so that any sensory signal specific to host finding is lost in the resulting barrage of sensory input.

In the case of the tsetse repellents reported here, mechanism (a) can be excluded because they are active in the absence of attractants, although interestingly this is the only mechanism that has ever been conclusively demonstrated. DEET reduced the responses of receptors on mosquito antennae to the feeding attractant, lactic acid (Davis & Bowen, 1994) and the oviposition attractant, ethyl propionate (Kuthiala *et al.*, 1992). With regard to mechanisms (b), (c) and (d) it should be noted that both 2-methoxyphenol and pentanoic acid are produced by host animals. 2-Methoxyphenol is a very minor component of cattle urine (Bursell *et al.*, 1988), occurring at very much less than 1% of the major phenolic component, 4-methylphenol. Its release rate in whole ox odour is thus typically less than 0.03 mg/h (cf Torr *et al.*, 1995), compared with the 5–10 mg/h used in these studies. However, addition of 2-methoxyphenol at these low rates of release to AOP blends caused only a small, non-significant reduction in catch (Torr, Mangwiro & Hall, unpublished). Pentanoic acid is also present in ox odour at much less than 0.5 mg/h and addition of a mixture of the carboxylic acids found in sweat at these low release rates to blends of AOP caused a slight reduction in catch of tsetse (*loc. cit.*). Mechanism (b) above thus seems unlikely, at least for 2-methoxyphenol and pentanoic acid, but mechanisms (c) and (d) cannot be excluded. The fact that two of the repellents are produced by host animals might suggest they play some definite role in tsetse-host interactions, perhaps activating specific receptors causing some other behavioural response as in mechanism (c) or possibly being produced in larger quantities by unsuitable hosts and activating specific 'noxious-substance' receptors, as in mechanism (d). Swynnerton (1936) reported that baboons and monkeys kill a 'fair proportion' of tsetse that attempt to feed on them and, more recently, Randolph *et al.* (1992) drew attention to the risk of mortality associated with feeding. It may therefore be adaptive for tsetse to be able to recognize, and thus avoid, those hosts that have a high probability of killing tsetse attempting to feed.

Preliminary electrophysiological evidence (C. den Otter & K. Voskamp, personal communication) indicates that 2-methoxyphenol and acetophenone activate several receptor types that also respond to attractive compounds. This suggests that these repellents might act by mechanism (e), causing a barrage of sensory input that jams any sig specific to host finding whether olfactory, visual or a other type. 2-Methoxyphenol obviously has some structu similarities to the attractant phenols, 4-methylphenol a 3-*n*-propylphenol, and acetophenone was originally test by Vale (1980) as an analogue of the attractant keto acetone.

Practical implications

The present study underscores a problem recentl highlighted by Vale (1993) concerning the use of traps t make deductions about tsetse behaviour – or indeed th behaviour of any insect. The initial studies using trap indicated that the repellents studied were potent and migh therefore be effective in protecting animals against try panosomiasis. However, analysis of the responses of tsets attracted to and then feeding on an ox revealed that th effect was relatively slight. Adding 2-methoxyphenol an pentanoic acid to a trap resulted in a pronounced decreas in trap efficiency but there did not appear to be a equivalent and large close-range effect with a host. Clearly making deductions regarding the behaviour of tsetse, base solely on their responses to traps, must be done ver cautiously.

The repellents studied here halved the number of tsets attracted to a host, but none had an effect on landing, and only pentanoic acid had a slight and significant effect or feeding. These data suggest that baiting an ox with these chemicals would only halve the number that are attracted to the ox and, at best, reduce the proportion that subsequently feed by *c.* 25%. So the net reduction in biting rate afforded would then be *c.* 60%.

The probability of a tsetse bite resulting in an infection is the product of the prevalence of infection in the tsetse population (p) and the probability of a bite by an infected fly resulting in an infection in a host which Rogers (1988) termed b_1. At Rekomitjie, the prevalence of *Trypanosoma vivax* is *c.* 3% (Ford & Leggate, 1961; Woolhouse *et al.*, 1993) and Rogers (1988) estimated b_1 as being 0.29. Thus the overall probability of infection per bite would be 0.0087 and the probability of not being infected therefore 0.9913. If a host is bitten by n flies then the probability of an ox not being infected is 0.9913^n and hence the chance that they are infected is $1-0.9913^n$. At Rekomitjie a stationary ox might be typically visited by 600 flies per afternoon (Vale, 1977a, table 1) of which 45% feed successfully. Such an animal might be conservatively estimated to receive 270 bites a day. Baiting the animal with a repellent that reduced the bites/day by 60% would reduce the daily probability of

Table 7. Percent feeding efficiency ($\pm$SE) for *G. pallidipes* feedin on an ox $\pm$ various repellents.

Odour	Feeding efficiency		Replicates	P
	Ox	+repellent		
2-Methoxyphenol	46.8 (664)	40.8 (409)	24	ns
Acetophenone	45.3 (547)	45.1 (563)	13	ns
Pentanoic acid	59.2 (299)	43.8 (194)	29	

Feeding efficiency is the total catch of fed flies from the inside o the ring of nets expressed as a proportion of the total (fed+unfed) catch (n). Asterisks indicate that the means are significantly different from AOP ($P < 0.05$, F-test). For release rates of repellents see table 1.

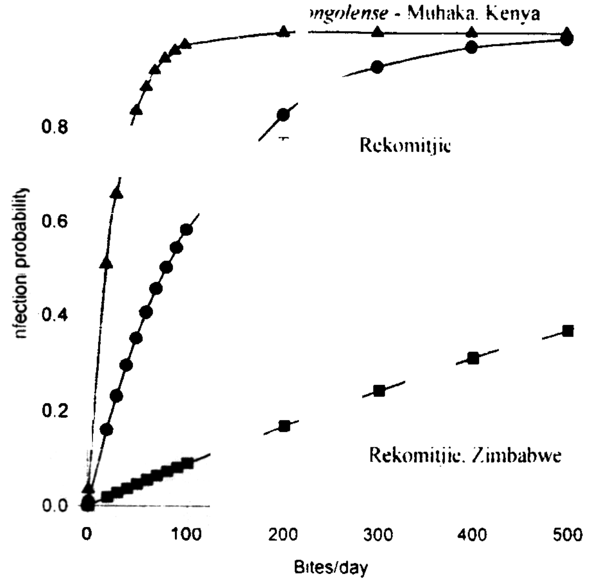

Fig. 1. The daily probability of an ox contracting trypanosomiasis with given infection rates in tsetse (p), transmission coefficients (b_1) and fly densities. Given that proportion p of tsetse are infected, that the probability of a bite from an infected fly producing an infection is b_1, and an ox is bitten by n flies, then the daily probability of an ox contracting trypanosomiasis is $1-(1-p.b_1)^n$. Illustrative examples of p and b_1 for *Trypanosoma brucei* (p=0.0015, b_1=0.62) and *T. vivax* (p=0.03, b_1=0.29) are from Woolhouse *et al.* (1993) and Rogers (1988) and from Tarimo *et al.* (1985) and Rogers (1988) for *T. congolense* (p=0.07, b_1=0.46).

infection with *T. vivax* from 0.91 to 0.61. The known repellents are clearly useless in these circumstances.

The efficacy of a repellent will vary according to tsetse challenge. To illustrate this, it is pertinent to consider three epidemiological scenarios based on a 'high' infection rate of 7.6% (*T. congolense* at Muhaka, Kenya; Tarimo *et al.*, 1985), a 'medium rate' of 3.1% (*T. vivax* at Rekomitjie, Zimbabwe; Woolhouse *et al.*, 1993) and a 'low' rate of 0.16% (*T. brucei* at Rekomitjie, Zimbabwe; Woolhouse *et al.*, 1993). The transmission co-efficients (b_1) for these species of *Trypanosoma* are 0.46, 0.29 and 0.62 respectively (Rogers, 1988).

Considering a range of fly densities (fig. 1) shows that at high infection rates a repellent exerts a proportionally greater reduction in disease risk at lower densities of tsetse. For instance, with daily biting rates of 500 bites/day a repellent that reduced the biting rate by 90% would reduce the risk of contracting *T. congolense* by 17% to 0.83. At densities of 10 bites/day the same repellent would reduce the risk by 88% to 0.03. At low infection rates the non-linear response between tsetse density and disease risk is not so apparent. Using the same repellent with a daily biting rates of 500/day or 10/day would reduce the risk of infection with *T. brucei* by 82 and 90% respectively. The medium infection rate (*T. vivax* at Rekomitjie) lies between these two extremes with a clear curvilinear relationship between bites/day and infection probability. Thus repellents might be useful in situations with low fly densities and/or low infection rates.

Where cattle are kept in tsetse infected areas of Zimbabwe the tsetse density is low with mean daily catches of <1 tsetse/trap/month and cattle are treated with diminazene if they become infected with typanosomiasis (Barrett, 1994). In such areas, a repellent that reduced the biting rate by 95% could significantly reduce disease incidence and hence drug costs. Low infection rates are typical for *T. brucei* (Rogers, 1988) and thus a repellent might also be particularly useful in protecting people against sleeping sickness.

Vale (1977a) showed that placing men adjacent to an ox halved the numbers of tsetse attracted and reduced the proportion that fed by 75% giving an overall reduction in biting rate of *c.* 90%. This reduction is largely a response to human body odour (Vale, 1979) and thus significant reductions in challenge are apparently achievable through the use of such repellents and work is currently underway to identify these chemicals.

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References

Barrett, J.C. (1994) *Economic issues in trypanosomiasis control: case studies from Southern Africa.* PhD Thesis, University of Reading, 485 pp.

Bursell, E., Gough, A.J.E., Beevor, P.S., Cork, A., Hall, D.R. & Vale, G.A. (1988) Identification of components of cattle urine attractive to tsetse flies, *Glossina* spp. (Diptera: Glossinidae). *Bulletin of Entomological Research* **78**, 281–291.

Davis, E.E. (1985) Insect repellents: concepts of their mode of action relative to potential sensory mechanisms in mosquitoes (Diptera: Culicidae). *Journal of Medical Entomology* **22**, 237–243.

Davis, E.E. & Bowen, M.F. (1994) Sensory physiological basis for attraction in mosquitoes. *Journal of the American Mosquito Control Association* **10**, 316–325.

Den Ouden, H., Thenunissen, J. & Heslinga, A. (1984) Protection of cabbage against oviposition of cabbage root fly *Delia brassicae* L. by controlled release of naphthalene. *Zeitschrift für Angewandte Entomologie* **97**, 341–346.

Dethier, V.G., Browne, L.B. & Smith, C.N. (1960) The designation of chemicals in terms of the responses they elicit from insects. *Journal of Economic Entomology* **53**, 134–136.

Ford, J. & Leggate, B.M. (1961) The geographical and climatic distribution of trypanosome infection rates in *G. morsitans* group of tsetse-flies. *Transactions of the Royal Society of Tropical Medicine and Hygiene* **55**, 383–397.

Francis, B., Green, M. & Payne, C. (1993) *The GLIM system (release 4 manual)*. 821 pp. Oxford, Clarendon Press.

Green, C.H. (1994) Baits methods for tsetse fly control. *Advances in Parasitology* **34**, 229–291.

Hargrove, J.W. & Brady, J. (1992) Activity rhythms of tsetse flies (*Glossina* spp.) (Diptera: Glossinidae) at low and high temperatures in nature. *Bulletin of Entomological Research* **82**, 321–326.

Hargrove, J.W. & Langley, P.A. (1990) Sterilizing tsetse in the field – a successful trial. *Bulletin of Entomological Research* **80**, 397–403.

Holmes, P.H. & Torr, S.J. (1988) The control of animal trypanosomiasis in Africa: current methods and future trends. *Outlook on Agriculture* **17**, 54–60.

Jordan, A.M. (1986) *Trypanosomiasis control and African rural development*. London and New York, Longman.

Kuthiala, A., Gupta, R.K. & Davis, E.E. (1992) Effect of the repellent DEET on the antennal chemoreceptors for oviposition in *Aedes aegypti* (Diptera: Culicidae). *Journal of Medical Entomology* **29**, 639–643.

Laveissière, C., Vale, G.A. & Gouteux, J.-P. (1990) Bait methods for tsetse control. pp. 47–74 *in* Curtis, C.F. (*Ed.*) *Appropriate technology for vector control*. Boca Raton, CRC Press Inc.

Randolph, S.E., Williams, B.G., Rogers, D.J. & Connor, H. (1992) Modelling the effect of feeding-related mortality on the feeding strategy of tsetse (Diptera: Glossinidae) *Medical and Veterinary Entomology* **6**, 231–240.

Rogers, D.J. (1988) A general model for the African trypanosomiases. *Parasitology* **97**, 193–212.

Rutledge, L.C., Sofield, R.K. & Moussa, M.A. (1978) A bibliography of diethyl toluamide. *Bulletin of the Entomological Society of America* **24**, 431–439.

Swynnerton, C.F.M. (1936) The tsetse flies of East Africa. *Transactions of the Royal Entomological Society of London* **84**, 579 pp.

Tarimo, S.A., Snow, F.W., Butler, L. & Dransfield, R. (1985) The probability of tsetse acquiring trypanosome infection from single blood meal in different localities in Kenya. *Acta Tropica* **42**, 199–207.

Thomson, J.W., Mitchell, M., Rees, R.B., Shereni, W., Schoenfeld, A.H. & Wilson, A. (1991) Studies on the efficacy of deltamethrin applied to cattle for the control of tsetse flies (*Glossina* spp.) in southern Africa. *Tropical Animal Health and Production* **23**, 221–226.

Torr, S. J., Hall, D.R. & Smith, J.L. (1995) Responses of tsetse flies (Diptera: Glossinidae) to natural and synthetic ox odours. *Bulletin of Entomological Research* **85**, 157–166.

Vale, G.A. (1974a) The response of tsetse flies (Diptera: Glossinidae) to mobile and stationary baits. *Bulletin of Entomological Research* **64**, 545–587.

Vale, G.A. (1974b) New field methods for studying the response of tsetse flies (Diptera: Glossinidae) to baits. *Bulletin of Entomological Research* **64**, 199–208.

Vale, G.A. (1977a) Feeding responses of tsetse flies (Diptera: Glossinidae) to stationary hosts. *Bulletin of Entomological Research* **67**, 635–649.

Vale, G.A. (1977b) Field responses of tsetse flies (Diptera: Glossinidae) to odours of men, lactic acid and carbon dioxide. *Bulletin of Entomological Research* **69**, 459–467.

Vale, G.A. (1980) Field studies of the responses of tsetse flies (Glossinidae) and other Diptera to carbon dioxide, acetone and other chemicals. *Bulletin of Entomological Research* **70**, 563–570.

Vale, G.A. (1993) Development of baits for tsetse flies (Diptera: Glossinidae) in Zimbabwe. *Journal of Medical Entomology* **30**, 831–842.

Vale, G.A. & Hall, D.R. (1985) The role of 1-octen-3-ol, acetone and carbon dioxide in the attraction of tsetse flies, *Glossina* spp. (Diptera: Glossinidae), to host odour. *Bulletin of Entomological Research* **75**, 209–217.

Vale, G.A. & Hargrove, J.W. (1979) A method for studying the efficiency of traps for tsetse flies (Diptera: Glossinidae) and other insects. *Bulletin of Entomological Research* **69**, 183–193.

Vale, G.A., Hargrove, J.W., Cockbill, G.F. & Phelps, R.J. (1986) Field trials of baits to control populations of *Glossina morsitans morsitans* Westwood and *G. pallidipes* Austen (Diptera; Glossinidae). *Bulletin of Entomological Research* **76**, 179–193.

Vale, G.A., Hall, D.R. & Gough, A.J.E. (1988) The olfactory responses of tsetse flies, *Glossina* spp. (Diptera: Glossinidae), to phenols and urine in the field. *Bulletin of Entomological Research* **78**, 293–300.

Woolhouse, M., Hargrove, J.W. & McNamara, J.J. (1993) Epidemiology of trypanosome infections of the tsetse fly *G. pallidipes* in the Zambesi Valley. *Parasitology* **106**, 479–485.

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