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.
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 et al., 1988) have been shown to reduce the catch of human and animal try'Panosomiasis rely on insecticide-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 x 1 m) flanked with 0.5 x 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 were killed or stunned and fell onto the tray where it became stuck. Tsetse generally fall vertically (Vale, 1974b) and so, by recording the numbers of tsetse caught directly below the netting and cloth panels, it was possible to gauge 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-methylphenol (0.8 mg/h) and 3-n-propylphenol (0.1 mg/h) at rates known to increase the catch of tsetse in Zimbabwe (Vale & Hali 1985; Vale et al., 1988) and henceforth this blend of odour is termed AOP. Acetone was dispensed from an open bottle and octenol and the phenols were dispensed from sealed sachets of low density polyethylene, 0.15 mm thick with surface area of 50 cm² (Laveissiere 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 or 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 x 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 x 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 polyethylene sachets. Unless reported otherwise, the odours were placed on the ground 30 cm downwind of the trap, target 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 or an incomplete ring (8 m dia.) of six electric nets (1.5 x 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...
Repellents for tsetse

Effects of repellents on trap catch

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

<table>
<thead>
<tr>
<th>Chemical</th>
<th>2-Methoxyphenol</th>
<th>Acetophenone</th>
<th>Hexanoic acid</th>
<th>Pentanoic acid</th>
<th>Lactic acid</th>
<th>Acetic acid</th>
<th>Butanoic acid</th>
<th>Formic acid</th>
<th>Propionic acid</th>
<th>3-methyl butanoic acid</th>
<th>DEET</th>
<th>treated cloth (20 x 30 cm)</th>
<th>Naphthalene</th>
<th>Trace</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>10</td>
<td>5</td>
<td>5</td>
<td>10</td>
<td>100</td>
<td>10</td>
<td>10</td>
<td>10</td>
<td>20</td>
<td>10</td>
<td>10</td>
<td>10</td>
<td>10</td>
<td>6</td>
</tr>
<tr>
<td>Catch (n)</td>
<td>14</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>6</td>
</tr>
<tr>
<td>Catch transformed ± SE</td>
<td>2.03 ± 0.0648</td>
<td>2.09 ± 0.0648</td>
<td>1.83 ± 0.069</td>
<td>1.82 ± 0.0553</td>
<td>2.03 ± 0.053</td>
<td>0.778 ± 0.0738</td>
<td>1.22 ± 0.065</td>
<td>1.34 ± 0.0720</td>
<td>2.13 ± 0.0807</td>
<td>1.30 ± 0.0366</td>
<td>2.03 ± 0.053</td>
<td>1.25 ± 0.0833</td>
<td>2.11 ± 0.0724</td>
<td>1.63 ± 0.0797</td>
</tr>
<tr>
<td>Catch P index</td>
<td>0.14 ***</td>
<td>0.31 ***</td>
<td>0.36 **</td>
<td>0.55 *</td>
<td>0.56 ***</td>
<td>0.70 ns</td>
<td>0.72 ns</td>
<td>0.87 ns</td>
<td>0.80 ns</td>
<td>0.83 ns</td>
<td>0.91 ns</td>
<td>1.29 ns</td>
<td>1.04 ns</td>
<td>1.13 ns</td>
</tr>
</tbody>
</table>

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. \( \text{A} = \) acetone (500 mg/h), \( \text{O} = 1\text{-octen-3-ol} \) (0.4 mg/h), \( \text{P} = 4\text{-methylphenol} \) (0.8 mg/h) + 3-n-propylphenol (0.1 mg/h).

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 acid 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 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 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).

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 x sites x 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 data for the sexes are therefore pooled henceforth.

The catches (\( n \)) were transformed, accompanied by their detransformed 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 \( \chi^2 \). 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.
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).

<table>
<thead>
<tr>
<th>Bait</th>
<th>Detransformed</th>
<th>Transformed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Experiment 1 (12 reps)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>AOP only</td>
<td>37.4</td>
<td>1.584a</td>
</tr>
<tr>
<td>AOP+2-ME</td>
<td>6.3</td>
<td>0.863b</td>
</tr>
<tr>
<td>AOP+2-ME+PEN</td>
<td>5.4</td>
<td>0.806b</td>
</tr>
<tr>
<td>AOP+2-ME+ACETO</td>
<td>8.5</td>
<td>0.978b</td>
</tr>
<tr>
<td>AOP+2-ME+PEN+ACETO</td>
<td>7.9</td>
<td>0.949b</td>
</tr>
<tr>
<td>None</td>
<td>5.2</td>
<td>0.792b</td>
</tr>
<tr>
<td>Transformed SE</td>
<td></td>
<td>0.0874</td>
</tr>
<tr>
<td>Experiment 2 (12 reps)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>AOP only</td>
<td>61.2</td>
<td>1.794a</td>
</tr>
<tr>
<td>AOP+PEN</td>
<td>33.6</td>
<td>1.539b</td>
</tr>
<tr>
<td>AOP+PEN+2-ME</td>
<td>6.5</td>
<td>0.875c</td>
</tr>
<tr>
<td>Transformed SE</td>
<td></td>
<td>0.0552</td>
</tr>
<tr>
<td>Experiment 3 (12 reps)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>AOP only</td>
<td>123.1</td>
<td>2.094a</td>
</tr>
<tr>
<td>AOP+ACETO</td>
<td>38.2</td>
<td>1.593b</td>
</tr>
<tr>
<td>AOP+ACETO+2-ME</td>
<td>19.0</td>
<td>1.314c</td>
</tr>
<tr>
<td>None</td>
<td>33.6</td>
<td>1.539b</td>
</tr>
<tr>
<td>Transformed SE</td>
<td></td>
<td>0.0622</td>
</tr>
</tbody>
</table>

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-methyl-phenol (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 were baited with natural ox odour. The results (table 5) were broadly in accord with those from the AOP-baited target. Addition of 2-methoxyphenol had a clear and significant effect, reducing the catch by c. 50%, while acetophenone also reduced the catch of tsetse but the effect was smaller and only significant in one experiment. Pentanoic acid had no significant effect.

**Effect of repellents on trap efficiency**

The results from the traps and targets indicated that pentanoic acid reduced the catch in traps but not at target. Addition of 2-methoxyphenol and acetophenone reduced the catch by both. This might be due to differential effects of repellents on this variable. The results (table 6) show that 2-methoxyphenol and pentanoic acid reduced the efficiency of the traps.
Table 4. The detransformed mean catch (transformed ± SE in brackets) of Glossina pal/idipes, and mean percentage (± SE) alighting on the cloth panel, from targets baited with AOP with or without various repellents.

<table>
<thead>
<tr>
<th>Bait</th>
<th>Mean catch</th>
<th>Percent landing</th>
</tr>
</thead>
<tbody>
<tr>
<td>AOP</td>
<td></td>
<td></td>
</tr>
<tr>
<td>AOP + 2-methoxyphenol</td>
<td></td>
<td></td>
</tr>
<tr>
<td>AOP + pentanoic acid</td>
<td></td>
<td></td>
</tr>
<tr>
<td>AOP + acetophenone</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Each treatment was repeated for 12 replicates. Asterisks indicate that the means are significantly different from AOP (P < 0.05, F-test). A = aceton (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 m²) 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.

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).

<table>
<thead>
<tr>
<th>Repellent</th>
<th>n</th>
<th>Ox odour only</th>
<th>Ox odour + repellent</th>
<th>Transformed mean</th>
<th>SE</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>2-Methoxyphenol</td>
<td>12</td>
<td>63.4 (1.809)</td>
<td>57.1 (1.581)</td>
<td>0.0265</td>
<td></td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>53.6 (1.737)</td>
<td>45.9 (1.228)</td>
<td>0.0387</td>
<td></td>
<td>***</td>
</tr>
<tr>
<td>Acetophenone</td>
<td>12</td>
<td>107.9 (2.037)</td>
<td>97.9 (1.947)</td>
<td>0.0283</td>
<td></td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>83.9 (0.968)</td>
<td>73.9 (0.919)</td>
<td>0.0694</td>
<td></td>
<td>ns</td>
</tr>
<tr>
<td>Pentanoic acid</td>
<td>12</td>
<td>79.3 (1.905)</td>
<td>68.4 (1.841)</td>
<td>0.0317</td>
<td></td>
<td>ns</td>
</tr>
</tbody>
</table>

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 behavioural 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-methoxyphenol. 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 cut (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 hypothesis 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 such as mechanism (c) or possibly being produced in larger quantities by unsuitable hosts and activating specific ‘noxious-substance’ receptors, as in mechanism (d). Swynnerton (1930) 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 acetaldehyde 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 signal specific to host finding whether olfactory, visual or a different type. 2-Methoxyphenol obviously has some structural similarities to the attractant phenols, 4-methylphenol and 3-n-propylphenol, and acetaldehyde was originally tested by Vale (1980) as an analogue of the attractant ketone acetone.

Practical implications

The present study underscores a problem recently highlighted by Vale (1993) concerning the use of traps to make deductions about tsetse behaviour — or indeed the behaviour of any insect. The initial studies using traps indicated that the repellents studied were potent and that therefore be effective in controlling trypanosomiasis. However, analysis of the responses of tsetse attracted to and then feeding on an ox revealed that the effect was relatively slight. Adding 2-methoxyphenol and 3-n-propylphenol to a trap resulted in a pronounced decrease in trap efficiency but there did not appear to be an equivalent and large close-range effect with a host. Clearly, making deductions regarding the behaviour of tsetse, based solely on their responses to traps, must be done very cautiously.

The repellents studied here halved the number of tsetse attracted to a host, but none had an effect on landing, and only pentanoic acid had a slight and significant effect on 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. At Rekomitjie, the prevalence of infection in G. palpalipes is c. 3% (Ford & Leggate, 1961; Woolhouse et al., 1993) and Rogers (1988) estimated b, 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, 1977) and of these 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 infection by 60%.

Table 7. Percent feeding efficiency (± SE) for G. pallidipes feeding on an ox ± various repellents.

<table>
<thead>
<tr>
<th>Odour</th>
<th>Feeding efficiency</th>
<th>Replicates</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ox</td>
<td>+ repellent</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2-Methoxyphenol</td>
<td>46.8 (664)</td>
<td>40.8 (409)</td>
<td>24</td>
</tr>
<tr>
<td>Acetaldehyde</td>
<td>45.3 (547)</td>
<td>45.1 (563)</td>
<td>13</td>
</tr>
<tr>
<td>Pentanoic acid</td>
<td>39.2 (299)</td>
<td>43.8 (194)</td>
<td>29</td>
</tr>
</tbody>
</table>

Feeding efficiency is the total catch of fed flies from the inside of 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.
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 coefficients (b_i) 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 10 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 trypanosomiasis (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.

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