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BEHAVIOURAL STUDIES OF *GLOSSINA MORSITANS* WESTW USING TANTALUM-182

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The behaviour of insects that are not readily visible may be studied with the aid of isotopes emitting strong gamma-radiation (Jenkins, 1962, 1963; Schmidt & Smith, 1963). Cobalt-60 has been used to follow the movements of Elaterid larvae, cutworms (Fuller & others, 1951), the white pine weevil (Sullivan, 1953) and of boll weevils (Babers, Roan & Walker, 1954); on the other hand, tantalum-182, which has a relatively short half-life, was preferred by Banks and his co-workers for their studies on Coccinellid larvae and adult senn bugs (Banks, 1955, 1962; Banks, Dezfulian & Brown, 1961). This paper describes investigations, using tantalum-182, into movements of *Glossina morsitans* Westw. in large field cages.

Methods

Tantalum-182 emits strong gamma-radiation within the range 0·0334–1·454 MeV. and has a half-life of 111 days. It was obtained as 0·4-mm. diameter wire, covered with a 0·1-mm. sheath of platinum; this was pre-cut into 1·0-mm. lengths the specific activity of which in different trials ranged from 85 to 250 μc. per mm. A mark consisted of a single length of the wire glued to the centre of the thorax of a fly with artists' oil paint; most other adhesives tested proved to be toxic. The weight of a mark, about 0·07 mg., was negligible since 30 mg. blood may be ingested by a 20 mg. male fly (C. T. McCabe, pers. comm.) without apparently affecting its capability for flight.

The effects of tantalum-182 on survival were determined on flies emerging from pupae held in the laboratory and maintained at 25°C. and about 70 per cent. relative humidity. The flies were immobilised by a short exposure to carbon dioxide soon after eclosion, and the tantalum-182 wire, held in long forceps, was attached to the thorax. Individual flies were held in 3 × 1-in. glass vials closed with cotton mosquito mesh through which they were allowed to ingest blood from a guinea-pig for 30 min. each day. Survival of these marked flies was compared with that obtained from unmarked flies held in a similar manner.

Relatively few flies were used in the field trials. Male flies, of unknown age, with some blood visible in the gut and apparently ready to feed, were caught in the bush. They were held gently between the fingers while the tantalum-182 wire was applied to oil paint on the thorax. Each fly was held in a 3 × 1-in. vial for four hours so that the paint could dry before release. Paints of different colour were used to identify individual insects. Panax radiation monitors, type TM 64GS, were used to locate the flies at hourly intervals throughout the day at ranges of between five and twelve feet.

Observations on the behaviour of marked and unmarked flies were made in three types of field cage. Cage 1 (8 × 100 × 100 ft.) was made of wire mosquito

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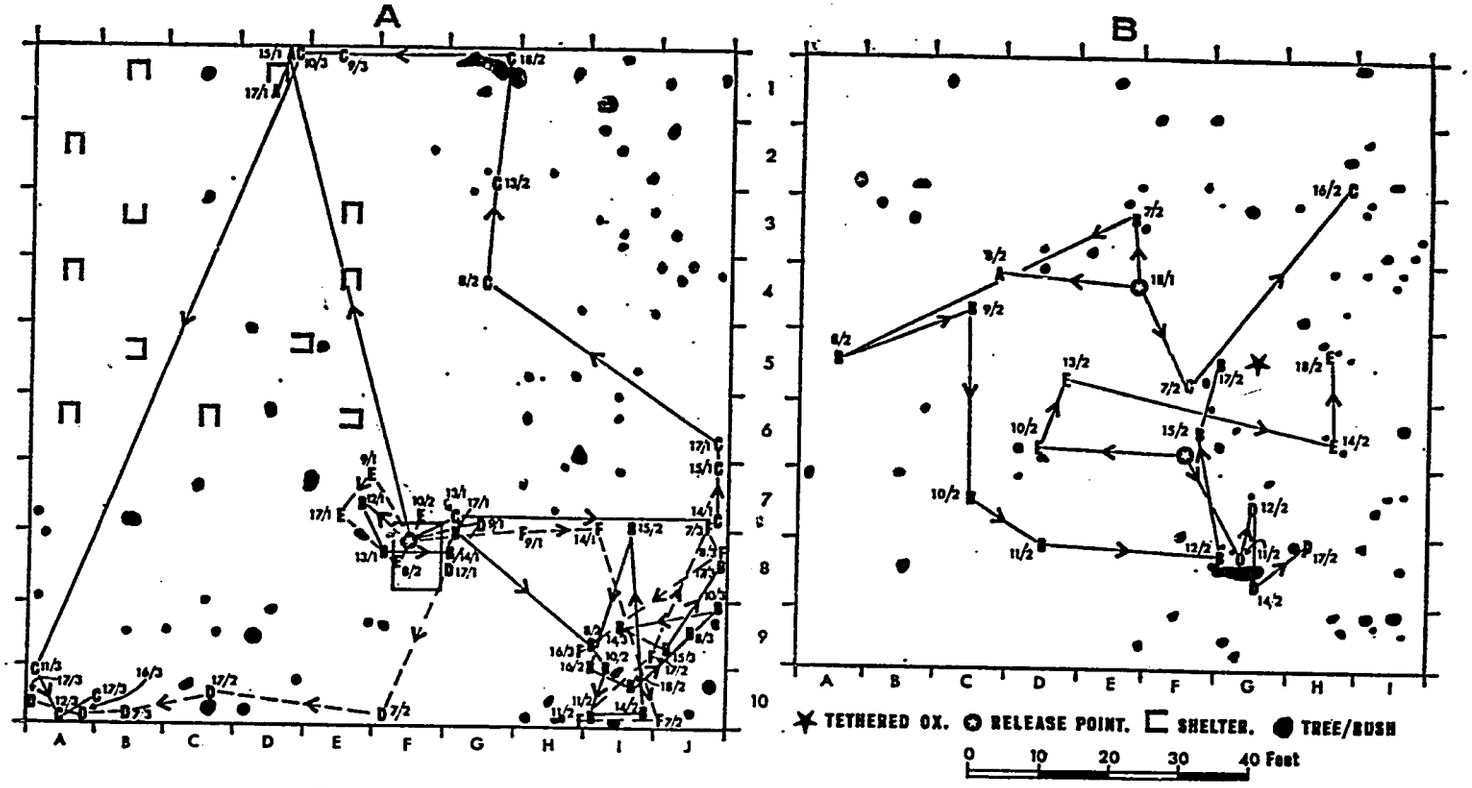

Fig. 1.—Movement of males of *G. morsitans* tagged with tantalum-182 and liberated into cage 1 (A) and 2 (B). Numbers before and after the oblique line refer to hour and day after release, respectively, of sighting in a new position. Sectors A–J and 1–10, and A–I and 1–9 for cages 1 and 2, respectively, referred to in Tables II and III, are indicated.

mesh on a metal frame, and was covered entirely with hessian (burlap) except for a 500-sq. ft. area in the centre of the roof. It enclosed a lower bush canopy of *Combretum*, *Boscia* and *Cleistochlamys* and was overshadowed by taller specimens of *Colophospermum mopane* and *Kirkia acuminata*. There were also twelve brick shelters with thatched roofs to act as additional roosting sites (fig. 1A). The host animals, two bush-pigs and five oxen, were tethered or allowed to roam within a 4-ft. security fence next to the cage wall. Cage 2 (8 × 90 × 90 ft.) was of similar construction and enclosed similar vegetation, but was not covered with hessian; a single tethered ox was used as a host. The position of the flies in these cages was plotted by means of a grid with 10-ft. intervals designated A–J and 1–10, and A–I and 1–9, in cages 1 and 2, respectively (fig. 1). The number before the oblique line in the figures denotes the time that a marked fly was first seen in a new position, and the final number indicates the number of days after release (*e.g.*, 9/2 = 0900 hr. on the second day).

The vertical cage, made of wooden posts covered with wire mosquito mesh, was about 30 ft. in diameter and 36 ft. high. It enclosed two trees, one of *Tamarindus indica* and the other of *Diospyros kirkii*, both about 35 ft. high and providing suitable shade for tsetse flies. Ladders built around the inside of the cage enabled most of the volume to be inspected. A wart-hog or an ox was tethered inside as a blood donor.

Only three or four marked flies were liberated into a cage during a single trial because it was difficult to locate individuals roosting within about 15 ft. of each other when using tantalum-182 with such a high specific activity. Large numbers of unmarked flies were released into these cages at the beginning of each trial. Observed roosting sites of marked and unmarked flies were recorded between 0600 hr. and 1800–1830 hr. A few attempts were made at night to locate marked flies in the vertical cage. Releases were made at 0900 hr. in cage 1, and at 1700 hr. in cage 2 and the vertical cage.

Results and conclusions

Survival of tsetse flies marked with tantalum-182

Two groups of ten male flies were marked with tantalum-182 at initial activities of about 250 and 195 μc., respectively, and then held under constant insectary conditions. For the first three weeks the survival of marked and unmarked flies was similar, but in the sixth week all marked flies were dead

TABLE I. *Per cent. mean survival of marked and unmarked males of* G. morsitans

	Week no.					
Treatment	1	2	3	4	5	6
Marked	85	75	65	35	20	0
Unmarked	95	75	70	60	30	20

Two replicates.
Ten males in each replicate.

whereas 20 per cent. of the unmarked flies were still living (Table I). The dosage received (rads per hr.) by a marked fly surviving more than five weeks, estimated from the formula

$$\frac{6{\cdot}8A}{d^2}$$

where A = radioactivity (μc.) of the source and d = distance (cm.) from the source, was equal to about 8,800 at one millimetre from the tantalum mark. Adult males

of *G. morsitans* given dosages of gamma-radiation of up to 18,000 rads as a single dose in two hours generally lived longer than untreated flies (Dean & Wortham. 1969), so that flies labelled with tantalum-182 at an activity level detectable at several feet would live long enough for field trials.

Horizontal movements of tsetse flies

Two groups, each of three marked flies, were released into cage 1 during August and September, respectively. Some flies tended to remain for a while around the release point (fig. 1A). Most observed roosting sites were on the wire mesh of the roof and walls, and flies were seen on vegetation on only two occasions. Generally, the flies moved to the darker perimeter of the cage, and their distribution did not appear to be associated with the vegetation, brick shelters or host animals. Observations on the roosting position of 299 unmarked

TABLE II. *Typical example of the number of unmarked individuals of* G. morsitans *in each sector of cage 1*

	Sector									
Sector	A	B	C	D	E	F	G	H	I	J
1	8	1	0	1	2	0	7	3	2	11
2	2	0	0	1	0	0	10	0	0	0
3	1	0	0	0	1	0	0	0	0	0
4	3	0	0	0	2	0	3	0	0	0
5	5	7	1	4	4	0	13	3	1	1
6	23	1	2	1	0	0	6	0	0	0
7	2	1	0	2	1	0x	1	0	0	0
8	3	0	0	1	1	0	7	0	0	2
9	3	3	0	0	1	1	1	0	0	27
10	34	7	2	1	1	0	11	12	2	43

The orientation and sectors of the cage are as in fig. 1A.
x refers to release point.

TABLE III. *Typical example of the number of unmarked individuals of* G. morsitans *in each sector of cage 2*

	Sector								
Sector	A	B	C	D	E	F	G	H	I
1	20	5	11	2	3	11	8	6	20
2	2	2	1	0	2	0	3	17	1
3	3	0	1	2	6	3	18	5	14
4	0	2	1	2	0	4	7	1	4
5	0	1	0	7	3	1	4	16	2
6	3	0	1	16	14	2	1	12	6
7	3	0	2	6	2	8	5	3	6
8	5	3	4	1	17	11	4	3	1
9	7	6	9	23	29	31	38	17	35

The orientation and sectors of the cage are as in fig. 1B.

flies during the two trials showed a similar preference for the perimeter of the cage (Table II). However, more flies (27%) appeared to roost in the centre of the cage and a few were seen on branches and boles of trees.

There was a single trial in cage 2 during August when groups of three and two marked flies were released (fig. 1B). The movement pattern of these flies

TABLE IV. *Number and length of displacements made by males of* G. morsitans *marked with tantalum-182*

Fly	Total period of observations[a] (hr.)	Number of displacements observed	Mean time in single location (hr.)	Total straight-line displacement (ft.)	Displacements between observations (ft.)		Mean hourly[a] displacement (ft.)
					Mean	Range	
			Cage 1				
A	9[b]	2	4·5	82	41·0	(6– 76)	9·0
B	34	16	2·1	192	12·0	(2– 29)	5·6
C	34	12	3·0	288	24·0	(5–104)	8·5
D	34	7	5·0	98	14·0	(6– 26)	2·9
E	14[b]	4	3·5	37	9·0	(7– 11)	2·6
F	34	8	4·3	140	17·5	(5– 31)	4·1
Mean	—	8	3·8	—	17·1		5·3
			Cage 2				
A	3[b]	1	—	21	—	—	7·0
B	13·5	8	1·7	181	22·5	(11– 50)	13·4
C	13·5	2	6·7	55	27·5	(16– 39)	4·1
D	13·5	4	3·4	43	11·0	(5– 17)	3·2
E	13·5	4	3·4	86	26·5	(11– 41)	6·4
Mean	—	4	3·0	—	20·3	—	6·8

(a) 0600–1830 hr.
(b) Fly died or tantalum-128 wire fell off.

showed that they tended to move and roost near the centre of the cage, and none was seen to visit the perimeter walls. Out of 19 observed roosting positions, eight were on bushes and trees and 11 were under small patches of leaves on the roof of the cage. Observations on 555 unmarked flies indicated a preference for the perimeter of the cage (Table III) but 40 per cent. were found roosting away from the walls.

Data collected every hour between 0600 and 1830 hr. showed that two marked flies (B and C) in cage 1 during August moved position more frequently than the others (Table IV). Flies A and C apparently covered much larger distances between successive observations. The mean length of time between successive movements, mean length of individual straight-line displacements, and mean hourly displacement tended to be similar for the two cages. However, the flies in the first trial (August) in cage 1 appeared to be more active than those used in the second trial during September. Fourteen observations on marked flies in the two cages showed that they did not move from their roosting positions during the night, or until after 0600 hr. the next morning. Pilson & Leggate (1962) reported that they were unable to find any resting individuals of *G. pallidipes* Aust. at first light and concluded that this species uses some unknown resting site at night.

Vertical movements of tsetse flies

Preliminary trials with marked flies in the vertical cage during the late dry-season and wet season were started with tantalum-182 at an activity of about 85 μc. per mm. The detection range was low and some tantalum-182 wires fell off within a few hours, possibly because of the poor quality of the oil paint used as adhesive. The few results obtained did not disagree with those recorded in subsequent trials. After dark it was extremely difficult to see marked flies in the light from torches even after their general position had been determined with the radiation monitors, and thereafter this was not attempted. However, two flies were seen roosting after dark on the undersides of leaves at 5 and 18 ft. above ground level.

Two major trials were done in the following August and September and each lasted for about three days (0600–1830 hr.). Unmarked male flies were released with the three marked flies in each trial. The tantalum-182 wire again fell off some flies, and this resulted in fewer observations than were expected, especially in the late afternoon and early morning.

TABLE V. *Total numbers of males of* G. morsitans *seen roosting in different sites at different levels during two trials in the vertical cage*

Height (ft.)	Number of flies on			
	Trees	Posts	Walls	Total
0–5	11	5	28	44
6–10	15	11	109	135
11–15	1	4	25	30
16–20	1	1	9	11
21–25	0	0	1	1
26–30	1	1	1	3
Total	—	—	—	224

Unmarked flies were found at all heights between ground level and the top of the cage (>30 ft). A mean of 60 per cent. of these unmarked flies roosted between six and ten feet above ground level (Table V), and the majority seen were resting on the gauze walls. However, there tended to be a movement

TABLE VI. *Summary, from two trials, of resting sites and heights above ground during the day of eight marked and 200 unmarked individuals of* G. morsitans *in the vertical cage*

		Unmarked flies						Marked flies		
		Number seen on								
Time (hr.)	Total no. flies seen	Host animal	Trees	Posts	Walls	Range of height (ft.)	Mean height (ft.)	No. of observations	Range of height (ft.)	Mean height (ft.)
0600–0700	107	15	1	9	82	1–23	7·4	5	5– 7	6·0
0700–0800	102	36	5	11	50	1–30	8·9	7	4–30	9·3
0800–0900	98	41	10	7	40	1–30	7·4	11	4–30	8·9
0900–1000	119	22	9	13	75	0–30	8·0	9	5–11	7·5
1000–1100	99	24	19	15	41	2–26	8·8	12	2–11	6·6
1100–1200	82	14	32	17	19	2–15	5·7	14	0– 9	6·1
1200–1300	78	11	24	12	31	1–17	5·9	13	0–11	6·7
1300–1400	34	2	5	6	21	1–21	6·3	12	3–11	6·7
1400–1500	39	1	11	16	11	1–25	6·2	12	0–11	6·5
1500–1600	49	14	16	4	5	1–30	7·4	11	0–11	6·6
1600–1700	67	23	5	11	28	2–30	7·8	7	6–12	9·0
1700–1800	78	26	6	3	43	3–30	9·7	9	6–18	11·3
1800–1830	—	—	—	—	—	—	—	5	7–20	12·0

from the walls to the posts and boles of the trees after about 1000 hr. and a return to the perimeter of the cage after 1600 hr. (Table VI). The number of flies visiting the host animal decreased between 1100 and 1500 hr. and increased again in the late afternoon, and this agreed with the results obtained in another study by Dean, Paget & Wilson (in press).

There did not appear to be much difference in the recorded resting heights between the three main site categories (trees, ladders and posts, and wall) and the data were combined (Table VI). The mean resting height of both marked and unmarked flies tended to increase between 0600 and 0700 hr. Between 0900 and 1100 hr., the mean height and the maximum height of individual resting flies tended to decrease. The data for the marked flies also indicated a decrease in the minimum roosting height, but this trend was not obvious in the more numerous data for the unmarked flies. In the late afternoon (1500–1700 hr.), the general level of resting sites began to rise again and reached a peak, with the marked flies, after 1800 hr. No observations were made after 1830 hr., but the lower levels of resting sites at 0600 hr. indicated that there must have been some activity during the night.

Pilson & Leggate (1962) concluded that during the late dry-season most individuals of *G. pallidipes* rest on branches in the early morning, prefer rot-holes, if available, between 1145 and 1245 hr., move to the boles of large trees at about 1445–1545 hr., and re-occupy the branches after 1645 hr. These diurnal movements generally agreed with the results presented above and may be due to the reactions of the flies to high temperatures at midday.

Marked flies released into cages 1 and 2 were found to remain in the same sites between dusk and early the next morning. However, Pilson & Leggate (1962) could not find any roosting individuals of *G. pallidipes* at dawn and concluded that they moved to unknown sites during the night. The decrease in the mean roosting height of marked and unmarked flies in the vertical cage also indicated some activity during the night but flies were always found at 0600 hr. in typical sites. Several other workers (Jewell, 1958; Rennison, Lumsden & Webb, 1958, 1959; Southon, 1959) marked various tsetse species with reflecting paints and during the night located with torches flies resting on leaves, while Pilson & Leggate (1962) found two individuals of *G. pallidipes* sitting on small vertical twigs.

Summary

Investigations, using tantalum-182, into the behaviour of *Glossina morsitans* Westw. in large field cages are described. Individual straight-line displacements occurred on average about every three hours and were generally small and erratic in direction. The perimeters of the cages tended to 'trap' an enclosed population, but flies appeared to move to the walls more quickly when they were shaded by an outer covering of hessian. Horizontal distribution and movements of flies did not appear to be associated directly with the enclosed vegetation, artificial roosting sites or host animals. Observations on vertical displacements indicated diurnal movements to and from boles of trees and changes in roosting heights. The majority of flies rested between six and ten feet above the ground, though individuals were seen from ground level to 30 ft. Few observations were done at night, but two flies were seen on the underside of leaves.

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