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Catches of tsetse (*Glossina* spp.) (Diptera: Glossinidae) from traps and targets baited with large doses of natural and synthetic host odour

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Abstract

In Zimbabwe, catches of *Glossina morsitans morsitans* Westwood and *G. pallidipes* Austen, at an odour source produced by up to 60 tonnes of cattle, fell by 90% from April to October 1987. With the time effect removed, the catches were: positively correlated with daily maximum temperature; up to twice as high with a trap as with an electrified target; and unaffected by the presence of an incomplete ring of electrified netting (11.5 m diameter) around the catching site. Catches increased as a power of bait mass in accord with the theory of odour dispersal. The power was ca. 0.32–0.44 for *G. pallidipes*, ca. 0.15 for post-teneral *G. m. morsitans*, 0.67 for Stomoxyinae and 0.48 for non-biting muscids. Earlier results from dose-response studies accord with the new model. Tsetse catches were 1.7–4.5 times higher with 20 tonnes of cattle as bait than with a synthetic simulate of this dose, consisting of carbon dioxide, acetone, butanone, octenol and phenolic residues. Important olfactory components thus remain to be identified. Trap efficiency for *G. m. morsitans* rose from 10–20% to 40% with increasing bait mass between 0 and 5 tonnes; thereafter bait mass had no effect. Increased efficiencies were also seen in Stomoxyinae (5 to 60%) and in post-teneral *G. pallidipes* (45 to 70–80%). Increases in catch for bait mass greater than five tonnes were due to increased attraction rather than increased efficiency. Targets were 60–66% efficient for *G. pallidipes*, regardless of dose; for *G. m. morsitans* the efficiency was ca. 54% when unbaited and 24–35% when 60 tonnes of cattle were used as bait. The probability that *G. pallidipes* landed on the cloth part of the target, rather than colliding with the flanking nets, increased as the square of the bait mass for both sexes–from 0.11 to 0.22 for males and from 0.06 to 0.15 for females. There was no effect of bait mass on landing probability for *G. m. morsitans* and no difference between the sexes; ca. 11% of the catch landed on the cloth portion of the target. Efficiency and landing behaviour were independent of climate and season.

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Introduction

The cost-effectiveness of bait systems for surveying and controlling (Diptera: Glossinidae) tsetse *Glossina morsitans morsitans* Westwood and *G. pallidipes* Austen (Diptera:Glossinidae) has increased *c.* 100-fold in the past decade (Vale, 1993a). About half this improvement is due to the use of attractants identified from host odour (Vale, 1982; Vale & Hall, 1985; Owaga *et al.*, 1988; Vale *et al.* 1988a). It is desirable to know how the cocktail of available odours compares with natural host odour and, *inter alia*, what scope there is for improvement by optimising odour doses and using attractants as yet unidentified. We investigate here the catches obtained using a wide range of doses of natural host odour, and simulates consisting of the main attractants so far identified.

In calculating the expected efficacy of control by baits, we need to know the proportion of the population treated per device per unit time (Hargrove, 1988). It is also important to estimate the numbers of tsetse which visit a given device but *fail* to be caught, killed or otherwise treated by it, since such knowledge should suggest ways in which the device can be improved. The present study investigated how trap and target efficiency varied over a wide range of doses of natural and artificial host odour.

Study area and methods

Natural odours

Studies were made in April–October 1987 in *Colophospermum mopane* (Leguminosae) woodland near Rekomitjie Research Station, Zambezi Valley, Zimbabwe, in the habitat of *G. pallidipes* and *G. m. morsitans*. During sampling, cattle (or artificial) odour was evacuated from a shed (fig. 1) by three fans, regulated to produce a flow of 200 l/min/t of cattle. This was discharged, via a 0.75 m (i.d.) pipe, at ground level in the centre of an arena ca. 30 m from the shed. The pens closest to the exhaust were filled first; an auxiliary fan was used for the 40 or 60 tonne treatments, to ensure that air from the back of the shed was pushed to the exhaust. A trap or target was sited 2 m downwind of the pipe exit. A 10 m tall scaffolding tower was erected near the capture arena. Observers sitting on the top of the tower monitored the progress of the experiment, collected samples using a vacuum cleaner and took measurements of the wind direction at the capture site for use in other parts of the study (Holloway, unpublished data).

Up to 200 cattle of both sexes and all ages were used in the experiments. Each animal was identified and weighed at the start of the experiment and monthly thereafter. Different bait masses were obtained by selecting animals from the herd to make up the mass required. Animals were fed on hay and concentrate while in the shed, into which they were herded one hour before catching started each day. At the end of each day all manure and straw was cleaned out of the shed. When not in use, the animals grazed in the bush well away from the experimental area. At night they were kept in a kraal 750 m south-east of the shed.

Artificial odours

Two simulates of cattle odour were produced and tested against natural ox odour. One was estimated to be the equivalent of 60 tonnes of cattle, the second of 20 tonnes. (It was reasoned that any difference in effect between natural and synthetic doses of odour would be detected most easily at high dose rates). The 60 tonne simulate was produced entirely artificially in Pen 1 (fig. 1) of the cleaned shed. Carbon dioxide was released from pressurized cylinders, ketones from open bottles, and phenols and octenol from heat-sealed polythene sachets (Hall *et al.*, 1991). The 20 tonne simulate was only partially artificial; the CO_2, ketones and octenol were dispensed as described above, but the phenolic component of the simulate was derived from fresh residues produced by keeping 20 tonnes of cattle in the shed for three hours and removing them 30 min before starting the experiment.

Rates of release of acetone and butanone were measured by the weight loss of their containers during the experiments. Rates of release of the phenols and octenol were assessed by drawing air from the pit outlets at 2 l/min

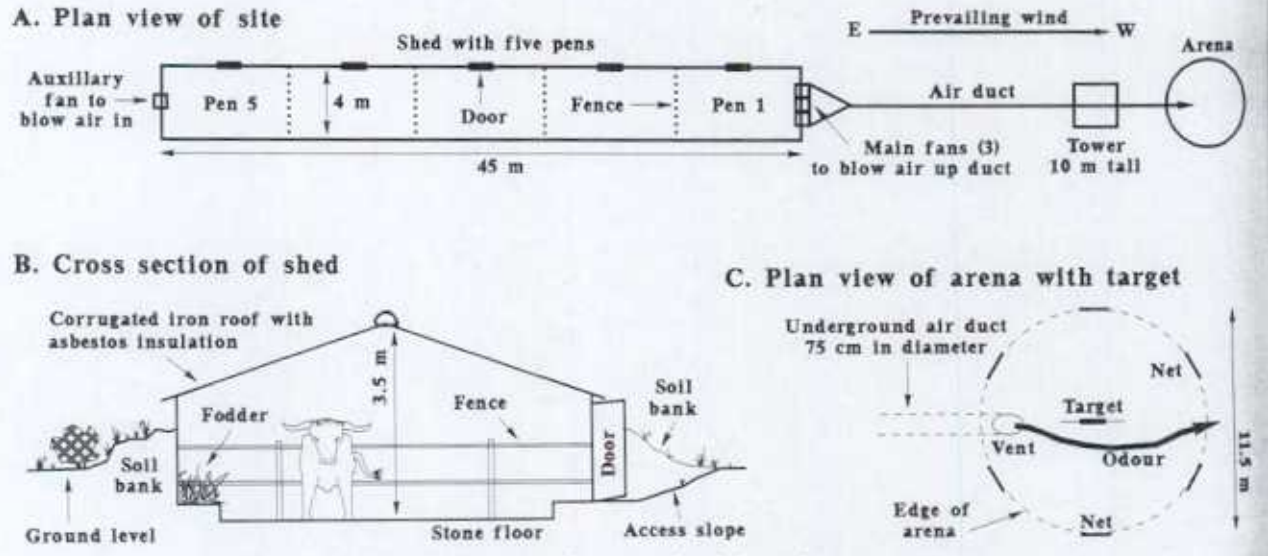


Fig. 1. Experimental set-up at the shed sampling site.

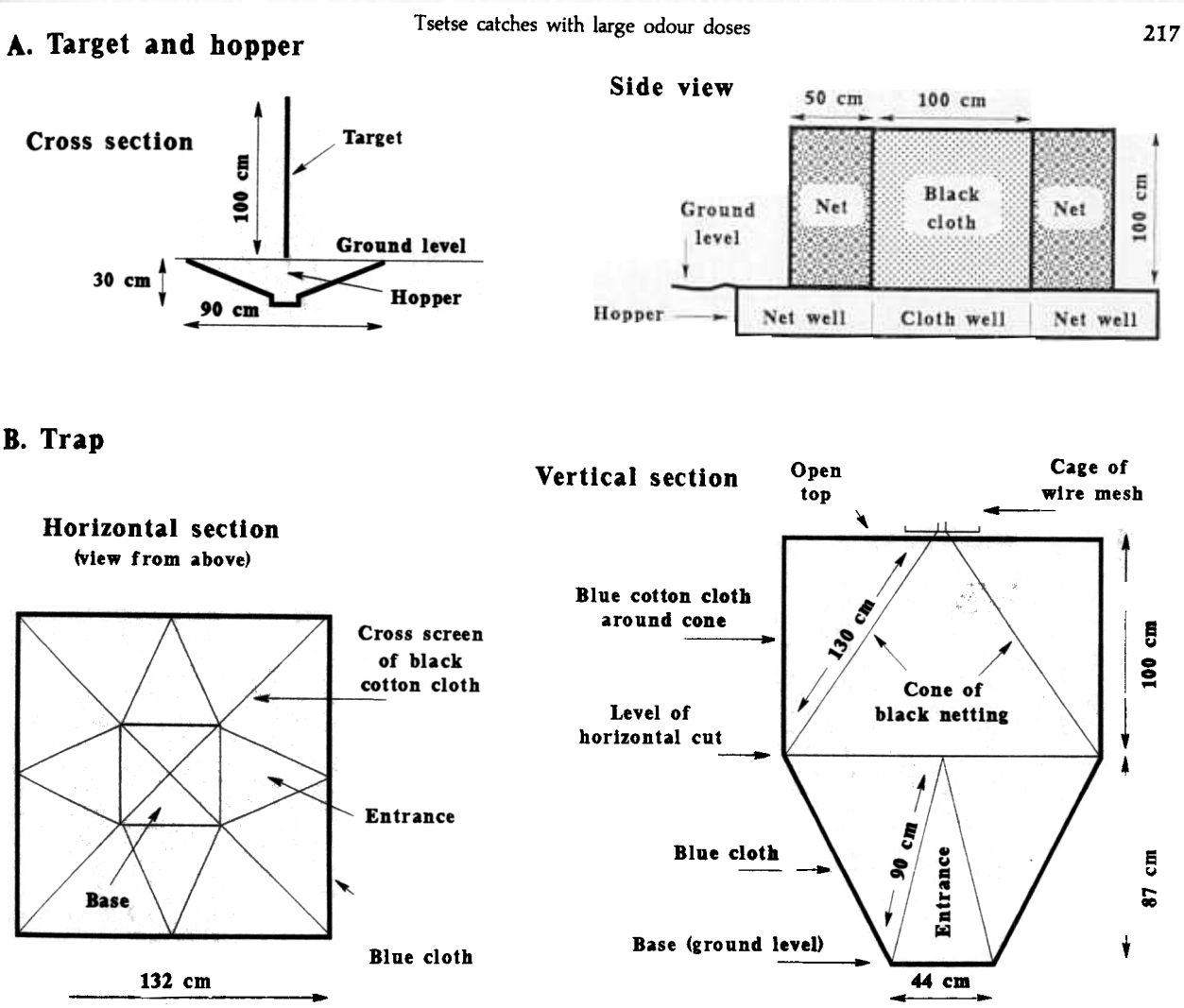


Fig. 2. Capture systems used at the shed sampling site.

through filters containing 100 mg Porapak Q (Waters, Milford, MA 01757, USA; 50-8- mesh). Trapped volatiles were removed with purified dichloromethane (3×0.1 ml) and the resulting solutions analysed by capillary gas chromatography linked to mass spectrometry using decyl acetate (10 µg) as internal standard.

Traps and targets

Insects were caught in an H11 trap (fig. 2B), with the collecting cage changed hourly, or on a target (Vale *et al.*, 1988b) comprising a central black cloth panel measuring 1×1 m with a netting panel 1×0.5 m at each flank (fig. 2A). Insects stunned by an electric grid covering the target surface fell into hoppers on the ground; they were sorted into those landing on the cloth and those colliding with the upwind or downwind netting panels. In addition to tsetse, *Stomoxys calcitrans* (Linnaeus), low numbers of *S. niger* Macquart, non-haematophagous Muscidae and various other (unidentified) insects were also collected.

As controls, H11 (fig. 2B) and F3 traps (Flint, 1985) were deployed ca. 2 km south of the shed, and another pair ca. 9 km north-north-east of the shed at the Nyakasakana Gate on the Rekomitjie River. They were baited with acetone, released at ca. 200 mg/h, and 1-octen-3-ol (octenol), 3-n-propyl-phenol and 4-methyl phenol released at ca. 0.05, 0.4 and 0.8 mg/h, respectively.

Experimental design

Experiments ran for three hours in the afternoon, i.e. when tsetse were most available to stationary baits at this time of year (Hargrove & Brady, 1992). The exact starting and finishing times varied slightly with season, but typically were 1500 and 1800 h respectively. The H11 trap was tested with odour produced by the following bait masses (in tonnes; numbers of replicates for each mass in parentheses): nil (17), 0.5 (6), 5 (7), 10 (6), 20 (19), 40 (7) and 60 (13); for the target the masses used were nil (8), 10 (2), 20 (2), 40 (2) and 60 (8) tonnes. No attempt was made to use the same number of replicates for each treatment; emphasis was placed on the 0 and 60 tonne treatments. Within months, treatments were allocated at random to available days. Replicates of treatments were tested throughout the study, except in September and October when there were no 60 tonne treatments.

Preliminary analysis indicated a power function relationship between catch and bait mass, i.e. a linear relationship between the logs of these two variables. This creates a problem because both catch and bait were zero on occasion. To circumvent this problem we added one to each daily catch and 0.1 tonne to each odour dose before performing the log transformations. The addition to the odour dose may be regarded as allowing for the visual stimulus of the trap or target which was present even when the odour dose was zero.

Efficiency

The ability of a device to capture flies attracted to it has been termed its *efficiency* (Vale & Hargrove, 1979; Hargrove, 1980) and we use the term only in this sense. Catches can be increased by attracting more flies to the device and/or by increasing its efficiency. The device under test in the arena was surrounded with an incomplete ring (diameter 11.5 m) of six electrified nets (1.5 × 1.5 m) covering 25% of the ring's circumference (fig. 1C). The efficiency was defined as the number of insects caught by the test device as a proportion of those entering the area bounded by the ring of nets. Following Vale & Hargrove (1979) it was estimated for the jth experiment by $\hat{e}_j = x_j/(x_j + 4I_j)$ where x_j is the catch of the test device and I_j is the total catch on the inside of the nets in the circle. For data pooled within each odour dose the pooled estimate of the efficiency is given by:

$$\hat{E} = \sum_{j=1}^{n} x_j / \left(\sum_{j=1}^{n} (x_j + 4I_j)\right)$$

Interpretation of tables

Preliminary analysis indicated that the logarithm of fly catches (n) varied approximately as a linear function of season (t) and daily maximum temperature (T) and that there were separate effects due to the locality (L) in which trapping was carried out and the type of trapping system (S) used. Moreover, catch appeared to increase as a power of odour dose (M). These observations led to the consideration of models of the type:

$$\log(n) = a + bt + cT + d \log M + eR + fS \qquad (1)$$

where a, b, c, d, e and f are constant coefficients. Taking antilogs of both sides we get the equivalent formulation

$$n = \mathrm{A}.B^t.C^T.M^d.E^R.F^S \qquad (2)$$

where $a = \log A$, $b = \log B$, etc. For each of the independent variables, except for M, it follows that the value of its coefficient in (2) (or the antilog of the coefficient in (1)) gives the proportional expected change in the catch for a unit change in the value of that variable. For example, the proportional expected change in catch ($n_{\tau+1}/n_\tau$) due to an increase in T from τ to $\tau + 1$ (for constant t, M, R and S) is given by:

$$n_{\tau+1}/n_\tau = C^{\tau+1}/C^\tau = C = \text{antilog}\,(c) = 10^c$$

As a numerical example, for female *G. pallidipes* (Table 1), the cofficient (c) of T is 0.055. We then have $C = 10^c = 1.14$. Thus the model predicts that catches increase by 14% for an increase in T of 1°C.

Independent variables such as sampling system or region are entered as *levels*. Each level has been assigned a dummy value of either 0 or 1 (e.g. in table 1, for trap type, F3 = 0, H11 = 1) which are entered into the equation exactly as for a continuously distributed variable. The antilog of the estimated coefficient thus gives the factor by which the catch changes between levels. For example, for female *G. pallidipes* (table 1), the coefficient of 'trapping system' is 0.28 with antilog 1.91. Catches of this fly were thus, on average, 1.91 times as high from the H11 as from F3. The dummy values 0 and 1 are convenient arbitrary choices. The reader may check that choosing different dummy values (1 and 2 say) affects the value of the coefficients, but not the expected difference between the catches for the different treatments in question.

In the case of the variable M the coefficient D (=antilog (d)) gives the factor by which the catch is expected to change for a *10-fold increase* in bait mass (for constant t, T, L and S). To see this, denote the catch at mass M by $n(M)$. Then:

$$n(10.M)/n(M) = (10.M)^d/(M)^d = 10^d = D$$

For example, for post-teneral female *G pallidipes* (table 2), the coefficient $d = 0.441$ so that $D = 10^{0.441} = 2.8$. Thus a 10-fold

Table 1. The effect of season, temperature, location and trap design on catches of tsetse from traps baited with acetone, octenol, 3-n-propyl-phenol and 4-methyl phenol (see Methods). April-Ocotober 1987.
Model: $\log(n+1) = a + b\,(t/100) + cT + dL + eS$

I Species	II Sex (r^2)	III a	IV $t/100$ (days)	V T (°C)	VI Locality	VII Trapping System
G. m. morsitans	male (0.57)	0.810	−0.483 ± 0.022 (490) (0.33)	N.S. (0.4) (−)	0.098 ± 0.027 (13.6) (1.25)	0.333 ± 0.027 (156) (2.15)
G. m. morsitans	female (0.66)	0.502	−0.660 ± 0.022 (913) (0.22)	0.027 ± 0.003 (69) (1.06)	N.S. (2.6 (−)	0.196 ± 0.026 (55) (1.57)
G. pallidipes	male (0.63)	0.553	−0.554 ± 0.027 (431) (0.28)	0.033 ± 0.004 (70.9) (1.08)	0.509 ± 0.032 (246) (3.23)	0.363 ± 0.032 (126) (2.31)
G. pallidipes	female (0.69)	0.120	−0.487 ± 0.024 (398) (0.33)	0.055 ± 0.004 (237) (1.14)	0.650 ± 0.030 (481) (4.47)	0.280 ± 0.030 (89.6) (1.91)

Key: t − day of experiment; T − maximum temperature; L − sampling locality (coding Nyakasakana = 0; Rekomitjie = 1); S − trapping system (coding F3 = 0; H11 = 1). Numbers in the body of the table are the estimated values of the coefficients a, b, c, d and e (± SE). Below each coefficient is its F value and the antilog of the coefficient (see notes on interpretation).

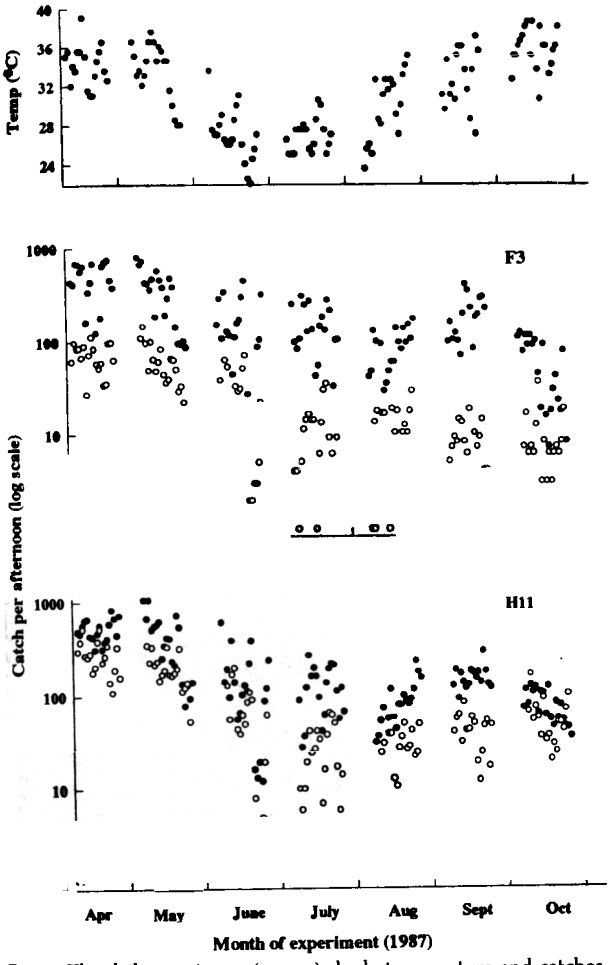


Fig. 3. The daily maximum (screen) shade temperature and catches of post-teneral female *Glossina pallidipes* from the control traps at Rekomitjie (dots) and the Nyakasakana Gate (circles) between 8 April and 25 October 1987. The traps were baited with acetone, octenol, 3-n-propyl-phenol and 4-methyl phenol (see Methods).

increase in bait mass leads to a 2.8-fold increase in the expected catch of this fly.

Unless otherwise stated, logarithmic transforms were to base 10 and references to statistically significant effects imply $P < 0.05$ after the application of an appropriate F test.

Results

All catches were influenced by a subset of the following factors: season, maximum temperature, capture device, experimental site, and the qualitative and quantitative makeup of the odour source. The complexities of the resulting models, compounded by necessary log transformation of the catches and of odour doses, cannot generally be illustrated in a single graph. To define the various models precisely we require tables. However, these are necessarily very detailed, interrupt the flow of the text, and give no easy intuitive sense of what is happening. Accordingly, while tables are included for completeness, readers are advised to ignore, at first reading, references to these tables. Rather they should refer to the text figures which provide simplified visualizations of the most important features of the study.

Control catches using traps baited with synthetic odour only

Catches of male and female *G. m. morsitans* and *G. pallidipes* from the F3 trap at the Nyakasakana Gate control site averaged ca. 10, 20, 40 and 70, respectively, per afternoon at the start of the experiment. They were 1.3–4.5 times higher than this at the Rekomitjie control site (table 1, col. VI) and catches from the H11 at each site were 1.6–2.3 times as high as those from the F3 trap (fig. 3; table 1, col. VII). The daily catch of tsetse at both control sites decreased by *c.* 90% during the course of the experiment (fig. 3) presumably due to seasonal population changes. When this trend was removed, catches at both sites increased with daily maximum temperature by 6–14% per °C (table 1, col. V). No quadratic effect of temperature was detected; this was probably because only a small number of very hot days (when catches are expected to decrease) occurred during the experiment.

Experiments at the shed

Catches with natural odour

The distribution of catches over the afternoon varied with season (fig. 4). At the hottest times of year, catches increased as the afternoon progressed and most flies were caught in the last hour. In the coolest months (June and July) they were caught throughout the afternoon (*cf.* Hargrove & Brady, 1992). These changes were independent of bait mass.

As with the control sites, catches at the shed generally declined during the experiment (fig. 5) and increased with maximum temperature (table 2, col. VI) by 4–9% per °C. At the start of the experiment, catches of male and female *G. m. morsitans* and *G. pallidipes* from the unbaited H11 trap, plus ring of nets, were ca. 10, 20, 50 and 120, respectively. When baited with the odour of 60 tonnes of cattle at this time the catches increased to 30, 60, 800 and 2000, respectively. Removal of the incomplete ring of electrified nets did not reduce tsetse catches, except those of male *G. m. morsitans* which fell by a factor of 2.25 (table 2, col. VIII). Substituting the black electrified target for the blue H11 trap made no difference to catches of *G. m. morsitans*, but cut *G. pallidipes* catches by 30–50% (table 2, col. IX). Catches of non-biting muscids were ca. 80% *lower* when the ring of nets was present and were 2.6 times higher from the target than from the trap (table 2, cols. VIII and IX).

If the effects of time and temperature are removed, we can illustrate the important result that catches increase as a power function of odour dose (fig. 6) and that the rate of increase of log catch with log dose was markedly higher for *G. pallidipes* than for *G. m. morsitans*. Detailed study of table 2 (col. VII) shows that the rates of increase differed by a factor of three between species, that the rate was ca. 15–25% less for teneral (not yet fed) than for post-teneral *G. pallidipes* and that, within each age category for both species, there was little difference between the sexes. Increased dose thus resulted in decreased percentages of tenerals and of *G. m. morsitans* in the catch, but did not affect the sex ratio. The model predicts that a 10-fold increase in dose leads to a 2.1- to 2.8-fold increase in *G. pallidipes* but only a 1.4-fold increase for post-teneral *G. m. morsitans* (table 2, col. VII).

For *G. pallidipes*, figure 6 suggests that the rate of increase of catch with dose is greater for the trap than for the target. In the tables presented in the text we restrict our view to models where no interaction terms are considered. Inclusion of first order interaction terms led to even more complex models than those presented and to considerable problems of interpretation. Accordingly, and because the more complex models did not explain much more of the variance, they are not presented here. However, we note that there was a significant interaction between capture device and odour-dose (see Discussion).

Since catch level and maximum temperature were both correlated with day of experiment, it may be objected that the qualitative and quantitative relationships between catch and bait mass estimated by multiple regression (table 2) are unreliable. This problem was investigated by repeating the analysis using, as the dependent variable, catches at the shed expressed as a proportion of the total catch at the control sites. Variance due to season and weather was thereby removed, and the effect of bait mass could be viewed in isolation. For post-teneral tsetse, particularly *G. pallidipes* for which the catches were greatest and least variable, catch index and bait mass were still apparently related by a power function (fig. 7) and the coefficients were similar to those obtained using multiple regression. There thus seems to be no reason to doubt the general validity of the effects of odour dose estimated in table 2.

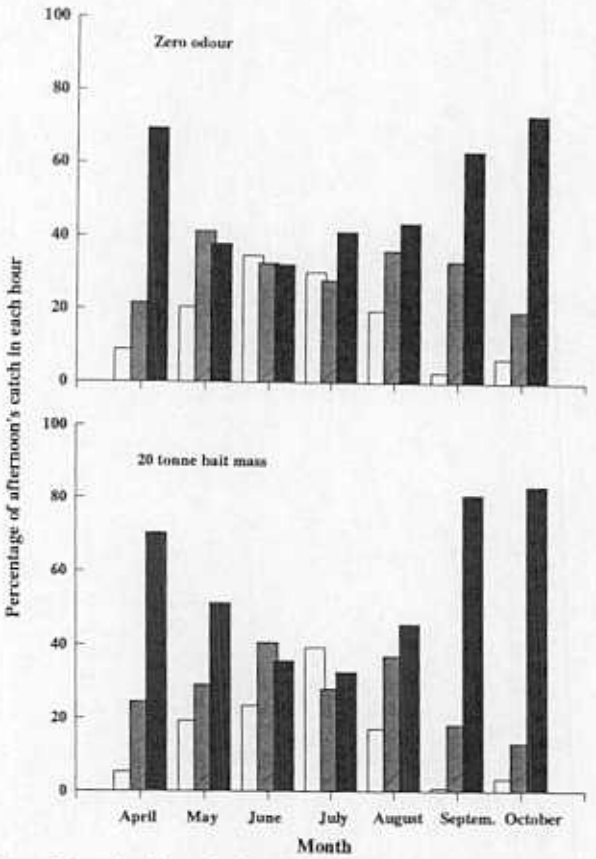


Fig. 4. Mean hourly catch distribution of female *Glossina pallidipes* in an H11 trap using no odour or 20 tonnes of cattle as odour source. The percentage catches in the first, second and third hour are denoted by blank, cross-hatched and solid histograms, respectively.

Measurements of odour dose

Production rates of natural attractants by cattle varied within fairly wide limits, but increased as the weight of cattle increased (fig. 8) and were generally of the same order of magnitude as the rates for the residues and the fully artificial odour (table 3). However, although octenol was detectable in all 14 collections of cattle odour, the amount produced was <0.01 mg/h/t. This is much less than the guess made at its concentration, before the start of the experiment, based on preliminary indications from Hall *et al.* (1984). Collections of octenol made at the exit of the air duct from live cattle, residues, or an artificial source showed that the amount of this chemical in the fully artificial simulate was ca. 100 times as high as the natural dose in this particular experiment.

Simulated host odours

When the partially artificial host odour was substituted for natural odour, mean catches of post-teneral *G. pallidipes* were approximately halved from 133 to 81 for males and from 411 to 200 for females. The corrected catches are shown in figure 6. Catches of Stomoxyinae and of non-biting muscids decreased by 70–80% (table 4). Catches of post-teneral *G. m. morsitans* and of all teneral tsetse were too low (<5 per trapping session) for meaningful analysis.

With the fully artificial simulate (with grossly elevated levels of octenol) tsetse catches were as high as those obtained with 60 tonnes of live cattle (fig. 6) but catches of Stomoxyinae and non-biting muscids were depressed by ca. 90% (table 5).

Analysis of earlier dose-response data

Hargrove & Vale (1978) modelled tsetse catches as a two-part linear function of bait mass, with a discontinuity in the rate of catch increase at the 0.5–1 tonne level (their fig. 1). However, when the model given in table 2 was applied to the original data, it accounted for 53–59% of the variance in the catches of *G. m. morsitans* and 89–93% in those of *G. pallidipes* (table 6). The results, particularly for *G. pallidipes*, suggest that the discontinuity was an unnecessary complication, and support present findings that catch levels increase as a power, rather than as a linear function, of dose. The relative sizes of the constant term and of the coefficients of log $(M+100)$ in tables 2 and 6 show that the overall catch levels, and the rate of increase of catch with bait mass, were higher in the earlier experiment.

Trap efficiency

Analyses of variance and covariance of individual estimates of the trap efficiency indicated that, for post-teneral *G. pallidipes*, efficiency was positively correlated with bait mass, but independent of climatic factors. Accordingly, mean efficiences and their variances were estimated from data pooled for each bait mass (see Methods). For all classes of fly tested, efficiency increased with increasing bait mass but (for female tsetse) only significantly for $M < 10$ tonnes

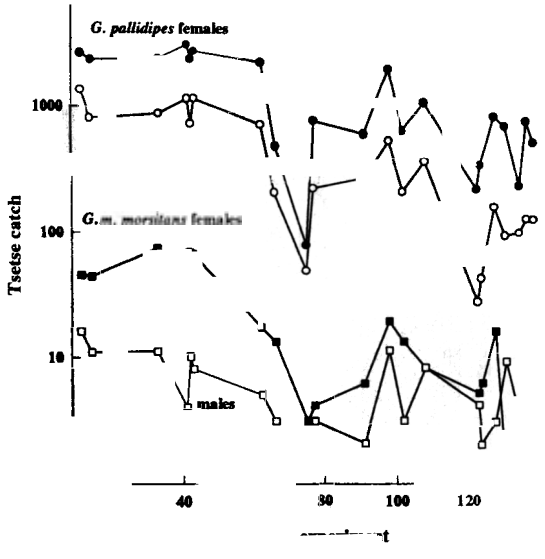
Table 2. Factors affecting catches of tsetse and other flies attracted to cattle odour. April-October 1987.
Model: $\log(n+1)=a+b\ (t/100)+cT+d\ \log\ (M+100)+eR+fS$

I Species	II Age	III Sex (r^2)	IV a	V $t/100$ (days)	VI T (°C)	VII log $(M+100)$ (kg)	VIII Ring of nets	IX Trap/target
G. m.	PT	male (0.58)	−0.032	−0.701 ± 0.088 (62.8) (0.20)	0.018 ± 0.007 (7.2) (1.04)	0.138 ± 0.024 (35) (1.4)	0.353 ± 0.107 (11.0) (2.25)	N.S. (0.1) (−
G. m.	PT	female (0.62)	0.052	−0.644 ± 0.055 (137) (0.23)	0.032 ± 0.008 (15.4) (1.08)	0.151 ± 0.030 (26) (1.4)	N.S. (0.4) (−	N.S. (0.6) (−
G. p.	Ten.	male (0.59)	−0.395	−0.130 ± 0.053 (6.0) (0.74)	N.S. (2.1) (−)	0.317 ± 0.028 (125) (2.1)	N.S. (0.1) (−	−0.289 ± 0.075 (14.8) (0.51)
G. p.	Ten.	female (0.64)	0.852	−0.191 ± 0.058 (11.0) (0.64)	0.018 ± 0.009 (4.3) (1.04)	0.374 ± 0.031 (148) (2.4)	N.S. (1.1) (−	−0.291 ± 0.082 (12.6) (0.51)
G. p.	PT	male (0.76)	−0.083	−0.390 ± 0.052 (56.7) (0.41)	0.031 ± 0.008 (16.7) (1.07)	0.422 ± 0.028 (234) (2.6)	N.S. (0.1 (−)	−0.263 ± 0.074 (12.7) (0.55)
G. p.	PT	female (0.76)	0.038	−0.242 ± 0.051 (22.2) (0.57)	0.037 ± 0.008 (23.5) (1.09)	0.441 ± 0.027 (260) (2.8)	N.S. (0.1) (−	−0.171 ± 0.073 (5.5) (0.67)
St.	−	− (0.82)	−1.586	N.S. (0.04) (−)	0.020 ± 0.009 (5.1) (1.05)			
NBM	−	− (0.87)	0.982	−0.006 ± 0.001 (27.4) (0.99)	N.S. (1.1) (−)			

Key: t − day of experiment; T − maximum temperature; M − mass of cattle used as odour dose; R − presence or absence of ring of nets (absence=0, presence=1); S − trapping system (trap=0 and target=1); *G. m.* − *G. m. morsitans*; *G. p.* − *G. pallidipes*; St − Stomoxyinae; NBM − non-biting Muscidae; Ten. − teneral; PT − post-teneral. Numbers in the body of the table are estimated values of the constants a, b, c . . ., f (± SE). Below each coefficient is its F value and the antilog of the coefficient (see notes on interpretation). For the coefficient of log $(M+100)$ the anti-log is the increase in cath expected for a 10-fold increase in bait mass. Total treatments=98. Numbers of teneral *G. m. morsitans* too small for analysis.

(fig. 9). For male *G. pallidipes* there was a quadratic effect of dose. For high odour doses the trap was 75–80% efficient for *G. pallidipes*, 60% for Stomoxyinae, 40% for *G. m. morsitans* and < 10% for non-biting muscids (fig 9).

Insufficient teneral tsetse were caught to estimate the effect of dose on trap efficiency in these flies. Pooled estimates for all doses suggested that efficiencies for teneral



Target efficiency and distribution of tsetse on targets

Data were obtained only for doses of 0 and 60 tonnes and for the fully artificial simulate. For *G. pallidipes*, target efficiencies were ca. 60–70% (table 7, rows 4 and 5) regardless of dose. For *G. m. morsitans* there was a suggestion, as there was with the traps (fig. 9), that capture efficiency actually declined at high doses (table 7).

Regression analysis of the data for post-teneral *G. pallidipes* showed that, for flies caught on the target, the probability of capture on the cloth surface increased with the square of the bait mass used (fig. 10). This factor accounted for 71% of the variance in the probability that a female *G. pallidipes* landed on the cloth, but only 27% in males. For *G. m. morsitans* there was no effect of bait mass on landing probability and no difference between the sexes; combined data for all doses and for both sexes showed that 10.7 ± 2.7% were caught on the central cloth panel. Temperature and time of year had no detectable effect on landing probability for any class of fly. There was no significant effect of bait mass on the proportion of tsetse colliding with the upwind and downwind sides of the netting wings of the target.

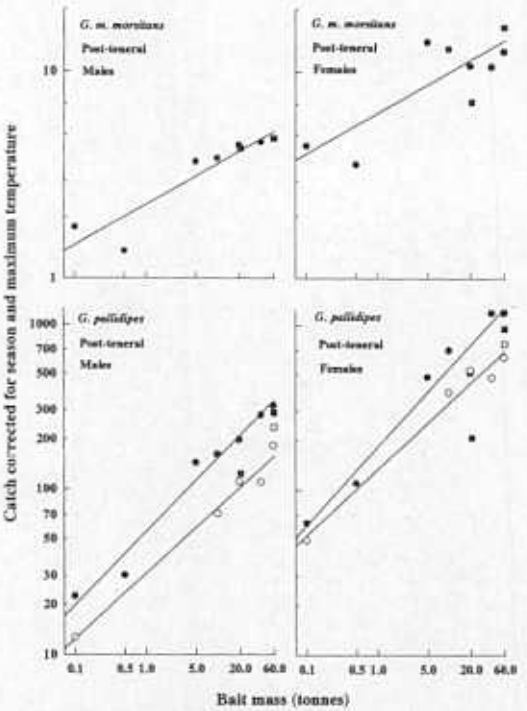


Fig. 6. The effect of bait mass on catches of post-teneral tsetse. Geometric means were calculated for each dose after catches were corrected for season and for the maximum temperature on the day of capture. For *Glossina pallidipes* mean catches from trap (dots) and target (circles) were calculated separately. Catches resulting from the use of simulates are indicated by square symbols; solid for trap catches, hollow for those from targets. Because of the small numbers, catches of *G. m. morsitans* from trap and target are not differentiated.

Discussion

The increase in tsetse catches with bait mass

Changes in trap and target catches of tsetse with increasing odour dose can be due to changes in the number of flies arriving at the device and/or to changes in the efficiency with which the attracted flies are caught. Trap efficiency increased for doses between 0 and 5 tonnes of cattle; thereafter there was little change. Increased catches associated with bait masses greater than five tonnes are thus presumably due to the larger number of flies approaching the trap, as a result of: better recruitment of flies from within a fixed area, and/or better navigation of recruited flies, and/or increasing odour plume length. It is not easy to separate these effects, but we note that the last possibility is consistent with Holloway's finding (unpublished data) that the distance at which tsetse were detected flying upwind towards the odour source increased with bait mass. It is also consistent with the theory of the dispersal of odour particles.

Theoretical issues

Under ideal conditions (no turbulence, flat ground with no trees, wind blowing in a constant direction) the concentration $C(x, y, z)$ of a chemical at a point x m downwind ($y=0$) from an odour source, at height W metres above the ground can be modelled as:

$$C=(E/(2\pi 3600VFG))[(\exp(-(W-H)^2/2G^2)+\exp(-(W+H)^2/2G^2)] \quad (1)$$

(Turner, 1970) where C = concentration (g/m^3), E = emission rate (kg/h), V = wind velocity (m/s), F^2 and G^2 are the variances in the y and z directions, and H and W are the heights (m) above the ground of the emission and receptor sites respectively.

In real situations, where plumes meander and have a filamentous structure, this idealization of the way in which odour concentration decays with distance from the source is inadequate (Murlis *et al.*, 1992). On the other hand, the current data give a rare opportunity to gauge the extent of the errors resulting from the simplification.

Equation 1 can be further simplified here, since the odour is being released at ground level and since most tsetse approach at <1 m above the ground (Vale, 1974) so that $W \cong H \cong 0$. The terms F and G depend on meteorological conditions but, for $H < 50$ m, are proportional to a power of x whose sum (f) lies in the region 1.4–2.0 (Turner, 1970). Thus:

$$C(x,y=0,\ z=0)=KE/(V.x^f) \quad (2)$$

where K (constant) is the product of 3600π and the proportionality constants for F and g.

Our practical results accord with the idea that the number of flies we attract to a point source depends on the distance downwind at which C falls below some constant threshold level (C_T, say). Beyond this threshold distance (x_T)

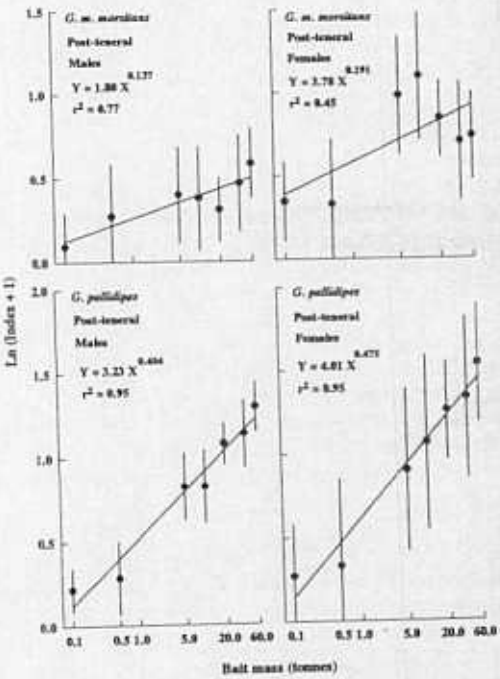


Fig. 7. The effect of bait mass on catch indices for post-teneral tsetse. Each catch at the shed was divided by the total catch at the control sites on that day; the means and standard errors were then calculated from these indicies.

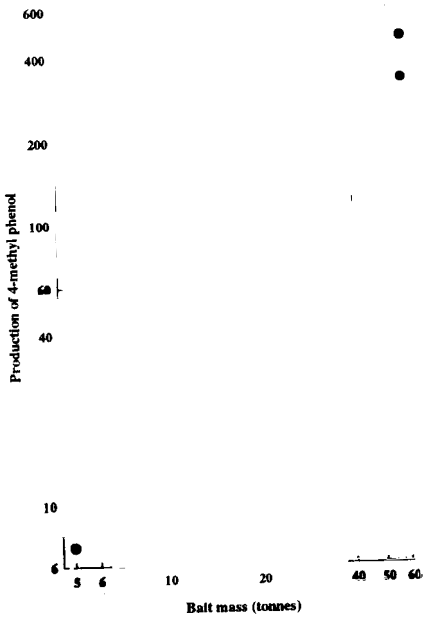


Fig. 8. Rates of production of 4-methyl phenol by different masses of cattle. Graphs for the production of other attractants (table 3) showed similar patterns.

flies in the plume will not detect the smell and will not turn upwind. Putting C_T and x_T into (2), rearranging, and taking logs we have,

$$\log x_T = K' + 1/f \log E - 1/f \log V \qquad (3)$$

where $K' = \log(K/C_T)$ and where $0.5 \leqslant 1/f \leqslant 0.7$.

Simply put, this equation says that the log of the threshold distance increases with the log of the odour concentration and decreases with the log of the wind speed.

Table 3. Mean rates of production of attractants in the actual and simulated odours per tonne of cattle, and from residues produced per tonne of cattle. Production figures are in l/min for carbon dioxide and mg/h for other attractants (UD, undetected).

	Natural	Odour Semi-artificial	Artificial
Months	May, June, October	June	May
Replicates	14	2	3
Chemicals:			
Phenol	0.54[a]	0.40[c]	0.28[d]
3-methylphenol	1.31[a]	1.17[c]	0.41[d]
4-methylphenol	3.32[a]	3.37[c]	2.02[d]
3-ethylphenol	0.09[a]	0.07[c]	–
4-ethylphenol	0.29[a]	0.16[c]	0.17[d]
3/4-n-propylphenol	0.20[a]	0.15[c]	0.23[d]
1-octen-3-ol	<0.01[a]	UD[c]	0.24[d]
Acetone	4[b]	10[e]	10[e]
Butanone	0.04[b]	0.1[e]	0.1[e]
Carbon dioxide	2.5[b]	2.5[e]	2.5[e]

Release rates measured by analysis of trapped samples from: [a]live cattle during experiment; [b]live cattle subsequently; [c]cattle residues during experiment; [d]artificial odours during experiment. Other rates [e] measured by weight loss of the containers during experiment.

If the number of flies entering the odour plume at some point in $[0,x_T]$ is directly proportional to x_T, and if all flies recruited are trapped thereafter with the same efficiency, then the expected catch should be directly proportional to x_T. To this extent there is good *qualitative* agreement between simple theory and our finding that log catch increases linearly with log bait mass.

For post-teneral *G. pallidipes*, in Hargrove & Vale's (1978) study, the estimated value for the coefficient linking log catch and log bait mass was 0.6 for both sexes (table 6), in the middle of the expected range on the basis of equation 3. In the present experiment, for the same classes of flies, the estimated coefficients were only 0.42–0.44. Similarly, Torr (1989) modelled catches of *G. pallidipes* as a power function of dose rates of carbon dioxide and acetone, and estimated coefficients of 0.35–0.43 when acetone was released at >5 mg/h.

In both cases the lower values could be due, in part, to site and seasonal differences and, in Torr's (1989) experiment, could also be due to the fact that he was using only two components of natural host odour. The more important sources of the discrepancy are likely to be the simplifications involved in equation 1. When there is turbulence, particularly due to heating close to the ground, it seems likely that the threshold levels will be reached closer to the odour source, so that the expected values of $1/f$ may be rather lower than indicated by equations 1–3.

In real plumes, molecules arrive at receptors in bursts, rather than in the smooth fashion indicated by equation 1. Measures of the strength of an odour – such as the number of molecules in each burst, the flux of the material moving past a receptor, the peak value of the flux, and the maximum peak measured in some constant time – all decline with distance from the source according to some simple power law (Murlis *et al.*, 1992). The pattern is thus qualitatively similar to that predicted by equation 1.

However, the various measures of odour strength decay at different rates (Murlis *et al.*, 1992). Thus, the mean flux (which is supposed to have a more direct impact on an insect than odour concentration) decreases more rapidly than peak values. If the flux also declines more rapidly than concentration this would explain why our measures of the coefficients linking catch and bait mass are lower than expected from the naïve approach.

The much lower values of the coefficients in *G. m. morsitans* (0.14–0.15) are not easily explained. It is tempting to invoke differences in behaviour linked to flight capability. *G. m. morsitans* appears to be less active than *G. pallidipes* and to depend more on the visual detection of hosts walking past its resting sites than on the location of essentially stationary hosts using olfactory cues (Hargrove, 1991). This may be linked in turn to their smaller size and strength which may mean they are unable to pursue odour trails for as far as *G. pallidipes*. The lower coefficients for teneral *G. pallidipes* (0.32–0.37) may have a similar cause since young flies have an incompletely developed flight musculature (Bursell, 1961).

However, Hargrove & Vale (1978) found that the teneral percentage in trap catches was independent of dose, suggesting that tenerals had no trouble finding their way up the longest plumes produced in that experiment. One could perhaps ascribe this to the fact that the maximum dose (11 tonnes), and hence the maximum distance the plume travelled, was much smaller in that experiment. On the other

Table 4. Comparison of catches of tsetse and other flies between treatments where the odour of 20 tonnes of cattle, a partially synthetic simulate of this dose, were used as an attractant. October 1987.
Model: $\log(n+1)=a+b\ (t/100)+cT+dS$

I Species	II Age	III Sex (r^2)	IV a	V $t/100$ (days)	VI T (°C)	VII Odour
G. m. morsitans	PT		0.120	N.S. (0.03) (−)	N.S. (0.1) (−)	N.S. (0.6) (−)
G. m. morsitans	PT		2.638	N.S. (0.1) (−)	−0.060 ± 0.028 (4.4) (0.87)	N.S. (0.01) (−)
G. pallidipes	Ten.	male (0.51)	14.61	−0.058 ± 0.014 (17.4) (0.87)	−0.087 ± 0.036 (5.9) (0.82)	N.S. (0.02) (−)
G. pallidipes	Ten.	female (0.38)	10.24	−0.051 ± 0.015 (11.3) (0.89)	N.S. (2.3) (−)	N.S. (0.4) (−)
G. pallidipes	PT	male (0.20)	2.123	N.S. (1.7) (−)	N.S. (1.4) (−)	−0.214 ± 0.094 (5.2) (0.61)
G. pallidipes	PT	female (0.32)	2.614	N.S. (17.9) (−)	N.S. (0.2) (−)	−0.314 ± 0.104 (9.1) (0.49)
Stomoxyinae		– (0.46)	1.763	N.S. (0.3)	N.S. (3.4) (−)	−0.626 ± 0.158 (15.6) (0.24)
Non-biting Muscidae		– (0.59)	−5.363	0.036 ± 0.011 (11.0) (1.09)	N.S. (0.8) (−)	−0.439 ± 0.112 (15.5) (0.36)

Key: t − day of experiment; T − maximum temperature; S − odour (natural odour=0; simulate=1); Ten − teneral; PT − post-teneral. Total treatments=18. Numbers in the body of the table are the estimated values of the constants a, b, c and d (± SE). Below each coefficient is its F value and the antilog of the coefficient (see notes on interpretation).

hand, we still found a difference between the coefficients for *G. m. morsitans* and *G. pallidipes* (table 6) indicating that one should be wary of any simplistic explanations of differences based on differential flight capability.

Real and artificial odour

The wholly artificial simulate caught as many tsetse, of all classes, as the highest dose of natural odour used in this experiment, but the amount of octenol dispensed was ca. 100 times as great as that expected in the odour from 60 tonnes of cattle. In the presence of ox odour, increasing the octenol dose from 0.05 to 5 mg/h doubled tsetse catches (Vale & Hall, 1985). Torr *et al.* (in press) found similar effects with both natural and synthetic ox odour for 2 mg/h octenol, relative to 0.014 mg/h from the ox.

When all identified attractants were dispensed at apparently appropriate levels, catches of post-teneral *G. pallidipes* were ca. half of that expected from the equivalent mass of live cattle (table 4). Thus while a number of attractants for

Table 5. The effect on catches of tsetse and other flies of substituting the odour of 60 tonnes of cattle with a totally synthetic simulate of this dose. (Note that the simulate contained 100-fold excess levels of octenol).
Model: $\log(n+1)=a+b\ (t/100)+cT+dP+eR+fD$

I Species	II Age	III Sex (r^2)	IV a	V $t/100$ (days)	VI T (°C)	VII Odour	VIII Ring of nets	IX Trap/target
G. m.	PT	female (0.72)	0.396	−0.823 ± 0.121 (44.4) (0.15)	0.032 ± 0.008 (15.4) (1.08)	N.S. (0.7) (−)	N.S. (0.4)	N.S. (0.1)
G. p.	T	male (0.74)	−0.914	N.S. (1.1) (−)	0.069 ± 0.010 (47.0) (1.17)	N.S. (3.8) (−)	N.S. (0.6) (−)	−0.535 ± 0.076 (49.6) (0.29)
G. p.	T	female (0.72)	−0.925	N.S. (0.0) (−)	0.079 ± 0.012 (47.5) (1.20)	N.S. (2.5) (−)	N.S. (0.3) (−)	−0.588 ± 0.087 (45.4) (0.26)
G. p.	PT	male (0.73)	2.058	−0.763 ± 0.110 (50.9) (0.17)	0.036 ± 0.012 (9.7) (1.09)	N.S. (0.2 (−)	N.S. (0.3) (−)	−0.168 ± 0.081 (4.3) (0.68)
G. p.	PT	female (0.68)	1.733	−0.442 ± 0.100 (17.9) (0.36)	0.056 ± 0.011 (24.6) (1.14)	N.S. (0.8) (−)	N.S. (0.02) (−)	−0.198 ± 0.079 (6.3) (0.63)
St.	–	– (0.74)	0.736	N.S. (0.1) (−)	0.049 ± 0.014 (11.7) (1.12)	−1.058 ± 0.107 (97.1) (0.09)	N.S. (0.4) (−)	N.S. (0.5) (−)
NBM	–	– (0.87)	3.027	N.S. (0.5) (−)	N.S. (2.3) (−)	−0.915 ± 0.100 (83.9) (0.12)	−1.094 ± 0.099 (123) (0.08)	0.286 ± 0.101 (8.1) (1.93)

Key: t − day of experiment; T − maximum temperature; P − odour type (natural odour=0; simulate=1); R − presence or absence of ring of nets (absence=0, presence=1); S − trapping system (trap=0 and target=1); *G. m.* − *G. m. morsitans*; *G. p.* − *G. pallidipes*; St − Stomoxyinae; NBM − non-biting Muscidae; Ten. − teneral; PT − post-teneral. Numbers in the body of the table are estimated values of the constants a, b, c, d, e and f (± SE). Below each coefficient is its F value and the antilog of the coefficient (see notes on interpretation). Total treatments=36.

Table 6. Factors affecting catches, on an electrified target, of tsetse attracted to the odour of 0-11 tonnes of cattle. Data from Hargrove & Vale (1978).

Model: $\log(n+1)=a+b\ (t/100)+cT+d\ \log\ (M+100)$

I Species	II Sex (r^2)	III a	IV $t/100$ (days)	V T (°C)	VI $\log(M+100)$ (kg)
G. m. morsitans	male (0.53)	0.766	N.S.	N.S.	0.270 ± 0.035 (58.2) (1.86)
G. m. morsitans	female (0.59)	0.689	-0.931 ± 0.225 (17.1) (0.12)	N.S.	0.457 ± 0.051 (81.2) (2.86)
G. pallidipes	male (0.93)	0.422	-0.983 ± 0.125 (62.2) (0.10)	0.016 ± 0.007 (4.8) (1.04)	0.612 ± 0.027 (513) (4.09)
G. pallidipes	female (0.89)	0.549	-0.623 ± 0.140 (19.7) (0.24)	0.018 ± 0.008 (4.8) (1.04)	0.608 ± 0.030 (399) (4.06)

Key: t – day of experiment; T – maximum temperature; M – mass of cattle used as odour dose. Numbers in the body of the table are estimated values of the constants a, b, c and d ($\pm$SE). Below each coefficient is its F value and the antilog of the coefficient (see notes on interpretation). For the coefficient of log $(M+100)$ the anti-log is the increase in catch expected for a 10-fold increase in bait mass.

tsetse have been identified, important components still remain to be discovered. Torr *et al.* (in press) arrived at the same conclusion using different techniques.

Catches of Stomoxyinae with the fully and partially synthetic simulates were only 9 and 24% respectively of those obtained with natural odour, and trapping efficiency was reduced by ca. 50% in the presence of the artificial odours. There is thus great scope for increasing catches of Stomoxyinae, both by identifying further components of natural odour important in their attraction, and in the development of efficient traps for these flies.

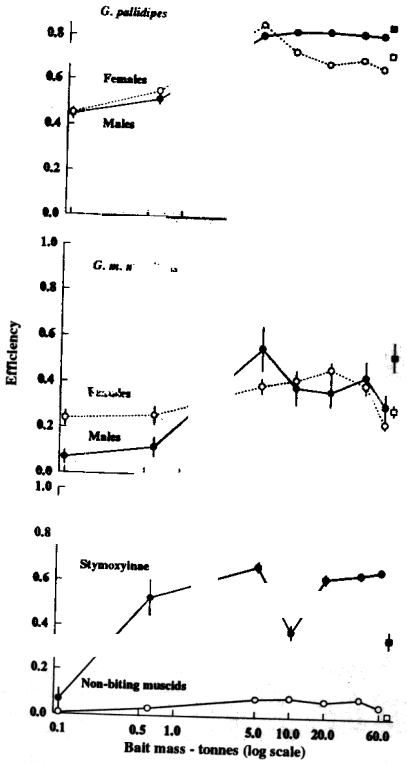


Fig. 9. The efficiency of an H11 trap in the presence of varying levels of natural host odour (circles and dots) or of the high octenol, fully synthetic, simulate (squares).

Catches from traps and targets

Catches of *G. pallidipes* were higher with the trap than the target (fig. 6), in accord with the finding that traps can be more *efficient* than an electrified grid for this species (Vale & Hargrove, 1979). This is partly because the grids fail to kill 100% of the tsetse contacting them (Packer & Brady, 1990). Such an effect would be expected to be aggravated when the number of flies present is highest, consistent with our finding that the discrepancy between the efficiency of the trap and target (and even between the absolute catches from the two devices) was highest in the presence of the greatest odour dose. The difference in efficiencies might also be due in part to differences in the visual stimuli presented by the two devices. Packer & Brady (1990) found that some tsetse visiting odour-baited targets flew around the targets and apparently did not alight, although figures from Vale (1993b) suggest that the effect was small with targets of the type used here.

Efficiency estimates

Packer & Brady (1990) suggest that trap efficiency estimates obtained using electric grids in incomplete rings will be greatly inflated because ca. 50% of tsetse either avoid electric nets or fail to be killed by them. The error can be quantified if their figure is accepted. Thus, the estimate for the H11 trap baited with the odour of 60 tonnes of cattle is based on 4755 flies in the trap and 251 on the inside nets, giving $\hat{E}=4755/(4755+(4\times251))=0.83$. If the ring of nets is only 50% efficient then we should really have caught $2\times251=502$ flies on the inside of the ring; the estimated efficiency is then 0.70 – only 0.13 less than our estimate. For a less efficient trap which caught, say, 476 flies with 251 flies caught on the inside nets we estimate an efficiency of 0.32, whereas we should have estimated 0.19 – again 0.13 less than our estimate, though a greater proportional error. The method thus correctly identifies efficient and inefficient devices, and the percentage error in the estimates decreases as the true efficiency of the test device increases. Moreover, incomplete rings of nets provide an absolute goal;

Table 7. Efficiency of capture (±standard error) of tsetse (*Glossina* spp.) by an H11 trap or an electrified target baited with different odours. The number below each estimate is the sample size on which the estimate is based. For the trap the teneral catches obtained with all natural odours have been combined. The simulate was the 60 tonne fully artificial cocktail in each case. The 'acetone+1:4:8' treatment refers to the use of the same odour dose as at the control sites (see Methods).

	Attractant source	*G. m. morsitans* Males	*G. m. morsitans* Females	*G. pallidipes* Males	*G. pallidipes* Females
Trap					
(Tenerals)	(cattle–all doses)	–	–	0.79±0.02	0.78±0.02
		4	11	274	568
(Tenerals)	simulate	–	0.20±0.13	0.83±0.05	0.87±0.03
		0	4	60	108
(Post-tenerals)	acetone+1:4:8	0.29±0.08	0.37±0.05	0.77±0.02	0.73±0.01
		16	43	582	1304
Target					
(Post-tenerals)	0	0.56±0.17	0.52±0.06	0.64±0.06	0.66±0.03
		48	48	160	70
(Post-tenerals)	60 tonnes	0.24±0.07	0.36±0.04	0.66±0.01	0.60±0.01
		18	98	1498	4578
(Post-tenerals)	simulate	0.47±0.06	0.49±0.03	0.72±0.01	0.69±0.01
		36	254	2139	5226

to wit, a trap which results in a zero catch on the inside of the electric nets. We emphasize again that it is at least as important to know how many flies a trap is missing as it is to know how many it is catching.

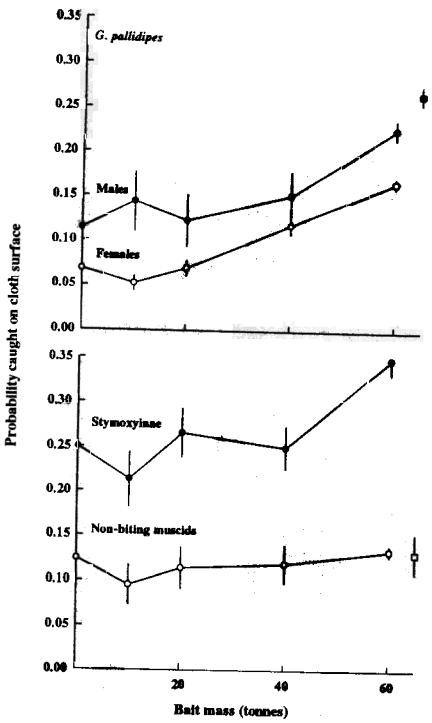


Fig. 10. The posterior probability that flies caught on an electrified target were caught on the central black cloth portion rather than on one of the flanking nets. Natural host odour (circles or dots); high octenol, fully synthetic, simulate (squares). For male and female *Glossina pallidipes* the regression equations relating landing probability (p_l) and bait mass (M in tonnes) are, respectively:

$$p_l = 0.0985 + M \times 0.0000308 \pm 0.000011 \text{ and}$$

$$p_l = 0.0554 + M^2 \times 0.0000292 \pm 0.0000043.$$

While estimates of trap efficiency clearly are inflated due to the above effect, they might be *deflated* because flies which fail to enter the trap at their first approach, and are then killed or stunned by the electric nets, do not get another opportunity to visit the trap. This would not be an important factor if flies made only one visit to the trap and then left the vicinity permanently if they were not caught. But if that were the case then the catch on the inside of the electric nets should accurately reflect the number of flies which would not have been caught in the central trap even if the nets had not been present. It follows that the trap-plus-nets should catch more flies than the trap alone. In fact this does not happen (except for male *G. m. morsitans*) and this is consistent with the idea that flies make more than one visit to the trap, and that the catch on the inside of the ring of nets includes a substantial proportion of flies which would ultimately have been captured at the centre had the ring not been present. In other words, our method may actually deflate the true efficiency of the trap, as concluded by Vale & Hargrove (1979).

We conclude that the H11 trap, even if it does not catch 100% of the flies which visit it, is a highly efficient device. Unfortunately, its size and design preclude its use in routine sampling. However, independent tests show that there is little difference between the *efficiencies* of the H11 and of the more convenient F3 and epsilon traps as devices for sampling *G. pallidipes* (Hargrove, unpublished data). The problem comes with *G. m. morsitans*, where the H11 is distinctly superior to the other two traps but, as this study shows, still disappointing in absolute terms. Although better traps have been developed for this species none has been shown to have an *efficiency* greater than 40–50% (R.J. Phelps, unpublished data). Moreover, it has been argued that the poor catches of *G. m. morsitans* in all stationary devices is due more to the failure of this species to visit the devices than to our failure to capture visiting flies (Hargrove, 1991). This results from the relatively less active nature of the species. If this is true then we should perhaps be concentrating on the improvement of mobile sampling techniques for *G. m. morsitans*.

Acknowledgements

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