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Observations on some possible attractants of tsetse flies (*Glossina morsitans* Westw. and *G. pallidipes* Aust.)

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Introduction

Tsetse flies are attracted to moving objects such as animals, black cloth screens and vehicles, and this behavioural characteristic has been used to develop methods of assessing relative sizes and distributions of their populations (Buxton, 1955; Glasgow, 1963). Harris (1932), Swynnerton (1933) and Morris & Morris (1949) investigated, with varying success, traps made to resemble host animals, while Vanderplank (1944) and Glover & Parks (pers. comm.) studied the possibility of increasing the effectiveness of these traps with pig extracts in various solvents. Buxton (1955) has reviewed research on the fly's visual response to potential hosts and light. It has also been claimed that tsetse flies were attracted to the exhaust gases from a lorry (Napier-Bax, 1937), new sacking and certain essential oils such as oil of cloves or essence of oranges (Buxton, 1955). However, the numbers of flies caught, and the ratio of males to females within a catch, can vary with the method used, and it has been concluded that each technique samples only certain segments of a population at any one time (Buxton, 1955). Investigations into the sterile-male principle as a possible means of eradicating this insect (Dame *et al.*, 1965) indicated that further information on attractants could be of value in devising more sensitive or accurate estimation techniques. This paper presents initial laboratory and field studies into some factors that might attract *Glossina morsitans* Westw. and *G. pallidipes* Aust., carried out in Salisbury and in the Zambezi Valley, Rhodesia, during 1967–68.

Methods and materials

Flies used in laboratory trials were obtained from puparia collected in the Zambezi Valley. Emerging male and female flies were sorted daily, and the sexes were held separately in 8 × 8 × 11-in. standard cages (Dame & Ford, 1966) at 25 ± 2°C and about 70% r.h. Virgin 3- to 5-day-old females and 7- to 9-day-old males that were sexually mature (Dame & Dean, unpublished) were used for all tests. They were offered a chance to feed for one hour every day on a guinea-pig placed into a mesh insert in the bottom of the cage.

In the laboratory the importance to tsetse flies of vision and olfaction in feeding were investigated using a guinea-pig under a standard cage. While the flies were inactive in a 2°C room, the compound eyes were covered with black enamel paint, or the antennae and aristae were removed at the basal segment with fine scissors. In one trial the antennae were also painted with black enamel paint. The treated flies were placed in cages and offered a guinea-pig for one hour every day, and results were assessed by recording survival at weekly intervals. Responses to 'host animals' were also investigated under field conditions in a *Colophospermum mopane*—riverine ecotone. A tethered ox or a black cloth screen enclosed within an open 8-ft-high reed screen, a tethered ox within a similar reed screen under a roof two feet above the top

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of the walls, and a control ox in the open bush were sited within 100 yd of each other. Comparative catches of flies were made at each point between 07.00 and 18.00 h on successive days, and each fly captured was marked with a paint spot on the thorax before release to prevent duplicate recording on the same day. Batches of 200 marked, unfed, wild flies were also released 100 yd down-wind from these sites, and recapture data from these flies indicated their response to the 'hosts' at each catching point.

Pregnant rather than non-pregnant host animals might be more attractive to tsetse (Nash *et al.*, 1966), and this possibility was investigated by comparing the number of flies caught off an ox and a cow, four months before parturition, tethered within 50 yd of each other in a stand of *Colophospermum*.

The response by tsetse to different colours and shades was investigated in four ways. In the laboratory, an open-ended 3·5 × 48-in. glass tube was divided into twelve four-inch sectors, and the two open ends were covered with cotton mosquito mesh. Initially alternate sectors were painted black, white, blue, yellow, red or grey, but in later tests every sector was painted except for a 1·5-in. gap on the top surface of the tube to permit observation into the interior. Fifty male or female flies were released into sector 1 and allowed to disperse under overhead diffuse lighting. Secondly, groups of 20 flies were offered a choice of the same types of painted surface, or black, white and three shades of grey, on the floor of a 7 × 10 × 14-in. glass tank. The position of these surfaces was changed after every trial. Thirdly, after releasing 100–200 flies the attractiveness of 3-ft^2 coloured surfaces was tested in a 6-ft^3 wire-mesh cage exposed to ambient conditions. Finally, a field test compared the numbers of flies caught between 07.00 and 18.00 h off an ox covered with thin, white tobacco-seed-bed cloth and off a control ox. Both animals were dark brown in colour and were covered alternately with the white cloth every other day in order to cancel any basic difference between them in attractiveness (*e.g.*, smell) to tsetse flies. Numbers of flies observed on test surfaces or caught off the oxen were recorded every half hour.

Attraction to different light sources was investigated initially in a light-proofed laboratory. A 3·4 × 48-in. glass tube was divided into 12 sectors, and Yellow Springs Instrument Co. thermistors and recorder were used to determine temperatures in each sector. In all tests, except for those with ultraviolet (black light), one end of the tube (sector 12) was placed against a transparent plastic jacket containing circulating cold water to reduce infra-red radiation from light sources positioned to shine down the length of the tube. In a separate series of trials, a one-kilowatt electric fire was turned on three to four hours after the start of the experiment to raise in one hour the temperature in sector 12 from the normal of 20–25°C to over the 45°C considered (Glasgow, 1963) lethal for tsetse flies. At the start of each test, groups of 50 male or female flies were released into the tube at sector 1 and allowed to disperse for a half hour under overhead diffused light. This light was left on during control tests, and turned off when the different light sources were used, namely blue (430–490 mμ), yellow (550–590 mμ), red (620–770 mμ) and white Osram 220/230 V, 40 W, and Philips—BL 230 V, 125 W (300–390 mμ) bulbs. The number of flies and temperature in each sector were recorded at half-hour intervals. No attempt was made to determine the light intensity from each source.

The attractiveness of light was investigated further in a 6-ft^3 field cage where red and blue Osram lamps or a Philips—BL bulb were incorporated into a trap with four radiating 6 × 12-in. vertical baffles joined at their top and bottom ends by solid surfaces. All surfaces were coated with a home-made tacky substance based on resin, vaseline and paratac (polyisobutylene). Tests in this cage were made between 16.30 and 08.00 h the next morning during a season when temperatures were above the minimum of 15°C required for flight (Dean, Paget & Wilson, 1969) until after midnight. A 'flap trap' designed by the United States Department of Agriculture, with four 6 × 20-in. vertical baffles and a Sylvania-BL 15-W tube was also tested. However, due to low ambient temperatures this trap was used only in a darkened room (10 × 10 × 8 ft) and tests lasted for periods of six hours during the day when temperatures were 20°–24°C. In

all trials, groups of 37–100 flies were released, and attraction to the light sources was assessed by the number of flies caught on the sticky surfaces. Finally, field trials were done with Sylvania-BL and General Electric-BLB 15-W tubes, powered by a 12-V battery, in a flap trap coated with the sticky material. A canvas bucket containing 50% isopropyl alcohol was slung underneath to catch falling insects, and the whole assembly was suspended at about four feet above the ground in an ecotone of *C. mopane*, *Combretum* spp. and *Terminalia* spp. The light was turned on between 17.00 h and 06.30 h the next morning. The tsetse fly population in this area was surveyed weekly by catches made off an ox led along a transect.

Results

Visual response to host animals in the laboratory

The survival of *G. morsitans* fed on guinea-pigs and held in standard cages under laboratory conditions indicated that painting the female's eyes increased longevity compared with untreated control flies; this was less evident with treated males until after the fourth week (Table I). Thus, the ability to see the immobile guinea-pig within

TABLE I. G. morsitans *survival under laboratory conditions after painting the eyes and painting or removing the antennae of flies held in standard cages and offered a guinea-pig daily*

Treatment	Sex	Mean no. flies	Mean percentage survival after indicated week							
			1	2	3	4	5	6	7	8
Eyes painted	Male	15	73	47	40	27	27	20	7	7
	Female	15	87	73	67	60	53	40	33	33
Antennae removed	Male	20	50	40	10	0	—	—	—	—
	Female	20	30	15	5	0	—	—	—	—
Antennae painted	Male	20	60	35	10	5	0	—	—	—
Untreated control	Male	20	80	65	60	20	10	10	5	0
	Female	20	75	55	50	35	30	25	10	0

Two replicates.

the mesh insert was apparently not essential for feeding success in this cage volume (704 in ^{3}). The activity of the blind flies was reduced and, consequently, they probably suffered less injury from collisions with the walls than untreated flies, and this may account for the increased longevity.

Olfactory response to host animals in the laboratory

Removing the antennae decreased longevity (Table I), and, as there are olfactory organs in the antennae (Jobling, 1933), this may have impaired the fly's ability to orientate to the smell from the static guinea-pig in the mesh mould. Nash (pers. comm.) considered that a response to an olfactory gradient in small cage volumes was an important factor if the fly was to orientate towards a host animal and obtain a satisfactory blood meal. *Glossina* may also have olfactory organs on the palps, but, if so, they alone do not appear to be capable of initiating a successful response. Poor survival rates after removing the antennae were probably not due directly to the operation since male flies with painted antennae also failed to live as long as the controls. From his field studies, Nash (1930) found that wild flies in small tubes fed more readily after their eyes had been painted than they did after their antennae had been removed. However, he concluded that painting the eyes was a more important factor against the survival of *G. morsitans* released in the bush than painting the antennae, presumably due to failure of accurate orientation to the host animal.

Field observations on responses to 'host' animals

The open reed screen described above concealed the ox from tsetse flies resting lower than 8 ft above the ground, while the screen with a roof 2 ft above the walls enabled flies to enter but concealed the ox from flies resting at any level on adjacent *Colophospermum* growing up to 50 ft high. A significant reduction in the daily mean number of *G. morsitans* caught off the oxen within both screens (Table II) indicated that

TABLE II. *Numbers of* G. morsitans *and* G. pallidipes *caught off different 'hosts' under described conditions*

	Trial 1				Trial 2			
	G. morsitans		*G. pallidipes*		*G. morsitans*		*G. pallidipes*	
	♂	♀	♂	♀	♂	♀	♂	♀
Screened ox under roof								
Total	229	111	7	42	—	—	—	—
Daily mean	16·4	7·9	0·5	3·0	—	—	—	—
Screened ox†								
Total	271	120	10	32	147	94	10	17
Daily mean	19·4	8·6	0·7	2·3	21·0	13·4	1·4	2·4
Black cloth screen within open screen†								
Total	162	67	5	17	—	—	—	—
Daily mean	18·0	7·4	0·5	1·9	—	—	—	—
'White' ox								
Total	—	—	—	—	379	144	13	12
Daily mean	—	—	—	—	25·3	9·6	0·9	0·8
Brown ox								
Total	421	167	9	18	970	462	28	74
Daily mean	30·1	11·9	0·6	1·3	64·7	30·8	1·9	4·9

†Ox or black cloth screen used on alternate days in Trial 1.

vision was important for locating a host. However, there was only a small difference between the catches made in the open or roofed screens, and this suggested that most flies were distributed at low levels on the surrounding trees. Associated studies using flies tagged with tantalum-182 showed that *G. morsitans* rested mainly between 6 and 10 ft above the ground (Dean, Williamson & Phelps, 1969). Flies caught within the reed screens may have been attracted visually to their mass rather than to the smell from the enclosed invisible ox, and this hypothesis was supported by the similar numbers caught off an ox or a black cloth screen placed within the open reed screen on alternate days. Thus, olfaction may not be as important as sight in the orientation of flights by *G. morsitans* to a hidden host; nevertheless, a residual smell from the ox used on alternate days, even after cleaning the area, may have biased the results. In all tests with the screens the catch of males was reduced more than that of the female flies. Only small numbers of *G. pallidipes* were caught, but the presence or absence of a screen around the ox seemed to make little difference to the numbers (Table II), and Fuller & Mossop (1929) obtained a similar result from their field investigations with the same species. Thus, smell may be almost as important as sight to *G. pallidipes* in locating a host animal, perhaps indicating a specific behavioural difference between the two species. However, it is possible that odours may act as arrestants as opposed to attractants.

During the first trial (Table II), 200 marked unfed flies were released 100 yd downwind from the three sites. Few marked flies were recaptured on the day of release (4–10·5%) but more were caught off the easily visible control ox than off the other two animals within the reed screens (Table III). This indicated again that vision was probably of greater importance than olfaction in finding a host animal at a distance. Lloyd (1935) reported that *G. swynnertoni* Aust. could locate a hidden calf, presumably by smell, at 25 yd but not at greater distances.

TABLE III. *Recapture of marked, unfed* G. morsitans *during trial 1 on different 'hosts'*

Release day	Screened ox	Screened ox under roof	Control ox
1	4	2	12
2	2	3	10
3	1	1	6
4	2	2	17
Total	9	8	45

Response to pregnant and non-pregnant animals

The apparent value of a pregnant goat as a host in breeding studies with *G. austeni* Newst. (Nash *et al.*, 1966) suggested that a pregnant cow might be more attractive to tsetse flies and, therefore, superior to an ox as a bait animal. However, there was no statistically significant difference between the numbers of flies caught off both animals during a trial in a stand of *Colophospermum* (Table IV). Thus a pregnant cow was not more attractive to tsetse than an ox, and Nash *et al.* (1967) retracted their earlier conclusion on the value of pregnant goats.

TABLE IV. *Total numbers of* G. morsitans *and* G. pallidipes *caught off a castrated ox and a pregnant cow during an 18-day period*

	G. morsitans		*G. pallidipes*	
Host	♂	♀	♂	♀
Pregnant cow	534	170	21	16
Ox	515	152	23	17

Response to colour and shade

Trial 1 in a 3·5×48-in. glass tube with alternate 4-in. painted or clear sectors showed that 15·0 and 14·8% of the male and female flies, respectively, rested on the grey surface (Table V) compared with a mean 8·3% if every sector was equally attractive. In trial 2 all the sectors were painted, but the results again indicated that tsetse flies did not respond to any particular colour or shade under these experimental conditions.

TABLE V. *Preferences shown by 50 male or female* G. morsitans *given a choice of resting surface in a 3·5×48-in. glass tube*

Surface (Trial 1)	No. flies resting on surface†								Surface (Trial 2)
	Trial 1				Trial 2				
	Male		Female		Male		Female		
	No.	%	No.	%	No.	%	No.	%	
Clear	25	2·5	27	4·0	96	10·5	148	17·7	Blue
Black	34	3·3	43	6·4	35	3·8	56	6·7	Black
Clear	82	8·2	14	2·1	62	6·8	79	9·4	Red
Grey	151	15·0	100	14·8	96	10·5	93	11·1	Grey
Clear	115	11·4	87	12·9	122	13·3	69	8·2	Yellow
White	74	7·4	33	4·9	114	12·4	75	8·9	White
Clear	101	10·0	81	12·0	88	9·6	46	5·5	Black
Blue	74	7·4	66	9·8	58	6·3	66	7·9	Blue
Clear	66	6·6	35	5·2	43	4·7	50	6·0	Grey
Red	89	8·8	86	12·8	47	5·1	33	3·9	Red
Clear	73	7·4	30	4·5	62	6·8	30	3·6	White
Yellow	76	7·5	34	5·0	94	10·3	93	11·1	Yellow
Clear	46	4·6	38	5·6	—	—	—	—	—
Total	1006	—	674	—	917	—	838	—	—

Totals of two replicates each of 7–10 observations.
†Flies resting on the ends of the tube are not included.

Observations on male *G. morsitans* that were offered a choice of similarly painted surfaces on the floor of a glass tank indicated that more flies rested on the blue and yellow than on the other colours (Table VI). However, a mean 46·6% of the observed resting sites were on the clear glass walls above the painted surfaces.

TABLE VI. *Preferences shown by 20 male* G. morsitans *given a choice of 3·5×4·5-in. painted surfaces on the floor of a 7×10×14-in. glass tank*

	No. flies seen on indicated surface							
Trial	Grey	Blue	Yellow	White	Black	Red	Other†	Total
1	44	15	35	17	5	9	55	180
2	4	14	15	7	17	8	75	140
3	2	32	31	11	22	11	131	240
Total	50	61	81	35	44	28	261	560
Per cent	8·9	10·9	14·5	6·3	7·9	5·0	46·6	—

Totals of three replicates of 7–12 half-hour observations.
†Clear glass walls.

In two tests with the glass tank painted half white and half black, 254 out of 358 (71%) of the observed resting sites of male *G. morsitans* were on the white surface. Subsequently, *G. morsitans* and *G. pallidipes* were offered a choice of black, white and three shades of grey surface on the floor of another similar-sized tank. Male flies of both species tended to occur more often on the white surface than on the others except for the glass walls (Table VII). The female flies appeared to rest almost

TABLE VII. *Preferences shown by 20 male or female* G. morsitans *and* G. pallidipes *given a choice of black, white and three shades of grey surface in a glass tank*

Sex		Black	Dark grey	Medium grey	Light grey	White	Other†	Total
G. morsitans								
Male	No.	29	20	7	39	78	227	400
	%	7·3	5·0	1·7	9·7	19·5	56·8	—
Female	No.	77	20	18	21	82	102	320
	%	24·1	6·3	5·6	6·6	25·6	31·9	—
G. pallidipes								
Male	No.	44	18	25	40	78	115	320
	%	13·8	5·6	7·8	12·5	24·4	35·9	—
Female	No.	82	51	13	11	55	108	320
	%	25·6	15·9	4·1	3·4	17·2	33·8	—

Totals of two replicates of 7–13 half-hour observations.
†Clear glass walls.

equally frequently on both the black and the white surfaces. In these laboratory tests no attempt was made to determine possible variations of light intensity from the painted surfaces, and this may have biased the results.

The attractiveness of painted 3-ft^2 surfaces to male *G. morsitans* released into a 6-ft^3 field cage indicated a preference for the black surface in two trials (1 & 2) and and for the blue in the fourth trial (Table VIII). However, only 88 (12·6%) out of the 700 flies released in the four trials were seen on all the squares combined; the remainder rested elsewhere in the cage. It seems unlikely, therefore, that any colour or shade is especially attractive to tsetse flies under these described experimental conditions. Conversely, a field trial showed that 'white' and dark brown oxen differed in their attractiveness as hosts, with higher daily mean numbers of *G. morsitans* caught off the brown ox than off the 'white' animal (Table II). A similar difference was detected between the two animals with the smaller numbers of *G. pallidipes* captured.

Response to light

Under laboratory conditions in a 3·5×48-in. glass tube, *G. morsitans* moved more readily towards the blacklight and blue source at sector 12 than toward the other sources (Fig. 1). There was a 50% response by both sexes to the blacklight within two hours, and 80% of the flies were in sector 12 after five hours compared with over

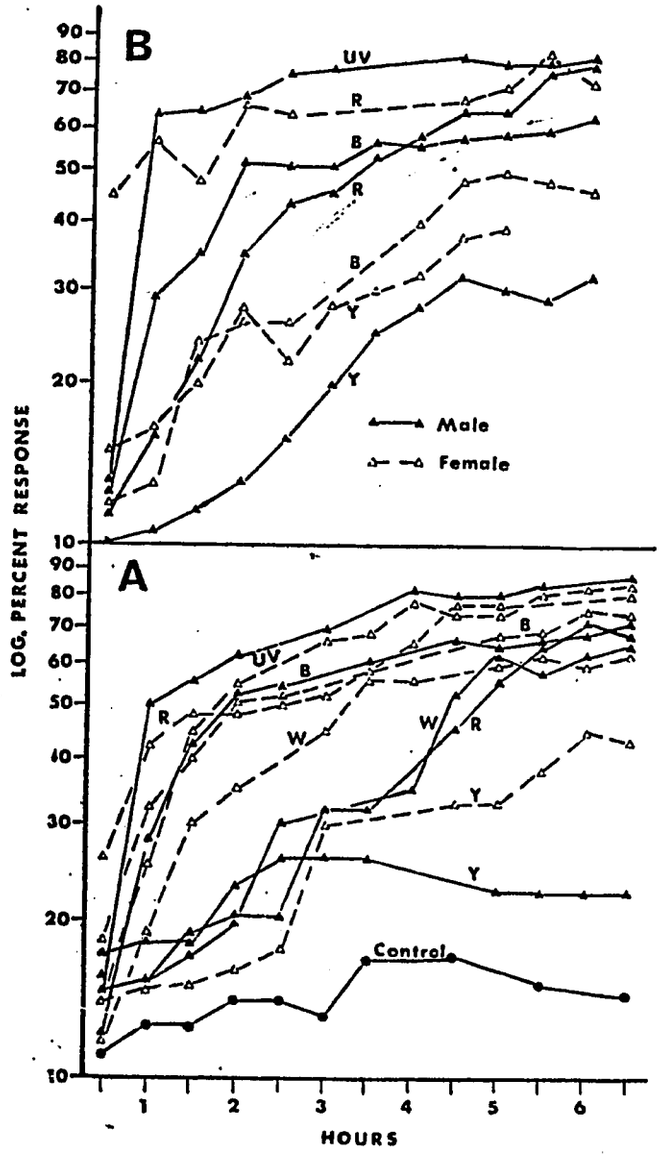

Fig. 1.—Mean log. percentage (two replicates) of 50 males or females of *G. morsitans* (A) and of *G. pallidipes* (B) seen at half-hour intervals in sector 12 of a 3·5×48-in. glass tube exposed to different light sources. (UV, ultraviolet or blacklight; B, blue; R, red; Y, yellow; W, white.)

TABLE VIII. *Preferences shown by* G. morsitans *offered a choice of six painted 3-ft² surfaces in a 6-ft³ cage*

Trial	No. flies released	No. flies on indicated surface					
		Grey	Blue	Yellow	White	Black	Red
1	100	0	0	0	0	7	0
2	200	2	4	4	0	21	5
3	200	3	2	1	1	6	1
4	200	4	18	1	4	4	0
Total	700	9	24	6	5	38	6

Totals of 7–10 half-hour observations in each trial.

six hours for a 70% response using a blue light. Female flies tended to move towards red and white light rather more readily than the males, while less than 50% of either sex were in sector 12 after six hours using the yellow light. Males of *G. pallidipes* appeared to respond more rapidly to the blacklight than those of *G. morsitans*, and 80% were in sector 12 within about four hours. Movement responses of *G. pallidipes* to blue and red sources in these tests were rather more erratic than with *G. morsitans*, while numbers found in sector 12 using yellow light were again low, though greater than observed with *G. morsitans*. Control tests with both species under uniform overhead illumination showed a relatively even distribution along the tube (Table IX).

Responses by male *G. morsitans* to different light sources were investigated further in the laboratory. About four hours after the start of a second series of tests, the temperature in sector 12 was gradually raised over a period of one hour to above the 46°C considered (Glasgow, 1963) lethal for tsetse flies. At the lower temperatures 72% of the flies moved towards the blacklight into sector 12, while two hours after starting to raise the temperature 42% of the total number released had stayed and died in sector 12 (Table IX). With the blue light, 48% responded initially at low temperatures and 32% were killed at high temperatures, compared with 44 and 16%, respectively, using a red light source. White light apparently was least attractive to male flies, and raising the temperature shifted the peak of fly numbers from sector 12 to sectors 9 and 10, and only 6% were killed. However, in a comprehensive study, Gui *et al.* (1942) found that the order of attractiveness to insects, from greatest to lowest, was blue, white, yellow and red. The temperature gradient was too steep to determine a lethal threshold but, with one exception, no live flies were found in sectors with temperatures above 43°C. Observations using the white light indicated that flies became sufficiently active above 35°C, in the absence of a stronger stimulus, for them to escape from sectors 11 and 12 when the slowly rising temperatures became too high for survival. These results confirmed the relative attractiveness of the different light sources tested, but no attempt was made to determine the light intensity emitted by each source and this factor may have biased the results.

In a 6-ft³ field cage, between 22·5 and 34·0% of the males of *G. morsitans* released, and 20·0 to 38·6% of those of *G. pallidipes*, were recaptured on the tacky surfaces around a Philips-BL (Table X). Two trials with a Sylvania-BL tube involved simultaneous releases of both male and female *G. morsitans*, and means of 27·4 and 24·4% of the two sexes, respectively, were recaptured. In tests with released males, the blue light caught on average only 4·6% of the males of *G. morsitans* and 8·8% of those of *G. pallidipes*, while the red light caught a mean of 4·7% of the male *G. morsitans*.

The ineffectiveness of Sylvania-BL and General Electric-BLB tubes in flap traps was demonstrated during two field trials. In the first, only one male and one female *G. morsitans*, and one female *G. pallidipes*, were trapped over a period of 15 days, and none were caught in a similar period during a second trial two months later. Numerous insects of other species were caught on the tacky surfaces and in the bucket of isopropyl alcohol, and temperatures up to midnight during both trial periods were

TABLE IX. *Sector preferences exhibited by 50 mature male* G. morsitans *after exposure for 3–4 h to light sources placed outside sector 12 of a 4-ft glass tube (1) at relatively constant temperature, and (2) after rapidly raising in one hour the temperature in sectors nearest the light source*

Light			Sector no. 1	2	3	4	5	6	7	8	9	10	11	12	Flies in sector 12 (%)	Flies dying in sector 12 (%)
UV	(1)	No. flies	0	0	0	0	1	1	2	1	2	3	4	36	72	—
		Temp. (°C)	23·5	23·7	23·8	23·8	23·9	23·9	24·0	24·1	24·2	24·4	24·5	24·9		
	(2)	No. flies	0	0	0	0	1	1	2	1	7	11	3 + 3*	21*	—	42
		Temp. (°C)	24·0	24·0	24·1	24·5	25·1	25·6	26·7	28·5	31·3	37·5	42·8	46·7		
Blue	(1)	No. flies	1	1	1	0	2	2	2	2	2	5	8	24	48	—
		Temp. (°C)	21·3	21·4	21·5	21·5	21·5	21·5	21·5	21·5	21·4	21·5	21·5	21·6		
	(2)	No. flies	3	2	0	1	1	1	5	5	6	3	6*	16*	—	32
		Temp. (°C)	22·0	22·0	22·2	22·7	23·2	24·0	25·4	27·6	31·1	38·3	48·7	50·0		
Red	(1)	No. flies	2	1	2	2	2	1	1	3	4	4	6	22	44	—
		Temp. (°C)	20·9	21·0	21·0	21·2	21·3	22·0	21·4	21·3	21·3	21·3	21·3	21·3		
	(2)	No. flies	1	1	2	2	1	0	5	6	6	6 + 1*	1 + 9*	8*	—	16
		Temp. (°C)	21·4	21·6	21·7	22·3	22·9	23·7	25·1	27·3	31·2	39·6	48·2	50·1		
White	(1)	No. flies	1	1	3	2	2	3	2	3	2	5	7	19	38	—
		Temp. (°C)	22·0	22·2	22·2	22·4	22·6	22·6	22·8	22·8	22·5	22·5	22·5	22·5		
	(2)	No. flies	0	0	1	1	1	3	4	5	16	16	0	3*	—	6
		Temp. (°C)	22·3	22·4	22·5	22·7	23·2	24·0	24·9	26·6	29·3	37·8	48·2	51·2		
Control†	(1)	No. flies	4	3 + 1*	1	3	0	5	7	8	7	4	2	5	10	—
		Temp. (°C)	21·3	21·2	21·1	21·1	21·0	21·1	21·1	21·1	21·1	21·1	21·1	21·1		

Two replicates.
†Overhead illumination.
*Dead flies.

TABLE X. *Recapture of* Glossina *spp. with a light-trap in a 6×6×6-ft outdoor cage*

Light source	Species	Sex	No. released	No. recaptured	Recapture (%)
Philips-BL	*G. morsitans*	♂	50	17	34·0
			80	18	22·5
			40	11	27·5
			43	10	23·3
	G. pallidipes	♂	70	27	38·6
			100	20	20·0
			63	24	38·1
			39	10	25·6
Sylvania-BL†	*G. morsitans*	♂	70	19	27·2
			58	16	27·6
		♀	73	15	20·6
			96	27	28·1
Blue	*G. morsitans*	♂	54	2	3·7
			37	2	5·4
	G. pallidipes	♂	68	6	8·8
Red	*G. morsitans*	♂	38	2	5·3
			50	2	4·0

†Conducted in slightly larger darkened room due to low outdoor temperatures.

above the minimum 15°C considered necessary for flight (Dean, Paget & Wilson, 1969). Surveys with a bait ox of the tsetse population at this site gave catches of two to five male *G. morsitans* per 100 yd of transect, and on most days flies were seen to follow the observer and to sit on adjacent trees when the blacklight was turned on in the late afternoon.

Discussion

Olfactory receptors on the antennae appear more important than vision for feeding and survival of tsetse flies in small cage volumes under laboratory conditions. However, in the field the ability to see the host animal is probably the more important sense to *G. morsitans*, though smell, particularly with *G. pallidipes*, may be used for orientating to an invisible host animal at shorter ranges. Other workers (Buxton, 1955) affirmed the importance of vision, and Napier-Bax (1937) reported that *G. swynnertoni* could see moving oxen up to 450 ft away. However, Chorley (1948) suggested that tsetse flies are guided by smell when he found that several species (*G. morsitans*; *G. pallidipes*; *G. pallidipes*, *G. palpalis* (R.-D.); *G. fuscipes* Newst. and *G. brevipalpis* Newst.) apparently congregate where elephant, buffalo or hippopotamus, respectively, lie up, probably because of the smell of dung or urine. According to Vanderplank (1944) more *G. pallidipes* were caught off a screen strongly scented with bush-pig than off one not scented, and Glover & Parks (pers. comm.) obtained similar results with screens soaked in solvents containing pig extracts. Differences in numbers of insects caught off these treated and untreated traps were not statistically significant, and recent studies by Dean, Paget and Wilson (1969) showed that *G. morsitans* and *G. pallidipes* did not concentrate around cattle permanently stationed for several months at fixed sites in the bush. However, results obtained by Persoons (1966) showed that significantly more *G. pallidipes* and *G. palpalis fuscipes* were caught off Langridge traps covered with hessian impregnated with benzene extract from pig-skin washings than off similar non-baited traps. Tsetse flies may be guided by smell to a host animal, but the relative importance of this factor compared with the, apparently, main orientation due to vision has not been determined, and may vary between species.

Laboratory and small field cage studies indicated that tsetse flies were not especially attracted to any of the colours or shades tested. However, larger numbers of flies were caught off a dark ox than a "white" animal, and similar results were obtained by Moggridge (1936), Fuller & Mossop (1929) and others. This would appear to be another example where tsetse flies do not respond in the laboratory when they might be expected to from field data, and the question of whether these insects possess a

sense of colour, or choose between differences in light and shade where there is a zone of optimum temperature still has to be determined.

Conversely, both *G. morsitans* and *G. pallidipes* showed a range of behavioural responses to different light sources under laboratory conditions. They were especially attracted to blacklight, but the proportion of flies moving to this source decreased in a 6-ft^3 cage, and virtually no response was detected in field trials. In the field cage tsetse flies were not seen to move towards the blacklight source during daylight, and the majority were trapped at dusk, while spontaneous activity by either species after dark was rarely recorded in other field behavioural studies (Buxton, 1955; Dean, Paget & Wilson, 1969). Thus, the apparent absence of flight in the dark, even at high air temperature, could explain the failure of the blacklight trap used in the field. The progressive failure of blacklight to attract tsetse flies in increasing experimental volumes may be attributed also to the light intensity decreasing with distance to below the minimum threshold level necessary to evoke a response. Foster (1957) found that *G. morsitans morsitans* would not feed below a minimum light intensity of 1–2 ft-candles, but members of the *fusca* (Wlk.) group are reported to be more active late in the day or at night (Buxton, 1955). According to Lewis (1950), *G. longipennis* Corti is attracted to light, as is *G. brevipalpis* (Lloyd, 1940) though not especially to ultra-violet radiation (Glasgow, 1956). Thus, the behaviour of different species may vary and the value of traps containing blacklight or other light sources as a possible sampling technique should be investigated for each species.

The tsetse fly almost "appears to have achieved a partial independence of its environment" (Bursell, unpublished) by its method of reproduction (Buxton, 1955; Glasgow, 1963), wide tolerance to temperature extremes, and development of control systems whereby the fly is mainly indifferent to environmental humidity (Bursell, 1960). It appears to require only a host animal on which to feed and behavioural mechanisms to keep it out of the sun and in shade where it can survive and deposit its larvae when temperatures are high. There does not appear to be a long-range attraction between the sexes (Dean, Clements & Paget, 1969) which is not surprising since male and female flies meet at the host animals. Thus, it would seem unlikely, in the absence of any other specific requirements for survival, that this insect would be especially attracted at a distance to stimuli other than objects resembling host animals.

Summary

Investigations into some possible attractants of *Glossina morsitans* Westw. and *G. pallidipes* Aust. have been described. In small cages (8×8×11 in.) under laboratory conditions, flies with painted eyes survived longer than those that were untreated, whilst removing the antennae decreased longevity. Olfactory stimuli were probably more important than vision in orientating a fly towards a static guinea-pig used as a host in a moulded mesh insert into the cage. Field observations indicated that tsetse flies were orientated towards an ox at a distance mainly by vision and few flies found oxen concealed by screens. Olfaction may be used at relatively short distances to find hidden host animals, and *G. pallidipes* may respond to smell more readily than *G. morsitans*.

Tests in the laboratory and small field cages (6 ft^3) indicated that tsetse were not attracted to any particular colour (red, yellow, blue) or shade (white, grey, black). However, in the field more flies were caught off a dark ox than a white ox. In the laboratory > 80% of male *G. pallidipes* responded to black light within four hours while with *G. morsitans* a similar proportion was attracted only after six hours. Responses by both species decreased with blue, red and white light and were least with yellow. In small field cages attraction to black light was reduced and only 20–38·6% of either species were caught by a "flap trap" in 6–13½-h test periods. Tests with either blue or red lights in these field cages trapped less than 9% of the released tsetse flies in similar periods. Field trials with black light indicated that this attractant was ineffective as a sampling technique since very few of a natural population were trapped.

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