Bulletin of Entomological Research (1992) **82**, 513–516

Flight behaviour of tsetse flies in thick bush (*Glossina pallidipes* (Diptera: Glossinidae))

Quentin Paynter and John Brady

Department of Biology, Imperial College of Science, Technology and Medicine, London, UK

Abstract

An odour-baited electric net placed in thick bush caught more *Glossina pallidipes* Austen when sited at ground level (0.2-1.2 m) than when sited in the top of the bush (1.4-2.4 m) or just above it (2.6-3.6 m). However, a similar net running concurrently 4 m away in a game trail through the bush caught far more flies. When electric nets were placed in the centre of two adjacent game trails in this bush and then one of the trails was barricaded with branches from nearby bushes, the catch declined in that trail and increased proportionately in the other. It is inferred that tsetse flies navigate up host odour plumes by finding gaps in thick vegetation rather than by flying over the top or through it, and that game trails are important forms of such gaps. The implications for siting traps and targets are noted.

Introduction

Tsetse flies locate hosts they cannot see in thick bush by flying up the plumes of host odour (see Brady *et al.*, 1989). At the speeds they fly in the open (up to 7.5 m/s, Gibson & Brady, 1985) it seems unlikely that they could navigate through thick bush without risking damage. Moreover, in typical tsetse bush the wind is light, directionally variable and can make odour plumes poor indicators of a host's position (Brady *et al.*, 1989). Tsetse flies may, however, alleviate these problems either by flying over the bush or by passing through gaps such as game trails or man-made paths (the wind there being faster and therefore straighter - Brady *et al.*, 1989). This paper reports a preliminary investigation of tsetse flies' use of these two strategies.

Methods

The work was carried out at the International Centre for Insect Physiology and Ecology Field Station at Nguruman, south-western Kenya (1° 50'S 36° 5'E, altitude 600 m). The area is in a generally semi-arid zone and is described by Owaga (1981) and Kyorku (1989). The experimental site was in dense thicket and gallery woodland along a perennial stream, the Oloibototo. Two species of tsetse fly were present: *Glossina pallidipes* Austen and *G. longipennis* Corti, but *G. pallidipes* was by far the most abundant, and all the results below refer to it alone, with the males and females aggregated. The data were collected over ten days (five for each experiment) in October and November 1990. Temperature and wind data, logged at 15-min intervals indicated no obvious effects on the results and are here ignored. The experiments were performed between 15.00 and 18.00 h local time, when *G. pallidipes* was most active.

Flies were caught with two 1 m^2 electric nets (external dimensions 1.1 m long by 1.2 m high) of the design described by Vale (1974a). The nets were baited with synthetic host odour. CO_2 was released at 2 1/min, from a 3 m long aluminium tube (drilled with thirty equally spaced 1.0 mm holes) placed between the two electric nets, threaded through the bush between 10 cm and 30 cm above the ground. From separate bottles, acetone was released at ca. 2,500 mg/h and the odour from aged cow urine at ca. 1,000 mg/h; a bottle of each odour was placed next to each electric net (fig. 1). These three odours together provide a reasonable simulation of cow odour (Dransfield *et al.*, 1986).

Experiment 1 - flight altitude

The area of dense bush used was ca. 2 m high with an over-storey of tall trees (*Ficus* spp., Moraceae). A large

Correspondence: Dr J. Brady, Imperial College, Silwood Park, Ascot, Berks, SL5 7PY, UK.

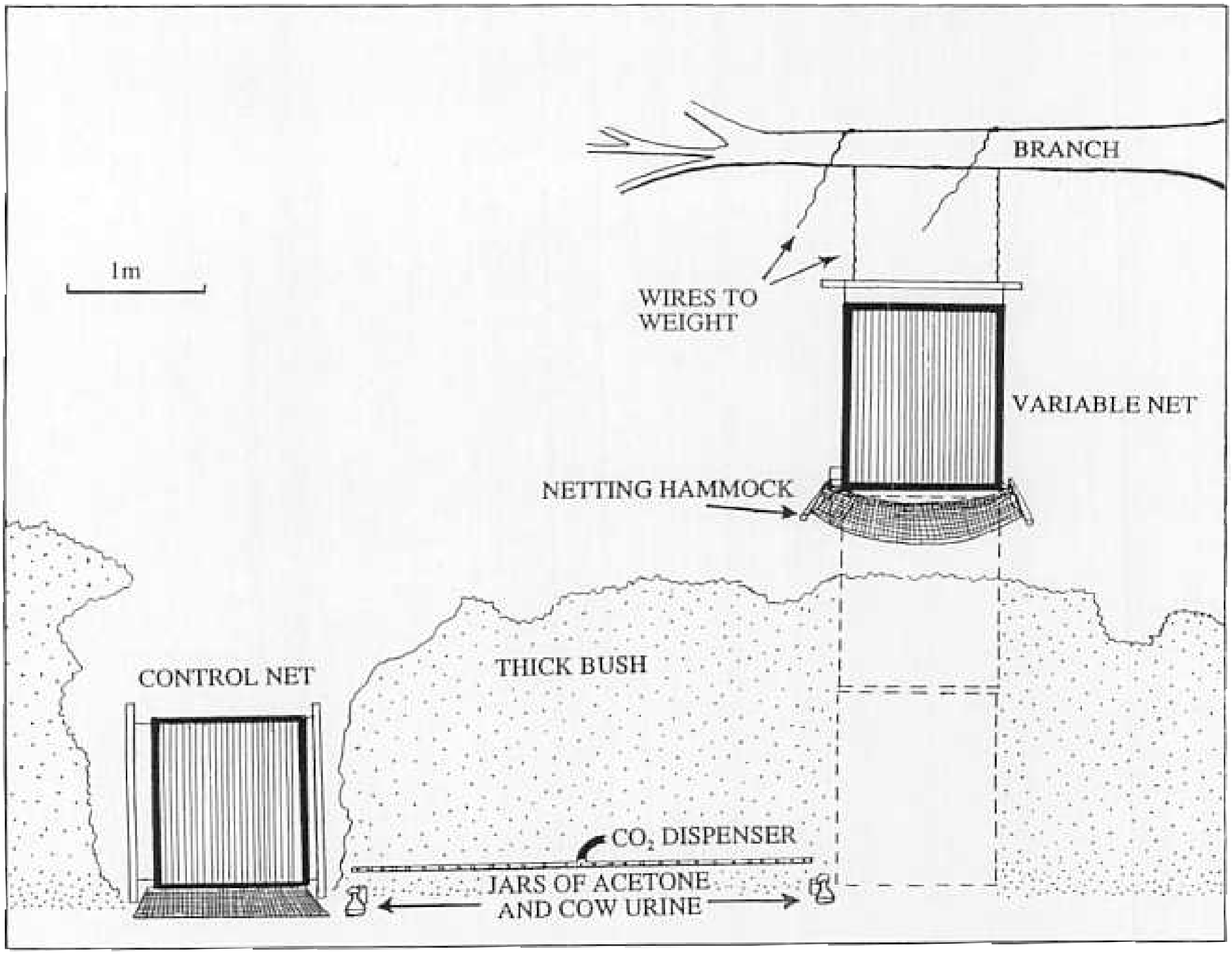

Fig. 1. Elevation view of the experimental set-up and positions of electric nets in Experiment 1

horizontal branch 5 m up was used to suspend an electric net at different heights in the bush. Two lengths of wire were hung over the branch and attached at one end to a counter-weight and at the other to the electric net. By moving the weight up and down, the net was raised or lowered (fig. 1). Three heights were tested: ground level (0.2-1.2 m), within the top of the bush (1.4-2.4 m), and just above it (2.6-3.6 m).

A mosquito netting hammock (1.0 x 0.6 m) suspended beneath the electric net caught the flies killed by it. A vertical slot was cut into the bush (1.5 m long by 1.0 m wide) to allow the electric net and its hammock to be raised and lowered. A small path was also cut to allow access for fly collecting, but this was blocked with branches cut from nearby vegetation during catches. An identical electric net was run at ground level in a game trail 3.5 m away. Collecting methods for both nets were identical.

The electric nets were run for 15 min, then switched off, the flies collected, and the height of the variable net adjusted for the next replicate. Observations were started at the same time each day and the variable electric net was set at a different height at the beginning of each day, to randomize the times it was set at a particular level.

Experiment 2 - flight in game trails

Two short game trails in the same patch of bush were used; they ran from a small clearing to a man-made vehicle track (fig. 2) and were ca. 7 m apart at the clearing end and 13 m apart at the track. The electric nets used in experiment 1 were placed across each trail to sample the flies passing along them. Synthetic host odour was released as in experiment 1, with the CO_2 pipe placed between the nets. Catches from the nets were collected (rapidly) every 15 min, and the catch on each side of the net (i.e. track-side or clearing-side) was counted separately. Trail 'A', was left clear during each run; trail 'B' was alternately left clear or blocked on one side with leafy branches collected from nearby bushes to make a barrier within the trail that was visually similar to the bush on either side. The barrier was placed about 1 m from the electric net.

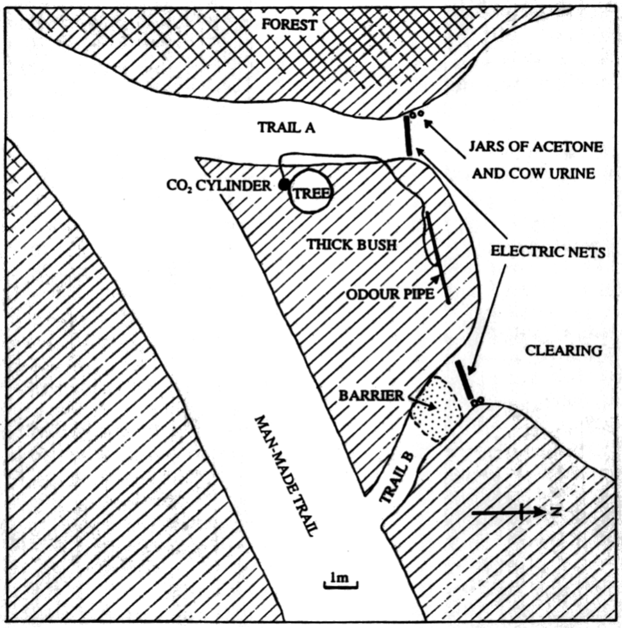

Fig. 2. Plan view of experimental site in Experiment 2; the wind direction was variable, but tended to be southerly.

Table 1. The mean number of *Glossina pallidipes* caught on electric nets placed at different heights in thick bush.

Height of net	Mean catch (±SE) Variable net (in thick bush)	Mean catch (±SE) Control net (in game trail)
Ground level (0.2-1.2 m)	12.6 ± 4.3	
High in bush (1.4-2.4 m)	2.0 ± 0.9	
Just above bush (2.6-3.6 m)	0.4 ± 0.2	

Number of replicates (= *n*) 9 or 10 for variable net, 28 for control net. For variable net, first and second means differ by $P < 0.05$, first and third by $P = 0.01$; means in row 1 differ by $P < 0.001$ (*t* test).

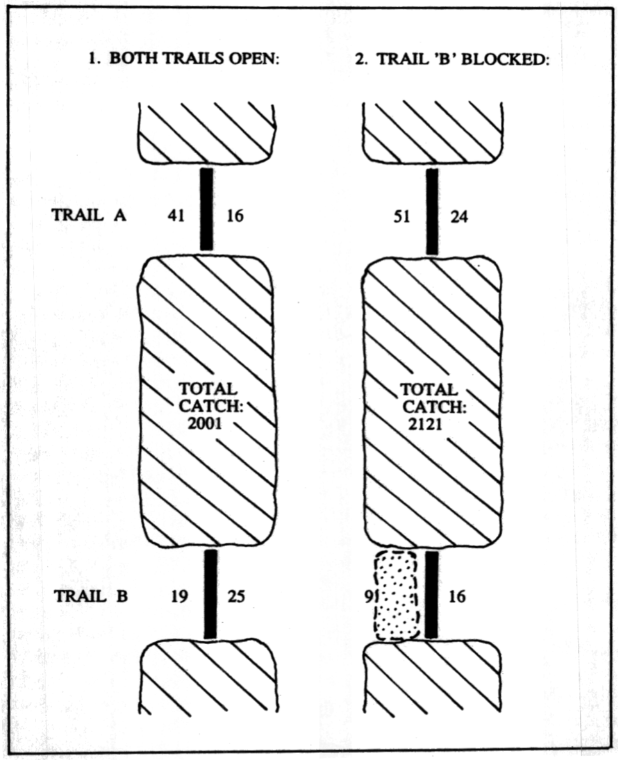

Fig. 3. Percentage distribution of the catch of *Glossina pallidipes* on both sides of electric nets placed in adjacent game trails in thick bush (see fig. 2); the figures in each diagram add to 100%. All equivalent pairs of percentages in diagrams 1 and 2 (e.g. 41% *vs* 51%) differ highly significantly (χ^2, $P < 0.001$).
Mean overall total catch (±SE) when both trails open = 125.1 ± 21.6, when trail 'B' blocked = 132.7 ± 22.2 (i.e. no significant difference $t = 0.35$). Overall decrease in trail 'B' when blocked =−19%, and the contemporary increase in trail 'A' =+18% (difference N.S.).

Results

The results of experiment 1 (table 1) show that many more flies were caught at ground level within the bush than higher up in it ($P < 0.05$), and highly significantly more than just above it ($P = 0.01$). However, over six times more flies were caught in the game trail less than 4 m away than at ground level in the bush.

In experiment 2, the ratios of flies caught at each net were highly significantly different with and without trail B blocked ($\chi^2 = 156.4$, $P < 0.001$). Moreover, although placing the barrier beside net B significantly reduced the catch in trail B (fig. 3), it produced no significant difference between the mean *total* number of flies caught in both trails in aggregate ($t = 0.35$); the reduction in the catch on net B (down 19%) was matched by an increase in the catch on net A (up 18%). Both sides of net B were affected, but, as expected, the greater reduction was on its barricaded side and the greater increase in trail A was on the same side (10% down and 10% up, respectively).

Discussion

Vale (1974b, 1982) reported 88% of tsetse flies approaching an ox over open ground at below 1.1 m, and 73% of *G. pallidipes* flying below 0.5 m when within 0.5 m of a 1 m high target. Similarly, Torr (1988) estimated that 80% of the flies he observed flew less than 50 cm above open ground. The present results are consistent with these findings, but, more importantly, indicate that this low flight behaviour is maintained even within thick bush, where 84% of flies flying there were caught within 1.2 m of the ground.

Experiment 1 also showed, however, that *G. pallidipes* in fact spent rather little time flying actually through thick bush; six times fewer flies were caught by the electric net placed at ground level within bush than at the same height in a game trail nearby. Moreover, although some tsetse were caught at ground level within the bush, significantly fewer were caught at or above the top of the bush. This suggests that they tend to avoid flying either through or over thick bush but instead are channelled into more open areas, such as game trails.

Experiment 2 examined this possibility directly. When one game trail was obstructed, the catch on the net there declined and the catch in the parallel trail increased in proportion. This suggests that flies that would have used the first trail, had it not been obstructed, were diverted to the second, and, as in experiment 1, did this in preference to gaining height and flying over the bush. This conclusion is strengthened by the fact that the 10% reduction in flies caught on the barricaded side of the net in trail B was precisely balanced by a 10% increase in flies caught on the same side of the net in trail A. This is particularly striking since the 'entrances' to the trails were about 7 m apart and the nets themselves at least 17 m apart (fig. 2).

The data in table 1 imply that in thick bush (at least at Nguruman) *G. pallidipes* spend over 80% of their flight time traversing gaps through the vegetation such as game trails. There may be several advantages in doing so, quite apart from avoiding the physical difficulty of flight in thick vegetation. As bush becomes thicker, wind in it becomes slower and therefore a less useful indicator of the direction to an odour source (Brady *et al.*, 1989). In game trails, on the other hand, the airflow is less obstructed, therefore faster, and must often be channelled along the trail.

Since a host is likely to be within or beyond a trail containing its odour, concentrating chemotactic behaviour in game trails should considerably reduce the area a fly needs to search, and the fly may be able to use much simplified wind information to find the host. If it flies upwind along the corridor of the trail from odour-free air to odour-permeated air, that will usually mean a host is located further ahead; it can then simply continue in the same direction, visually guided by optomotor cues from the walls of the trail (Colvin *et al.*, 1989). Alternatively, if it enters the trail from the bush at the side, its choice of which direction to turn (normally upwind or downwind - Gibson & Brady, 1988) may be simplified to up-trail or down-trail by the vegetation and thereby be made more precise.

There is little in the literature to suggest that game trails play an important part in tsetse fly host-location. It now seems that they may, at least in thick bush. If this behaviour is general, there are obvious implications for the siting of traps and targets.

Acknowledgements

We thank Prof. T.R. Odhiambo, Director, and Dr L. Otieno, Head of Tsetse Programme, the International Centre for Insect Physiology and Ecology, Nairobi, for the provision of research facilities at Nguruman. Dr R.D. Dransfield, Mr R. Brightwell and Dr N.T. Griffiths provided invaluable advice and assistance in the field. This work formed part of the PhD project, London University, of Q.P., who is grateful to the Medical Research Council for support. J.B. acknowledges financial support from the Overseas Development Administration of the Foreign and Commonwealth Office, under contract X.0138.

References

Brady, J., Gibson, G. & Packer, M.J. (1989) Odour movement, wind direction, and the problem of host-finding by tsetse flies. *Physiological Entomology* **14**, 369–380.

Colvin, J., Brady, J. & Gibson, G. (1989) Visually-guided, upwind turning behaviour of free-flying tsetse flies in odour-laden air: a wind-tunnel study. *Physiological Entomology* **14**, 31–39.

Dransfield, R.D., Brightwell, R., Chaudhury, M.F., Golder, T.K. & Tarimo, S.A.R. (1986) The use of odour attractants for sampling *Glossina pallidipes* Austen (Diptera: Glossinidae) at Nguruman, Kenya. *Bulletin of Entomological Research* **76**, 607–619.

Gibson, G. & Brady, J. (1985) 'Anemotactic' flight paths of tsetse flies in relation to host odour: a preliminary video study in nature of the response to loss of odour. *Physiological Entomology* **10**, 395–406.

Gibson, G. & Brady, J. (1988) Flight behaviour of tsetse flies in host odour plumes: the initial response to leaving or entering odour. *Physiological Entomology* **13**, 29–42.

Kyorku, C.A. (1989) Trapping studies on *Glossina longipennis* Corti at Nguruman, south-western Kenya. PhD thesis. University of Ghana, Legon.

Owaga, M.L.A. (1981) Ecological studies and laboratory rearing of the tsetse species *Glossina longipennis* in Kenya. *Insect Science and its Application* **2**, 197–200.

Torr, S.J. (1988) Behaviour of tsetse flies (*Glossina*) in host odour plumes in the field. *Physiological Entomology* **13**, 467–478.

Vale, G.A. (1974a) New field methods of studying the responses of tsetse flies (Diptera, Glossinidae) to hosts. *Bulletin of Entomological Research* **64**, 199–208.

Vale, G.A. (1974b) The responses of tsetse flies (Diptera, Glossinidae) to mobile and stationary baits. *Bulletin of Entomological Research* **64**, 545–588.

Vale, G.A. (1982) The improvement of traps for tsetse flies (Diptera: Glossinidae). *Bulletin of Entomological Research* **72**, 95–106.

(Accepted 30 April 1992)