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The Occurrence in Nature of Tsetse Pupae
(*Glossina swynnertoni* Austen).

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Contents **Pages**

Introduction.

SWYNNERTON (1923), working east of Mwanza, Tanganyika Territory, was the first observer to find pupae of the species which bears his name. They occurred under thickets, logs, and under the shelter of overhanging rocks. He wrote: "In its apparent partiality for thickets as a place of deposition, the fly would appear to resemble *pallidipes* and differ from typical *morsitans,* for in the west of the territory at any rate, few *morsitans* pupae, but many *pallidipes* are found in these thickets, while under logs in the grass outside them the proportions are reversed. Under single rocks near Ngasamo as many as 300 and 400 puparia were taken. The conditions were always dry."

LLOYD (1935) also mentions some breeding sites of *G. swynnertoni*. Near Shinyanga he found that, provided there was sufficient shelter, pupae were taken in greater numbers under logs, under leaning trees, or rock shelters, than in the rest of the thicket; under overhanging rocks they were found only round the bases of kopjes, never high up. Rock sites away from kopjes were favoured, as were logs, decumbent trees, hollows in the bases of trees, and the bases of baobabs. He thought the effort expended in his getting 31 live pupae of *G. swynnertoni* would have resulted in obtaining 500 to 600 of *G. morsitans* at Kikori. None the less records of JACKSON (1948) show that vast numbers of pupae of *G. swynnertoni* could be procured in the dry season. Thus between 17th and 27th August he had used 27,500 pupae for fly-release experiments. He informed me that these pupae were all obtained by native searchers during July and August in the north west corner of Block 9—the block of bush lying immediately north of Old Shinyanga (see SWYNNERTON 1936, Map 2).

During the rainy reason, however, the position is different. Pupae from which newly emerged flies continue to come have never been discovered in sufficient numbers to account for more than a fraction of the newly emerged flies encountered in the field. The explanation put forward for this is given by POTTS (1950, p. 9), who stated that the results which I (E. B.) had obtained for *G. swynnertoni* and *G. pallidipes* up to that time, "have confirmed the previous suspicion that during the rains the pupae of these tsetse are scattered so widely through the floor of the general woodland that searches by ordinary means produce but little result".

If SWYNNERTON (1936) is consulted one receives a different impression. He wrote (p. 94): "During part of the year at least *G. swynnertoni* breeds much on the thicket floors, but VICARS-HARRIS is finding that in the late wet season the largest numbers are under logs and at tree bases in the thickets, under rocks in kopjes and in rot holes in trees as much as six feet from the ground, in any nooks in fact in which real protection from the rain may be had... However the particular observation here referred to requires confirmation over a larger number of seasons." SWYNNERTON evidently thought that the wet season breeding grounds of *G. swynnertoni* had been discovered. Official reports reveal that this was due to the considerable numbers of live pupae and what appeared to him to be very recent shells which VICARS-HARRIS had found during June 1935 (that is, after the rains were over) in Block 11, south west of Old Shinyanga. He got 112 pupae und 608 shells in dry sites, mostly from rot-holes in baobabs near kopjes, or sheltered places under rocks in the kopjes themselves. As a result of these findings VICARS-HARRIS laid out two pupal rounds for regular search in Block 11, one associated with the upper Ninghwa fly round and the other with the Mantine fly round. The results during the following rainy season were disappointing. Thus he reported no pupae at all being found for the first three months of 1936; "negligible results" for April and only two pupae during May. This showed that the previous year's hopes for finding pupae in their wet season breeding grounds had been mistaken. The rains that year (1936) were heavy and well distributed. In previous seasons, when the rains were lighter and badly distributed, many more pupae had been found. Thus in the two years 1933-1934 during the corresponding period (January-May) Mr. W. H. POTTS had obtained 135 pupae.

The environment of Shinyanga.

The area in which my observations have been made lies close to Old Shinyanga situated in the western part of the Central Plateau of Tanganyika Territory (3½° S., 33° E.) at an altitude between 3800 and 3900 ft. The climate is semi-arid with an annual rainfall of about 30 inches. Meteorological data are recorded at Old Shinyanga. Accounts of the climate have been given by LLOYD (1935, p. 440) and by SWYNNERTON (1936, p. 95). The area is subjected to south-east trade winds in the dry season and the rains follow in the track of the sun, somewhat after the two periods when the sun has passed the zenith, with the result that the year is divided into two periods of about equal duration, when conditions are mainly wet, or are mainly dry. The rains usually break in November and tail-off in May, with typically a drier spell (the short dry season) lasting for about a month from January into February. Early morning temperatures are at their minimum in the early dry season, particularly in the month of July; the highest maxima occur in October, or until the rains break. The change of conditions from one season to another is usually abrupt.

The year may be taken as starting with the break of the rains. It can conveniently be divided into six bi-monthly periods, each with its characteristic features (Table 1).

There are three times during the year which are particularly likely to change the kind of breeding site chosen by parent female flies:

1. The break of the "short" rains and the flush of new foliage.
2. The change from rainy season to (early) dry season, when conditions are cool and there is progressive leaf fall.

3. The sudden reduction of shade as a result of grass fires at the end of July at a time when temperatures are rising, conditions become more arid and cool places very localised.

TABLE 1.

Division of the year at Shinyanga into six bi-monthly periods each having its characteristic features.

Period	Season	Soils and Vegetation
Nov.-Dec.	Short rains break	Leaf flush
Jan.-Feb.	Rains interrupted by short dry season	Soils at breeding sites all dry out
Mar.-Apr.	Long rains	Usually all soils wet
May-June	Cool: start of early dry season	Leaf fall
July-Aug.	Continues dry, but temperatures rising	Leaf fall continues grass fires at end of July
Sept.-Oct.	Hot and very dry	Few precursory showers accelerating leaf flush locally

During the period of the present investigation, rainfall decreased from 1946 to 1949. Late in 1948 the short rains failed almost completely. There was a fall of 90.4 mm. in a few hours on 27th October, but this was followed by only a total of 59.4 mm. throughout the entire two months of November and December. Drought continued to the end of the short dry season late in February 1949. The rainy season of 1950-1951 was normal, but ended suddenly at the beginning of May. The rains of 1951-1952 were unusually heavy and prolonged.

Within about a month of the breaking of the rains there is very little bare soil left except, of course, in such places as rot-holes in trees, under large logs and under dense thicket. Predominantly the soils round Shinyanga become dark coloured and tacky when wet and cling to small objects contained in them. This dark colour may be due to humus (as under dense thicket) but otherwise to the nature of the mineral content. Soils like those under riverine thicket which have suffered a good deal of inundation during the rainy season may be hard when they first dry out, but if so this hardness usually breaks down as a result of natural weathering within a few weeks, leaving the soil soft and powdery. Well drained soils, when they dry out, tend to be friable and quite light in colour.

LLOYD (1935) describes the country in the vicinity of Shinyanga as being gently undulating, the rises draining into rather open hardpan valleys; when it rains the water tends to lie about where depressions occur. The bush is of the "Nyika" type (*Acacia—Commiphora—Combretum*—other genera) traversed by river channels in which no water flows during the dry season, but which frequently overflow and inundate the country in their vicinity during heavy falls of rain. Two such seasonal streams, the Ngongho and the Mwakilendya, traverse the south west corner of Block 9 from north west to south east.

Large trees such as *Piptadenia hildebrandtii* and *Albizzia sericocephala* are prominent features along the water courses. Patches of dense riverine thicket contain a considerable proportion of evergreen species and afford shade in the hot dry season, the most important being the liana *Hippocratea obtusifolia.* There are three main vegetation communities, on respectively eluvial, hardpan (grey cemented soils of the lower colluvium) and illuvial soils, which may tend to occupy comparatively small areas forming rather a mosaic. Maps of such a mosaic pattern in Block 9 are given by HARRISON (1936). The most conspicuous tree scattered throughout the area as a whole is the baobab *(Adansonia digitata).* Hardpan bush is characterised by the small trees *Lannea humilis, Commiphora schimperi* and *Acacia drepanolobium,* together with bushes of *Combretum parvifolium.* A good example (fig. 1) occurs just across the Mwakilendya river three miles north east of Old Shinyanga. In addition to thickets associated with rivers, there are many other thickets scattered on the eluvium and hardpan, mostly only a few yards across and centred on a prominent tree or small group of trees (fig. 11). By contrast with the riverine type already mentioned these other thickets are composed mostly of deciduous species, but occasional evergreens such as *Thylachium africanum,* or the thorny climber *Capparis tomentosa,* may be present. The majority of deciduous species have lost their leaves by the end of July, though, in a few localities where the soil has not yet dried out so much, defoliation may be postponed a week or two longer, leaving patches of bush which are still green when the rest is already practically leafless.

Grass fires sweep through about the end of July and the aspect of the bush is profoundly changed as a result. In hardpan areas grass may be too sparse to support a fire, but the grass mat in most of the bush is over two and a half feet high. After burning, only bare soil is left, save for a few resistant stalks scattered about. Such foliage as still remains on the bush and was within reach of the heat of the flames gets destroyed or scorched; the scorched leaves tend to remain on the plant until the next rainy season. The fire may destroy a proportion of the tsetse breeding places completely, especially hollow trees and logs, and in other sites the remaining shade is of course reduced suddenly by removal, or scorching, of the foliage. New foliage in the bush begins to appear before the rains actually break, and there are usually precursory showers which help to bring on leaf flush. Such early rain is usually local and the areas where it falls show conspicuously green.

There were very few logs in the south west of Block 9, but they were abundant a few miles further north, both in the open and in thickets where *Acacia usambarensis* was numerous. This species is prone to develop rot-holes and also has a tendency to a decumbent habit, especially when near the edge of small thickets (figs. 8 and 9).

In the hot dry season the evergreen thickets still give protection from the sun; the only other protected sites (apart from large logs) are rot-holes, cavities at tree bases or under massive roots (fig. 13). Such sites seem to be almost confined to the trees *Piptadenia hildebrandtii, Commiphora mollis* and baobabs, the last sometimes with a projecting flange (fig. 14) round the trunk just above ground level.

Large game animals do not now much frequent the areas where these observations on breeding sites were made. Giraffe, for example, are very much fewer now than when HARRISON (1936) made his observations. Wart hog are quite numerous; impala and smaller antelope are frequent, but animals such as rhinoceros and elephant occur only very occasionally.

Methods of search.

A man named Shija Masanja was amongst those collecting the large number of *G. swynnertoni* pupae required by JACKSON (1948), mentioned above (p. 305). He lived near the north west corner of Block 9 and was remarkable in having found larger numbers of pupae in that area than anyone else. He, along with two others from the same locality, were recruited to work for me, along with a Shinyanga fly-boy who had an intimate knowledge of the local bush.

Throughout the work, apart from receiving some general indications from me, the men have been free to choose the sites for searching for themselves. Previously Mr. W. H. POTTS had found that Africans tended to get on very well in finding pupae as long as they were left alone, but when the European in charge chose the sites to be searched, they found many less. As the work progressed I have been impressed with the truth of this on many occasions. When I have taken it upon myself to choose new places to be searched, it has usually been with the object of consolidating the position round some particular site which the men had already located. Left on their own they will not do this, since they naturally object to "wasting time and energy" on places which they sense are unproductive. I selected a number of the most productive sites which had been located late in 1946 for routine examination. Searching these occupied about half the men's time and during the remainder of the month they were left to search new places. The problem which I wished particularly to elucidate was the location of pupae during the rainy season. The men themselves could offer no clue to this, despite their experience. Shija Masanja told me he had only *once* found a pupa during the rains, in the north west part of Block 9, where flies are very numerous, after a great deal of search. I was influenced by the account given by LAMBORN (1915) of how he found breeding places of *G. brevipalpis* in places "which differed in no wise" from the surrounding bush, save in being particularly frequented by animals. I imagined the same might well be true of *G. swynnertoni* in the ubiquitous shade afforded by the Shinyanga bush in the rainy season and that if pupae were concentrated anywhere, it would be near water-holes or near game paths, or places where animals lie up regularly. I instructed the searchers to bear these suggestions in mind in their choice of new sites for searching.

Until the end of 1949 the searching was done in the south west end of Block 9, in squares B, C, and their vicinity, with transfer of the work from time to time to square C2 in which the Mwakilendya locality lies (HARRISON 1936). The point at the meeting of HARRISON's squares E2, E3, D2 and D3 was the centre from which searches were carried out in 1951 and 1952, along with occasional visits back to the Mwakilendya locality. The reason for thus transferring the work further to the north was that *G. swynnertoni* then occurred there much more abundantly.

In sites which were big enough to permit of it, the invariable method of searching employed at all seasons up to the end of 1951 was first to remove larger objects obstructing the site, such as dead twigs, branches and dead leaves, and then to inspect the surface for possible shells. Afterwards the site was dug to a depth of about one inch with pointed wooden pegs and the loosened earth carefully searched through. When finished, the site was restored pretty much to the condition it was in at the start. Search of rot-holes in trees entailed scooping out the loose material from inside the tree on to the ground (see fig. 16), searching through it carefully and afterwards replacing it. In 1952 the customary method of searching described above was modified by giving much more attention to the surface of the soil. Instead of just inspecting it rather casually, it was very closely scrutinised inch by inch before digging was attempted. Eventually digging wet soil was abandoned as a method of search and the surface searching was followed by lightly scraping the soil surface.

Each site was indexed and records were made of its characters. Except in the case of very restricted sites like rot-holes, the place where each whole puparium was found was made obvious by the insertion of a wooden peg. Pupae were not handled, but were scooped up into a glass tube with the aid of a slip of paper and securely held with cotton wool so that they could not be disturbed again until they reached the laboratory where they were weighed. If the weight was a good deal too low for a live pupa, it could confidently be stated the pupa concerned was dead when found. All pupae having a reasonably good weight were kept singly in small glass tubes plugged with cotton wool and resting horizontally in shade on a table in the laboratory. If the fly did not emerge within a reasonable period, the pupa was re-weighed and counted as dead if now found to be grossly under weight.

Field results.

The wet season.

Up to 1952, very few viable pupae of *G. swynnertoni* were found during the wet season months January to April which separate one dry season "concentration" of pupae from another (Table 2). Thus in 1947 there were only four,—all from wet soil. One of these occurred by the peg at the foot of the erect *Acacia usambarensis* on the left of fig. 18. Despite their inability to find pupae in appreciable numbers during the rainy season, the searchers found substantial numbers of empty cases. Thus for example between January and April 1947 they got 782 shells of *G. swynnertoni* and *G. pallidipes* and similar numbers were obtained in subsequent years.

During the first four months of 1948 the total found was only two live pupae (none dead). Both pupae were discovered by Shija Masanja on 22nd April, during a long spell of cold, wet weather. The pupae were under a log of *Acacia rovumae* (fig. 2), part of which was covered by thicket and part lying in the open. The pupae were under the open part, where the trunk was a foot

TABLE 2.

The numbers of whole tsetse puparia found by ordinary methods of search during each bi-monthly period up to the end of 1951.

Period of observation		Rainfall at Old Shinyanga (m.m.)	Rainfall at Old Shinyanga No. of days	Total number of whole puparia found: Tsetse emerged from pupae collected during this period	Dead or died	Obviously dead when found
1946	from 24 Oct.	2.4	3			
	Nov.-Dec.	238.9	38	53	18	20
1947	Jan.-Feb.	348.8	34	3	0	3
	Mar.-Apr.	303.1	38	1	0	0
	May-June	49.5	9	16	4	0
	July-Aug.	17.4	3	44	11	5
	Sept.-Oct.	20.2	5	25	6	11
	Nov.-Dec.	123.9	23	25	3	4
1948	Jan.-Feb.	301.9	27	0	0	0
	Mar.-Apr.	282.2	36	2	0	0
	May-June	20.8	9	58	10	2
	July-Aug.	3.7	3	95	16	4
	Sept.-Oct.	136.1	11	59	11	3
	Nov.-Dec.	59.4	18	6	0	4
1949	Jan.-Feb.	176.2	26	30	1	0
	Mar.-Apr.	200.5	31	1	1	0
	May-June	17.7	5	13	2	1
	July-Aug.	Nil	0	68	3	1
	Sept.-Oct.	37.3	6	12	0	5
	Nov.-Dec.	200.6	20	9	0	1
1951	Jan.-Feb.	331.4	31	1	3	0
	Mar.-Apr.	451.4	38	5	3	1
	May-June	18.7	6	39	6	0
	July-Aug.	0.2	1	84	13	2
	Sept.-Oct.	20.4	4	45	10	4
	Nov.-Dec.	420.0	38	29	2	4

above the soil and one and a half feet in diameter. Herbage up to three feet high was growing up to the edges of the log, but immediately beneath it the soil was bare. The pupae occurred two feet apart, resting on the surface of two separate small flakes of bark about two inches square. The larvae could not possibly have climbed on to these flakes and must therefore have been deposited on them. A female and a male of *G. swynnertoni* emerged from these pupae 12 and 15 days later. This observation shows that:

1. The pupae must have been lying thus exposed on the surface, for about a month before they were found, without suffering injury from predators or their vitality being otherwise impaired.

2. The parents were different flies and they probably took their last meal prior to larviposition at the same time.

3. The mother flies were attracted by a certain type of furniture in the breeding site; their larvae were not deposited at random in the bush.

4. The larvae were born under conditions which led to pupation taking place without their making any appreciable effort to burrow. They only needed to crawl about one inch from where they were deposited to fall off the bark and reach the bare soil.

Early in 1949 on the other hand, far more pupae were found, in association with the virtual failure of the short rains late the previous year. While the amount of foliage on the bush was much as usual, herbage was scanty and arid conditions prevailed until late in February. From 10th January to 25th February, 1949, 31 "good-weight" pupae were found, in sites a shown in Table 3.

TABLE 3.

Pupae found in the short dry season of 1949.

Category of site	Number of pupae found
Rot-holes in trees	5
Logs under deciduous thicket	15
Logs in the open	1
At tree base	1
Under exposed tree root	1
Thicket	8

These finds showed the following important features:

1. A predilection by pregnant female flies for logs raised above the surface of the soil, particularly under a canopy of deciduous thicket.

2. One pupa occurred under a log in the open, as did the two wet season pupae of 1948 mentioned above.

3. Some flies sought out rot-holes in trees, despite the fact that these were situated in the centre of thickets amid a general shade canopy. The presence of shade alone was evidently not sufficient—they wanted a certain kind of furniture besides. From their emergence dates, one of these rot-hole pupae was evidently deposited in December and the other four in January.

By contrast with this record drought of 1948/49, the rains of 1950/51 were above normal. From January to April 1951, mostly about a mile north of the Mwakilendya river where *G. swynnertoni* was then abundant, only six viable pupae were discovered. They were all under logs, or decumbent trees, at the edges of small thickets. Many rot-holes were searched also, but no pupae (live or dead) were found in them. Also four non-viable puparia were obtained under *Fockea schinzii.*

On 3rd May 1951, just at the start of dry season, in conditions when the surface soil was still damp, an important discovery was made of three live pupae close together under an arched log of *Acacia usambarensis.* In May the log lay in open grass three feet high, so that only the upper portion was visible protruding above the grass layer. Judging from the dates of emergence of the flies, two of the pupae and possibly also the third had been deposited while the heavy rains of late April were still in progress. Like the observation in April 1948, here again was a case where deposition during the rains did not take place at random, the females having been attracted for larviposition to a certain very limited spot. This site was kept under observation and more pupae were found there during the early dry season, thus showing that a preference which had started during the late rains continued for a considerable period.

In about 50 sites which had been productive in the late dry season of 1946, only one viable pupa was found from January to April 1947. This occurred in a hollow baobab (Table 4, site 25). In the majority (mostly hollows in trees or evergreen thickets) the soil was wet very soon after the break of the rains, but some of the tree hollows kept dry for considerably longer. All soils eventually became sodden throughout Block 9, no matter how protected the site might appear. Thus there was no evidence that the initially drier and more protected sites were being sought out by the flies for breeding purposes before the general wetting became complete. (Compare VICARS-HARRIS's observation referred to on p. 306 above.) All sites dried out at times, particularly during the short dry season and then the negative results were undoubtedly valid, since there was no question of the presence of a pupa being obscured through earth clinging to it; and pupae would have been visible in rot-holes at all times even when wet, owing to the friable nature of the soil in them. The results therefore showed beyond doubt that the types of site used during the hot dry season were scarcely used at all during the rains.

As the wet season breeding sites had evidently so far escaped detection, trees were searched early and late in 1951, to try to find signs of the breeding of *G. swynnertoni* in this higher, well-drained and well-shaded stratum of the vegetation. Crevices of bark and places under loose bark were also closely scrutinised. Neither shells nor puparia were ever found in such places until the 12. 1. 52, when a small, non-viable pupa was discovered in a crevice of bark of *Acacia usambarensis,* four inches above the soil.

The dry season.

Foliage and shade are still abundant when dry season conditions set in, usually in May. Just over a week later pupae of *G. swynnertoni* abruptly appear again, not only under deciduous thicket but also in tree hollows.

After the break of the rains, if we judge from the dates of emergent flies, little, if any, larviposition goes on in the sites (of whatever kind) utilised during the late dry season. The number of whole puparia found each month in a series of twenty hollows in trees between November 1946 and June 1949 in the south-west of Block 9 is shown in Table 4. All except one deep natural hollow at the base of a baobab (No. 14) were rot-holes; No. 25 was a hollow baobab similar to that illustrated on Plate 24 by NEWSTEAD, EVANS, and POTTS (1924).

If we bear in mind that most November and December pupae in tree hollows were deposited before the rains began, Table 4 shows that the use of hollows in trees as breeding sites is confined almost entirely to the dry season. Normal short dry seasons (which divide the short and long rains) do not suffice to induce the flies to utilise such places, but after a quite abnormal drought had continued into early 1949 (page 307) a few pupae were found eventually in tree hollows. Table 4 also shows that whereas hollows in trees are being used only to a moderate extent until the time of grass fires at the end of July, their use thereafter is greatly increased.

In addition to the pupae occurring in classical sites in the early dry season numbers occur also under deciduous thicket, particularly species such as *Combretum parvifolium* and *Grewia fallax* whose stems tend to lean over the ground. If the plant has an erect habit it is not favoured. Pupae under thicket tend to occur in groups. Examples are shown in figs. 10 and 12. Observations made in 1947 (repeated and confirmed in 1948 and 1949) showed that pupae were quite numerous under the bushes of *Combretum parvifolium* on the Mwakilendya hardpan (fig. 1) during the early dry season and even as late as mid-August, when the bushes were leafless, but none was found subsequently, and deposition must have ceased several weeks earlier. Apparently therefore breeding shifted during July from these exposed places to rot-holes and other protected sites, thus helping to augment the numbers in rot-holes (fig. 15) during the hot dry season as indicated in Table 4.

TABLE 4.

Whole puparia found in 20 tree hollows searched usually at least once a month.

	Site:	14	25	26	27	28	29	30	31	34	35	37	39	40	42	43	109	162	183	284	292	Total
1946	XI	5	6	4	1	3	2	–	6	2	–	3	1	3	–	–						36
	XII	–	–	–	–	–	–	–	–	–	–	–	–	–								0
1947	I	–	–	–	–	–	–	–	–	–	–	–	–	–								0
	II	–	1	–	–	–	–	–	–	–	–	–	–	–								1
	III	–	–	–	–	–	–	–	–	–	–	–	–	–								0
	IV	–	–	–	–	–	–	–	–	–	–	–	–	–			Not searched					0
	V	1	–	–	–	–	–	–	–	–	–	–	–	–								1
	VI	1	–	–	1	–	–	–	1	–	–	3	–	–								6
	VII	2	–	1	–	1	–	–	1	–	–	2	2	–								9
																			Grass fires			
	VIII	1					Not searched															–
	IX	2																				–
	X	–	3	2	–	–	2	–	1	–	–	–	–	–	–	–						8
	XI	2	–	3	–	–	–	–	–	–	1	1	–	1	1	–	1	1	1	–	–	12
	XII	–	2	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4
1948	I	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0
	II	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0
	III	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0
	IV	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0
	V	1	1	1	–	–	1	–	1	–	2	2	2	–	–	1	–	–	–	–	2	14
	VI	2	–	–	1	–	2	–	–	–	–	1	1	–	–	–	4	1	1	–	1	14
	VII	2	–	1	2	–	–	2	1	–	–	–	–	–	2	2	–	–	–	–	–	12
																			Grass fires			
	VIII	–	5	–	–	2	4	3	4	–	–	–	1	–	–	–	–	–	–	–	–	19
	IX	1	2	–	–	–	1	2	1	1	5	–	1	–	–	–	1	6	1	–	–	22
	X	5	–	3	–	2	6	–	1	–	3	1	–	4	–	–	–	5	3	3	–	36
	XI	–	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	2	1	–	5
	XII	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2
1949	I	1	1	–	–	1	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	5
	II	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0
	III	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0
	IV	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2
	V	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
	VI	–	2	–	–	1	1	1	–	–	1	1	–	–	–	–	–	–	–	–	–	7

No pupae were found under riverine thicket during the early dry season (before grass fires), but they do occur there, chiefly at the edge and very sparsely, during the hot dry season. By contrast, *G. swynnertoni* prefers to seek out rot-holes in trees, even when growing in the centre of the riverine thicket, and to concentrate its pupae there. Despite the suitable appearance presented by the massive liana *Fockea schinzii* and the evergreen bush *Maerua johannis,* both growing on hardpan soils, I have found little evidence that these are favoured by *G. swynnertoni* for breeding purposes.

The work during the early dry season of 1951 was centered in the area well to the north of the Mwakilendya river, about the intersection of squares E2, E3, D2, D3 (HARRISON 1936). The first pupa was found in a rot-hole on 8th May just over a week after the change from very wet to dry season conditions. This evidently marked the real start of the dry season occurrences, since henceforth pupae continued to be found in numbers. Since three wet season pupae had been found under a log (No. 354) in the open on 3rd May, other places of this nature were searched. Out of 14, only two gave positive results (five pupae) between May and July, but none subsequently. Logs and decumbent trees at the edge of small thickets were much favoured as breeding sites during the early dry season, but as was the case with the deciduous thickets at Mwakilendya, such places had been largely vacated by the time that hot dry season conditions set in. Examples as they appeared in mid-June are shown in figs. 7 and 8, while fig. 9 shows the appearance presented by one of these places in the late dry season. The figures show how the pupae tend to occur immediately underneath a trunk, or log, lying more or less horizontally a few inches above the ground. This strongly suggests that the female flies seek out such places and perch there before larviposition. I have not yet discovered the role played by these perching places in relation to larviposition. When they were first noticed, it seemed to me that they supported SWYNNERTON's suggestion (1921) that the females drop their larvae from a height, but I have found no evidence to support such an idea and laboratory observation (below) points strongly against it.

G. swynnertoni evidently does sometimes use animal burrows, for three pupae were found in a disused wart hog burrow on 10th July.

An observation of great interest made on 20th August 1951 was the discovery of one live pupa and eight recent shells 20 ft. above the ground in soil in the crown of a baobab (fig. 17). This is the greatest height above the ground at which tsetse pupae have ever been recorded.

Observations in 1952: the discovery of *G. swynnertoni* pupae during the rainy season.

Searching in the first five months of 1952 was carried out in the area investigated the previous year. Sufficient indications of the occurrence of wet season pupae had been obtained by this time to induce me to exploit the observation made during the rainy season of 1948 and try to find pupae on the surface of the ground under suitable "perching places"—such as raised logs in the open, decumbent trees, or stout branches close to the ground. On 9th January the rains were suddenly interrupted by the start of the short dry season which lasted in the area of search until 11th February. Before that, the rains had been heavy and those that followed were exceptionally prolonged (27th May). During the short dry season, surface soils were dry for a month from 12th January and they dried out to some extent at intervals after that also until 13th April, after which they remained wet until the end of May. The numbers of *G. swynnertoni* pupae found each month and the number which produced flies are shown in Table 5.

TABLE 5.

The number of pupae found each month in 1952 up to the end of May, and the method by which they were found.

1952	Rainfall recorded at Old Shinyanga		Number of pupae found by searching					
			On surface		Scraping surface of soil		Digging	
	(m.m.)	Days	Total	Flies[1] emerged	Total	Flies[1] emerged	Total	Flies emerged
Jan.	27.7	8	7	4	not attempted		10	9
Feb.	187.8	17	9	8	not attempted		16	12
Mar.	183.8	16	23	22	not attempted		6	6
Apr.	164.3	12	7	5	3	3	6	6
May	213.9	13	56	39	33	21	not attempted	

[1] To 29. 6. 1952.

Table 5 shows that a total of 178 pupae were found up to the end of May. Of these, 102 were discovered on the surface of the ground, 56 during May when the soil was always wet, and only two were dead when found. It was only during this last month that the searching of sites in which the surface had yielded positive results was generally followed up by scraping the surface of the soil and 33 additional pupae were detected by this means. Of the 40 pupae obtained by digging, 20 were from dry soil during the short dry season. They occurred under perching places at the edge of small thickets as exemplified in fig. 7. Four pupae were found at this site on 4th February by digging, and three more on 25th February after the rains had set in again, but these latter pupae were on the surface of the soil. Since scraping of the surface was not practised until 27th April, there is doubt about the real depth of pupae found by digging, particularly in relation to wet soil, before then. Judging from the dates when the flies emerged, it appears that 29 of the 40 pupae obtained by digging and possibly four from the surface had been deposited during the short dry season. These pupae were found mainly under logs in thickets, as were those discovered at the same season in the dry year 1949 and also the earlier finds in the long dry season of 1951. The indication is that, provided breeding *is* taking place in an area, pupae can be obtained in dry soil under such perching places by ordinary methods of search.

In the early stages of the 1952 searching, a good deal of attention was given to inspecting the surface of flakes of dead bark lying on the ground under logs and trees, but nothing was found. The nearest approach to a repetition of the initial observation made by Shija Masanja in April 1948 was the finding of a single pupa resting on the surface of a fallen dead leaf; two other pupae were found resting on the surface of the soil underneath flakes of bark. A feature common to all wet season breeding sites was the presence of bare soil—small patches without grass or other herbage such as persist throughout the rainy season immediately beneath large logs and under low, drooping thicket, providing some form of semi-horizontal "perch" for the parent female, exemplified in the leaning stem of *Grewia fallax* at the base of the tree shown in fig. 3, or trunks of fallen trees as in figs. 4 and 6, or large branches as figs. 5 and 7. No positive result was obtained from searching the surface round 50 erect, clean stemmed trees.

It can be seen from the illustrations that there is little difference between the character of breeding sites used in the rains and those used in the short dry season or in the early part of the long dry season. There is a tendency for the former to be in the open, whereas the latter tend to be under a canopy of thicket; the essential difference lies not in the nature of the site, but in the actual location of the pupa in relation to the soil.

Under dry conditions the larva burrows almost at once to a depth of about half an inch and the presence of the pupa is revealed by digging because the dry soil does not adhere to it to any great extent. In tenacious wet soil, on the other hand, pupation evidently occurs on, or near, the surface and the pupa lies effectively hidden because it is embedded, partially or wholly, in this dark coloured tacky matrix. Even if pupation had occurred so as to leave the pupa completely exposed, it would soon become obscured by mud-splash as well as by getting beaten into the soil by the force of the rain. Such pupae are extremely difficult to detect (fig. 19), especially on wet soil; the earlier examples were found during periods when the surface of the soil was temporarily dry. Until mid-May, all but three of the pupae, on or near the surface, had been found by the one man Shija Masanja; after that the other men suddenly developed the knack also and were finding quite substantial numbers.

The meeting point of squares E2, E3, D2, D3 (HARRISON 1936) formed the focus of the searching in the rains of 1951 and 1952. During 1951 abundant evidence had been obtained that breeding was going on to the west. The site shown in figs. 8 and 17 were situated in the western area, whereas that shown in fig. 7 lies about a quarter of a mile to the east. In 1952 the two first-mentioned were searched many times and many other places besides, but the only evidence of breeding ever obtained up to the end of May was a single viable pupa on the surface. By contrast, 172 of the pupae shown in Table 5 (up to the end of May) were all in a comparatively small tract of country, half a mile wide and a quarter in width, extending about half a mile eastwards from the focal point at the meeting of the above squares. The reason for this was not discovered, but it suggests that breeding is restricted to certain zones of the bush even in the rainy season.

Site 394 (fig. 4) consists of a log of *Lannea humilis* lying in a small open glade in bush much frequented by wart hogs. No rain fell there between 5th and 13th April. On 9th April, eight pupae were found by Shija Masanja within an area of one square foot near the base of this log. He found five on the surface and the remaining three by digging. Unfortunately the practice of scraping the surface was not being used at that time. He inspected the surface and dug under the arched part of the log also, but found nothing further. The weather continued dry and on 12th April the site was searched again. No more pupae were seen on the surface but three more were found by digging under the central portion of the log (which had been apparently negative when it was dug over on the previous occasion). Flies emerged from two of these pupae two and six days later. This shows that the pupae had been present on the first occasion this site was searched but had remained undetected. The opening-up of the soil had probably resulted in its drying sufficiently to cause it to fall away from the pupae, whose presence had previously been masked through soil adhering to them. Seven more surface pupae were found at No. 394 before the end of the rainy season, all near the base of the log where the first ones were found, thus bringing the total found there during the rainy season to 18. Flies from these pupae emerged between mid-April and late June, showing that this log was being used as a breeding site over a considerable period.

Other productive sites nearby resembled No. 394 (figs. 5 and 6). It was remarked how strikingly aggregated the "clutches" of pupae were, separated into distinct groupings even under a single log (cf. fig. 3 also): in No. 394 fifteen occurred within an area of about a square foot. It was difficult to resist the suggestion that larvipositing females attracted others to use the same spot.

As has already been mentioned (p. 305) the main source of supply of large numbers of *G. swynnertoni* pupae in the dry season was the north west end of Block 9. During the latter part of May 1952 I sent Shija Masanja together with another man to search for pupae there. However, despite the fact that flies were abundant they only found four live pupae (included in Table 5) in two positive surface sites out of 32 searched.

On 19th March one malformed surface pupa (excluded from Table 5) was found still showing the hardened crenulations of the larva. Such malformed pupae are sometimes found in the laboratory but I have never before seen one from the field.

Possible association of breeding with wart hogs.

The sites where pupae were found in the south west of Block 9 did not occur at random throughout the bush. They tended to be restricted to certain localities, usually without any vegetational difference being apparent between positive and negative areas. It may have been largely a matter of availability of food and on occasions throughout the work it was noticed that sites productive of pupae were frequently associated with the presence of wart hog in the vicinity. The tree hollows, results from which are shown in Table 4, were all in the "positive" areas. Several eminently suitable looking sites situated in "negative" areas were also kept under observation. An example is afforded by a deep rot-hole in *Commiphora mollis*. When this was first searched in November 1946, seven shells were found in it. Thirty-four subsequent searches up to the end of 1949 yielded only one additional shell. There was a similar experience with a rot-hole at the base of a baobab standing inside, but near the edge of a thicket, only a few shells ever being recovered from it. Many other such negative examples were encountered, particularly from thickets. It was unusual for the men to search a site, which they themselves had chosen, without finding some evidence that tsetse had been breeding there. It may have been that these shells were relics from previous years when the flies had been more abundant, or that at the times when they were found the flies were not using the sites, possibly because of absence of suitable game animals in the neighbourhood.

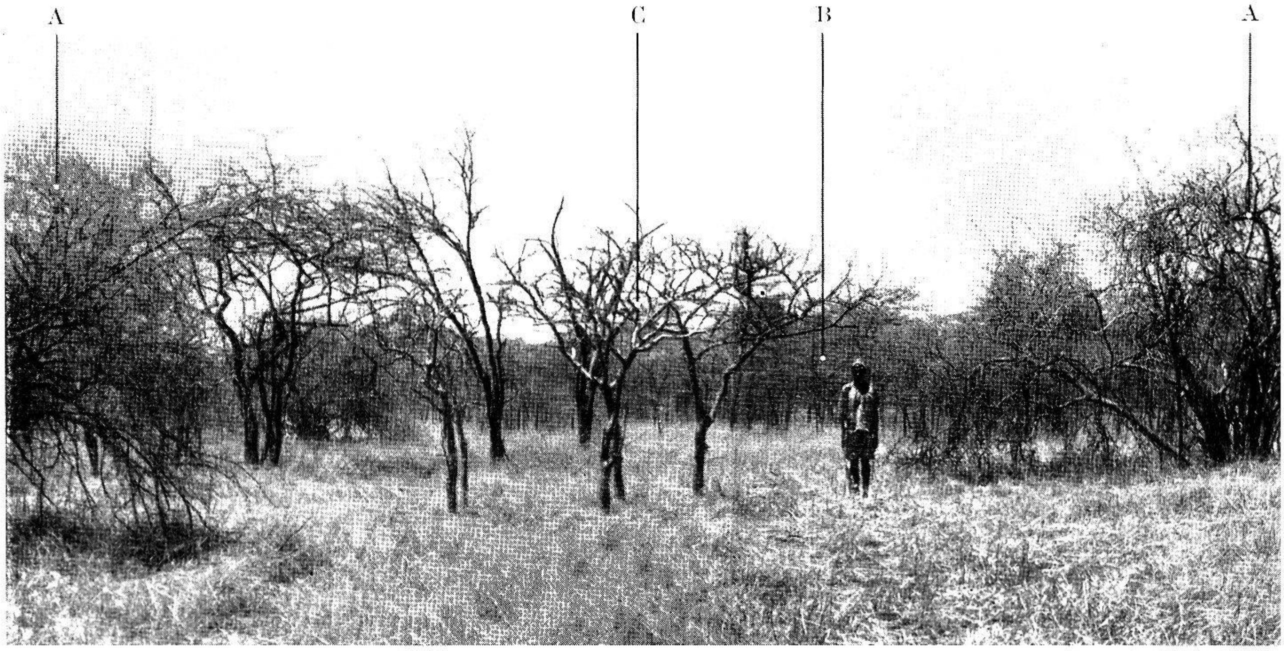
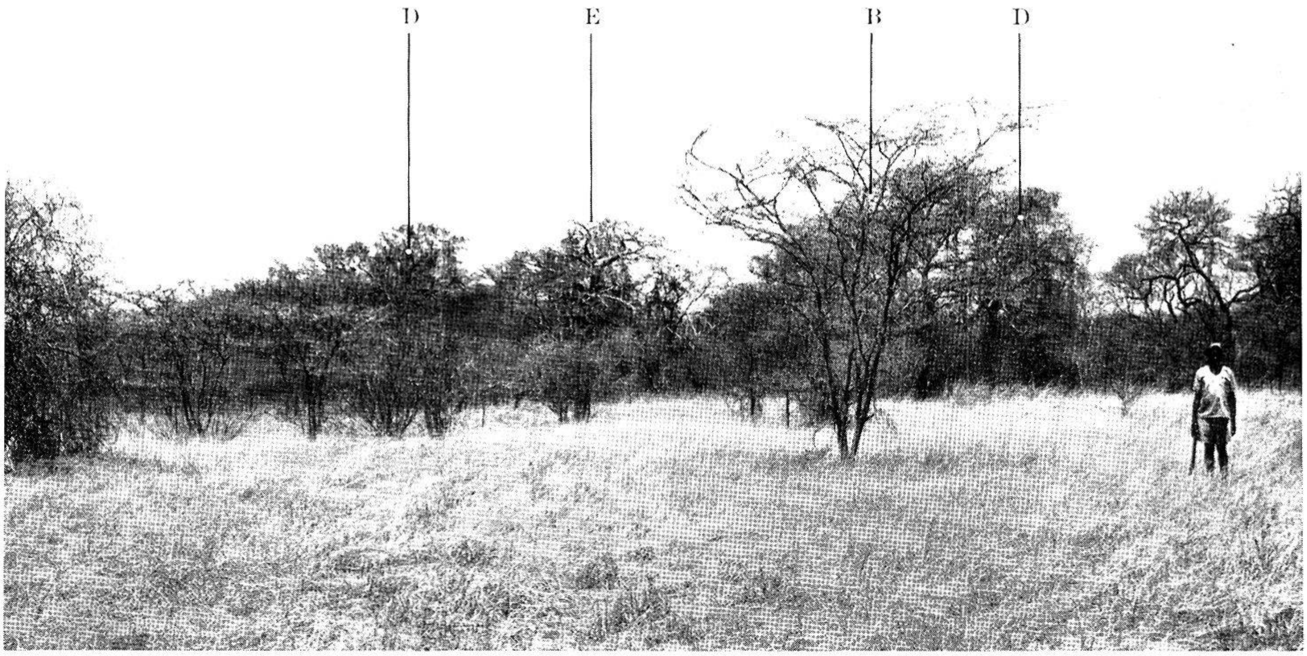


Fig. 1. The Mwakilendya hardpan in the dry season. (A) *Combretum parvifolium*, (B) *Acacia drepanolobium*, (C) *Lannea humilis*. The tall trees in the background, (D) *Piptadenia hildebrandtii* and (E) baobab, *Adansonia digitata*,

It was found that a place might suddenly spring into prominence as a breeding site for a brief period one year and not again be used. Thus in the south west of Block 9, where it was very unusual for as many as five pupae to be found in a single site at one time, site No. 160 contained a tree of *Acacia usambarensis* standing near the edge of a patch of deciduous thicket and on the ground a few feet away was an arched log formed by a branch which had fallen from it (fig. 18). A wet season pupa had been found near the base of this tree on 19th February 1947. The site was accordingly re-searched during March and April, but only four more shells were recovered. However, on 2nd July, eight pupae were found near the log as shown by the wooden pegs. Two of these pupae were dead and one failed to produce a fly. The first fly to emerge was a male on 16th July and the last was a female on 4th August. This site was re-searched 24 times up to June 1949 without any further pupae being found. There was a small water-hole 40 yards away which dried out completely early in July, but before this happened it was being much frequented by wart hogs.

The site shown in fig. 8, like No. 160 mentioned above, was near a small waterhole frequented by wart hog. Another similar example occurred about a mile to the south east, and a third also which comprised a *Manilkara densiflora* having a rot-hole at the



are in the riverine thicket. Pupae of *G. swynnertoni* were found under the spreading bushes of *C. parvifolium* in the early season to mid-August, but not during the hot dry weather afterwards.

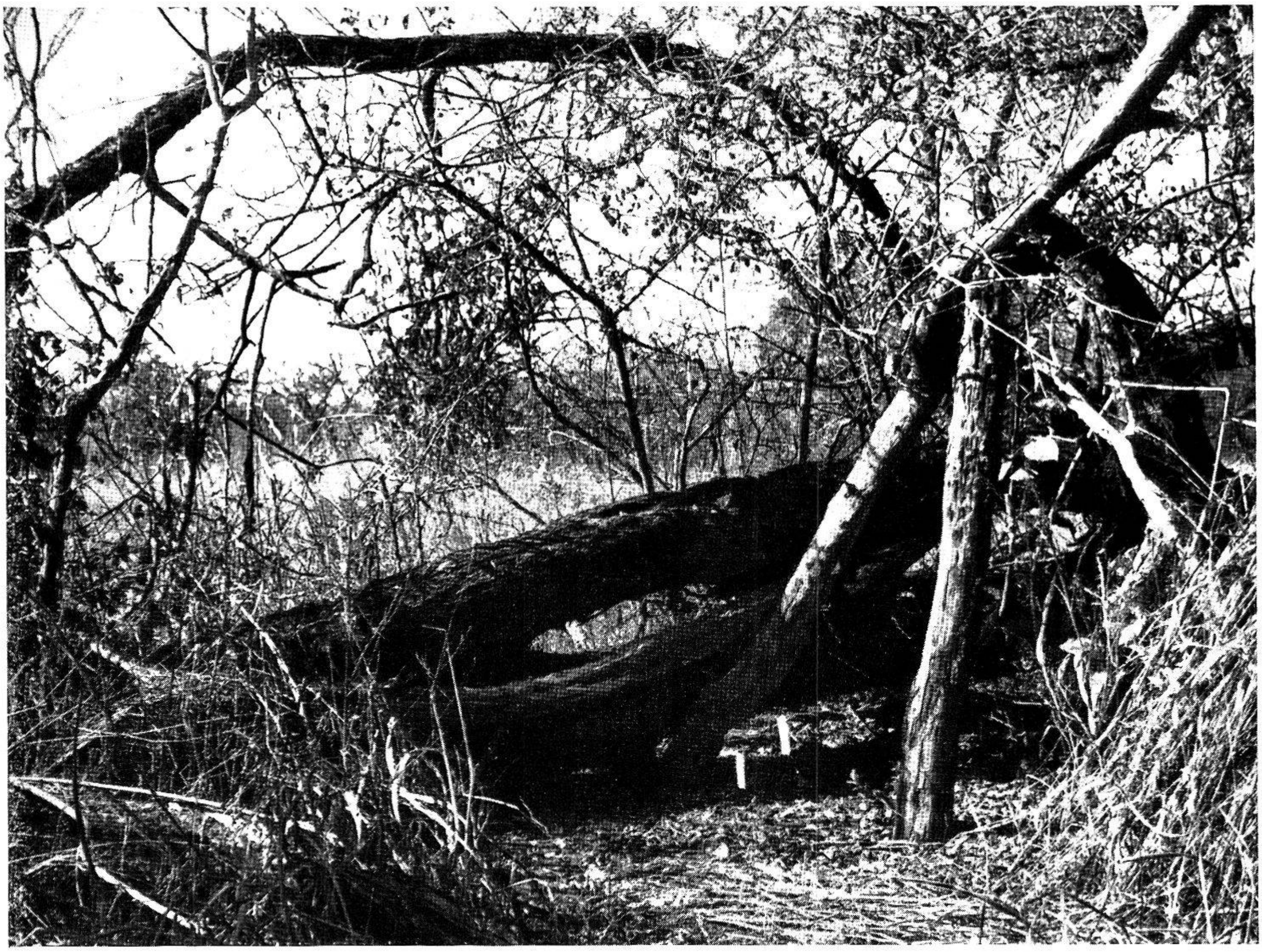


Fig. 2. Two viable pupae of *G. swynnertoni* were found here in cold wet weather. The log is *Acacia rovumae*, photographed six weeks after the pupae had been found in a spell of cold wet weather in April 1948. They were under the open part of the log. 2 ft. apart, each resting on a small flake of bark. The date when the flies emerged showed that the larvae were deposited about the same time.

Fig. 3

Fig. 4

Fig. 3. A wet season breeding site. The tree is *Albizzia harveyi* with a bush of *Grewia fallax* on one side at its base, with stout leaning stems. The pegs show where four pupae were found on the surface on 12th March (rains) 1952. Two others, similarly placed below another stem of *Grewia*, were found on the surface behind the tree on the same date.

Fig. 4. A wet season breeding site. A log of *Lannea humilis* in a small glade much frequented by wart logs. Eight pupae were found, all at the base of the log, on 9th April, 1952, five on the surface and three by digging. It continued dry, and three additional pupae on the right (see pegs) were found by digging on 12th April, though they had been missed on the first search perhaps because then the soil had been insufficiently dry to fall away from them. Seven pupae found subsequently to 12th May all occurred in the very restricted area at the base of the log, four on the surface and three by scraping the surface of the wet soil.

Fig. 5

Fig. 6

Fig. 5. A fallen *Commiphora ugogensis* in an open glade with branches crushed close to the ground, about 70 yards from the log shown in fig. 4. Twenty pupae were found here from 5th April to 29th May, ten on the surface, nine by scraping and one by digging; in the ensuing early dry season, six more were found by scraping. The figure shows only part of the site, one of the branches crushed to the ground when the tree fell.

Fig. 6. A log of *Ostryoderris stuhlmannii*, where 18 pupae were found during the rains, 14 on the surface and 4 by scraping the surface. Four more found on the surface in the early dry season (9th June) were dead, but three good-weight pupae were found by digging on the same day.

Fig. 7. A dead decumbent branch of *Acacia usambarensis*, near the edge of a small thicket. One pupa was found here in the rains early in 1951, six in the ensuing early dry season, and then no more until the short dry season early in 1952, when four were found by digging. Then in the long rains three were found on the surface.

Fig. 8. A decumbent *Acacia usambarensis* at the edge of a small thicket, near a water hole frequented by wart hog, photographed in early dry season. Twenty-three pupae were found in the dry season of 1951, the later ones near the base of the trunk, the latest being a nonviable pupa on 17th September.

Fig. 9. The site of fig. 8, still used in the late dry season.

Fig. 10. Perching sites composed of stems of small diameter, where *G. swynnertoni* pupae occur scattered like *G. pallidipes*. Thirteen pupae of *G. swynnertoni* (12 pegs are visible) were found here on 20th July, 1951, and no others nearby. The flies emerged over about a month, showing that larviposition had occurred over a considerable period.

Fig. 11

Fig. 12

Fig. 11. A thicket on hardpan soil centered on a large *Acacia rovumae*. In the left foreground is *Lannea humilis* and on the right a group of *Commiphora schimperi*. The breeding site is under a large spreading bush of *Grewia fallax* and a tree of *Commiphora mollis*, both cloaked with the thorny climber *Capparis tomentosa*.

Fig. 12. A close-up of the site shown in fig. 11. The stem and exposed roots in the foreground belong to *Commiphora mollis* (A). The pegs indicating finds of pupae occur under the spreading stems of *Grewia fallax* and the exposed roots of the *Commiphora*. All save two of the pupae found here are marked by the pegs seen in this figure, showing how restricted is the small area where larviposition occurred.

Fig. 13

Fig. 14

Fig. 13. The base of a baobab tree *(Adansonia digitata)*, searched 53 times over three years. Pupae were found in the early and late dry seasons, and one on 25th February, 1949.

Fig. 14. A baobab near the west edge of Block 9 where *G. swynnertoni* abounds. It is in meagre bush dominated by baobabs—the nearest about 70 yards distant from this one. The hollow at the base goes in for about 3 ft., and here in October 1946 I witnessed the discovery of 46 pupae within a few minutes. Every dry season since then this site has been productive.

Fig. 15

Fig. 16

Fig. 15. A rot-hole in *Piptadenia hildebrandtii* in a small hardpan thicket. Nine pupae were found here in the early dry season of 1948, and 28 in the late dry season of 1949; in 1951 none was found in the early season, but 36 in the later part of it.

Fig. 16. Material scooped out from the site shown in fig. 16. It has a high humus content and is friable even when wet. After searching the soil is replaced. Pupae collected are shown in the preground, on the small notebook.

Fig. 17. Soil was found 20 ft. up in this baobab, where the man can be seen. One viable pupa and eight shells were found here, and three more shells a month later. The site is water-logged in the rains.

Fig. 18. At the foot of the erect *Acacia usambarensis* shown on the left, one of the four viable wet season pupae of 1947 was found on 19th February, and later four shells. On 2nd July, eight pupae (no shells) were found orientated under the arched log (a fallen branch from the tree on left). At that time wart hogs were frequenting a small water-hole just outside this thicket. Twenty-four later searches up to June 1949 failed to discover any more pupae.

base with numerous logs from its dead branches lying about in a small hardpan thicket. Wart hogs frequented this thicket and numerous pupae were found under the logs and in the rot-hole in the tree, but little was found in other sites in the vicinity.

The suggestion of an association between breeding and the proximity of wart hogs was also strong in 1952, when the most productive sites were all situated in a small area in which, judging from spoor and dung, these animals abounded. Five recently fed flies from one such area were submitted to Mr. BERNARD WEITZ, of the Lister Institute of Preventive Medicine, London, who kindly consented to examine them by the precipitin test. He reports that in every case they had fed on pigs, which in the area concerned must have been either wart hog or bush pig *(Phacochoerus* or *Choiropotamus).*

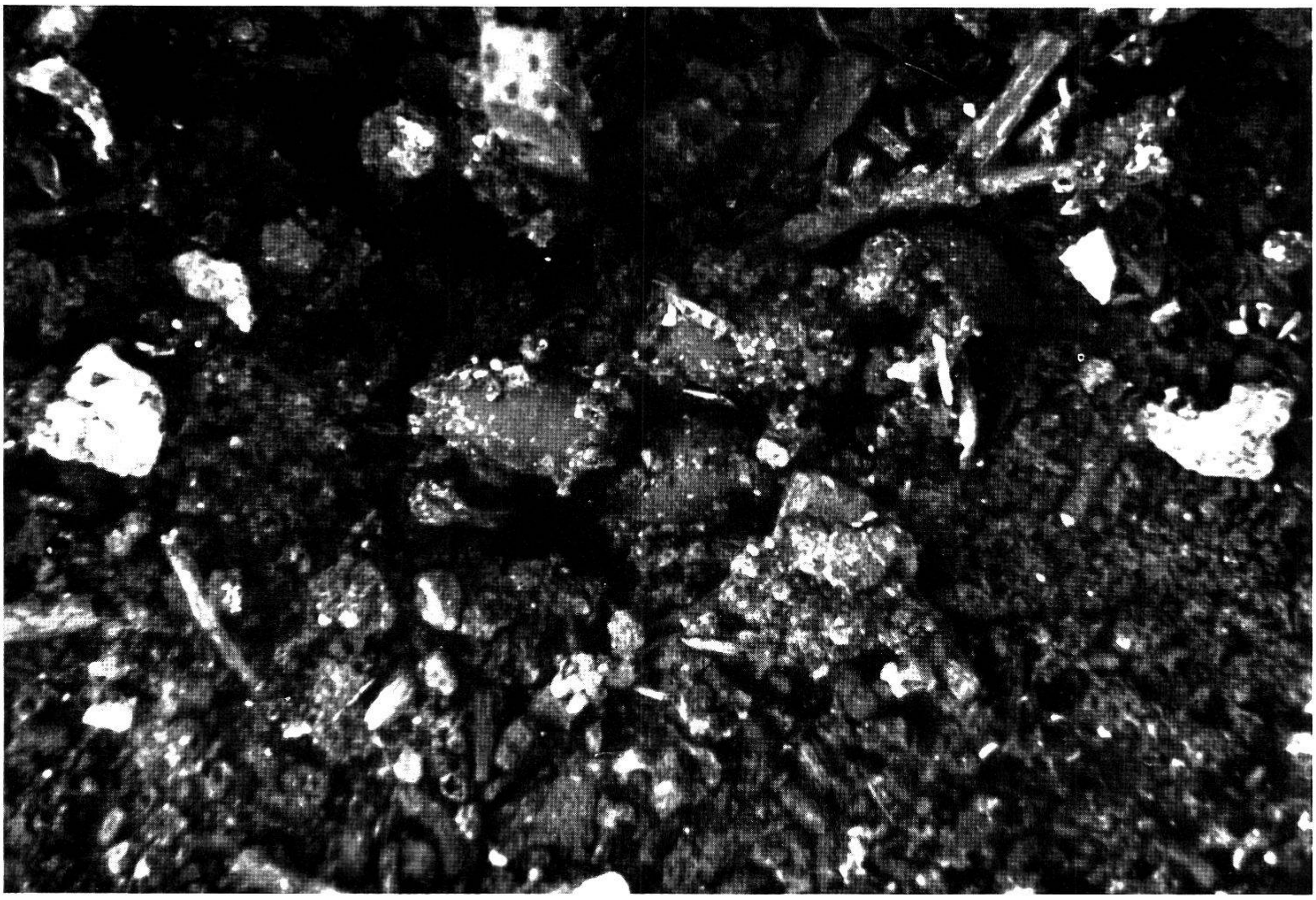


Fig. 19. Three surface pupae of *G. swynnertoni* deposited in captivity, in an outdoor cage. At first in wet weather these pupae were quite invisible, but they became apparent one after another with the drying of the soil. In this group, all three are touching each other.

Laboratory results.

Pupation in relation to wet and dry soil, to darkness and cold.

After the discovery of *G. swynnertoni* pupae on the surface in the field, tests were made on larviposition and pupation with respectively wet and dry soils in the laboratory.

Test A.

I used a cage 9 inches square and 18 inches high, having sides, top and bottom of metal mosquito gauze stretched on a rectangular wooden frame work. one side of which was the door. Earth from one of the recently discovered breeding sites in Block 9 was placed on the gauze bottom of the box to a depth of about two inches It was given a good wetting from a watering can and then left in the sun for two hours for the surface to dry somewhat. A small flake of dry bark (3 × 2 inches) was placed on the surface of the soil. The cage was kept on a stool under a large shade tree. Female *G. swynnertoni* collected from Block 9 were kept singly in 3 × 1 inch tubes in the laboratory and fed on rabbit. Single flies in which the larva could be seen to have developed black lobes were introduced at intervals into the cage between 10th March and 2nd April. When a female had evidently deposited her larva, another black lobed specimen was substituted, so that the exact number of depositions which had taken place was always known.

The first fly had not larviposited by 5 p.m. the day after its introduction into the cage and it rained shortly after this time. Next morning a pupa (already black) was seen fully exposed on the dark coloured wet surface. The soil in the cage was closely inspected every morning, but despite a total of 12 depositions having occurred by 30th March, nothing further was detected until then, when I saw a pupa lying partially embedded at the point which had been covered by the end of the bark flake. Further examination by another observer revealed that there was a second pupa almost touching the first, and one of these must have escaped detection for three days or more. By the 4th April, when this test was stopped, there had been 16 depositions, and six of the pupae had been found by inspecting the surface of the soil, four under the bark flake and two away from it out in the open. The two found close together mentioned above, had now been joined by a third (fig. 19). Photographic record was made at 11 a.m. of the position of all six of the surface pupae, after which the cage was replaced on the stool under the tree outside. It continued fine and dry and at 5 p.m. the next evening I was immediately able to locate two additional pupae in the cage both partly embedded in the open soil away from the flake of bark. These had certainly not been visible the previous day when the soil had been moister, but contraction from drying had evidently resulted in their becoming partially exposed subsequently.

Test B.

The same gauze cage was used and prepared with soil and flake of bark as in Test A, and a stem of *Albizzia* two inches in diameter was fixed across the top, inside the cage to serve as a possible perching place for the female flies. Instead of introducing flies singly, as in the previous test, I put twelve black lobed *G. swynnertoni* in together at 9 a.m. on 23rd April. The cage was left out in the open on a stool under a large shade tree as before. Air temperature was recorded and the flies in the cage were inspected frequently until all had extruded their larvae. This test began on a day of bright sunshine, but conditions deteriorated into prolonged drizzle the following day and showers of rain after that. After the flies had all deposited their larvae, the flake of bark was removed and the cage left in situ under the tree outside until after flies had finished emerging from the pupae.

The results obtained in this test are shown in Table 6.

Test C.

Some other observations on pupation in relation to wet soil were made at ordinary laboratory temperatures by putting black lobed females singly into glass jam pots containing wetted earth at the bottom to a depth of above one inch. A dried leaf, bent at right angles, was placed on the surface, so that the fly could rest on it, horizontally or vertically. Care was taken not to use water logged soil. If the surface was left rough (7 observations) the larva always managed to hide itself and the pupa could not be seen without scraping the surface of the soil (usually to a depth of about $^1/_8$ inch). If the wetted surface was smoothed lightly with a spatula (25 observations) the larva was unable to burrow into it and the resultant pupa was always visible, exposed on the surface, or partially embedded, when the pot was examined the following morning. Two similar tests were made with black-lobed *G. morsitans*. Both pupae were invisible the morning after larviposition, but they were only just embedded. Two further tests were made with this species using soil obtained from its breeding sites (in the Central Province). In one case the pupa was on the surface and in the other it was about ¼ inch below.

From the above tests it is evident that pupation took place on, or near, the surface when the soil was wet. Table 6 shows that such surface pupae were viable, even when deposited in cold wet weather and left exposed to wet outside conditions. The table also shows that larviposition could be delayed to over 50 hours after the lobes of the larva had blackened, but two out of five of such cases failed to pupate properly and a third failed to produce a fly. The flies were normal in the remainder. Larvae were observed to make prolonged attempt to burrow, but usually were unable to get deep enough to hide themselves before they had to pupate. Such prolonged activity on the part of the newly born larva, however, could not have accounted for the occurrence in the field (p. 312) of two pupae resting on the surface of small flakes of bark, when the larvae must have pupated where they were born, despite being on a hard surface. The nearest approach to this in the laboratory was Obs. 11 (Table 6) wherein I myself placed a larva on the bark and it forthwith pupated there. Since this observation was obviously inconclusive I carried out tests to discover (D) whether surface pupation resulted through the absence of light, and (E) whether animation of the larva was reduced under cold conditions.

TABLE 6.

The results from 12 black-lobed G. swynnertoni *kept in gauze cage in the open until all had deposited their larvae.*
Experiment started 9 a.m., 23. 4. 1952.

Obser-vation	Day	Larviposition Time (p.m.) (Between)	Temp. (°C).	Position of pupa	Hours female observed before larvi-positing	Notes
1	0	(12.10 to 12.30)	24.5	On surface under bark	3 1/4	Larva seen at 12.30
2	0	(12.30 - 1)	26.5	On surface under bark	3 1/2	This fly was sitting up side down underneath the bark 1/2″ above the soil at 12.30 p.m.
3	0	Night (?)	24.5 - 20.0	Half embedded in the open	> 9 1/2	Larviposited after 6.30 p.m. pupa black 7.30 a.m. of day 1.
4	1	(3.00-3.45)	20.0	On surface in the open	30	Larva seen at 3.45 p.m.
5	1	(4.30-5)	19.5	On surface under bark	31 1/2	
6	1	(5.00-5.30)	18.5	Half embedded in the open	32	Larva seen.
7	1	Night	(6 p.m. to 8 a.m.) 18.0	On surface under bark	> 33	(Last observation 6 p.m.) Pupa red at 8 a.m. of day 2.
8	2	(12.30-1)	24.0	On surface under bark	51 1/2	Failed to darken. Died.
9	2	(1.15-2)	24.5-26.5	Pupa under door of cage	52 1/4	Pupa was placed on soil.
10	2	(1.15-2)	24.5-26.5	Not detected	52 1/4	By exclusion this was the pupa found under the surface (20.0 mg. on 18. 6. 52.) Died later.
11	2	2.15-3	26.5	Larva under door of cage	52 1/4	Larva was placed on top of bark and had pupated where it was placed by 3.30 p.m.
12	2	6-7	22.0	Surface in the open	57	Female was resting vertically on corner wooden strut with larva half extruded. Birth completed by 7 p.m.; pupa not viable.
						3 males emerged after 45-50 days and 6 females after 42-44 days.

TABLE 7.

Test D. Pupation in the dark. The depth beneath the soil of ten G. swynnertoni *pupae, from flies kept in the dark on dry soil at ordinary laboratory temperatures.*

Observation	1	2	3	4	5	6	7	8	9	10
Depth of pupa (inches)	3/4	1/8	1/2	1/2	1/2	1/4	1/2	3/4	3/4	3/4
Period when larva was born	6.30 a.m. to 7.30 a.m.	11-12 a.m.	4-5 p.m.	10-12 a.m.	10-12 a.m.	12 a.m. to 4.30 p.m			11-12 a.m.	6 a.m. to 8 a.m.
Temperature (° C.)	24.0	25.5	26.0	25.0 to 26.0	25.0 to 26.0	24.5 to 26.0			25.0	24.0

Test D (Table 7) shows that the larvae observed all burrowed despite the absence of light, to depths varying according to the individual and not correlated with ordinary laboratory temperatures.

Test E. Forty-eight observations were made at moderately high temperatures, 24.5° C. to 26° C. and eight at much lower temperature, approximately 20° C. The results are shown in Table 8, which

TABLE 8.

The depth to which G. swynnertoni *larvae burrowed in dry soil at ordinary laboratory temperatures (24.5° C.-26° C.) and in similar soil kept at approx. 20° C.*

Depth	Surface	Just hidden	1/4 inch	1/2 inch	3/4 inch
24.5-26.0° C.	nil	1	6	22	19
Approx. 20° C.	2	1	4	1	nil

shows that surface pupation never occurred on dry soil at ordinary laboratory temperatures, the great majority penetrating to a depth of over half an inch. In dry soil kept at approximately 20° C., on the other hand, larvae tended to burrow less deeply and two out of eight pupated on the surface.

Times of larviposition.

Between June 1948 and December 1949 I made 384 observations on the time of larviposition in *G. swynnertoni* and 99 on *G. morsitans*. Each fly was kept singly in a corked 3 × 1 inch glass cylinder having the other end covered with cloth mosquito netting. When it could be seen that the larval lobes had blackened these tubes were rested obliquely on the rim of white enamel plates with the gauze-covered end downwards. The total results were examined in relation to seasons, but though they gave a slight suggestion that larviposition tended to be later between mid-May and mid-July, no marked correlation was apparent, neither was there any difference between results from wild females from the bush and females which had emerged from pupae in the laboratory and had mated there.

On 10th April 1952, two black lobed female *G. swynnertoni,* which had been in 3 × 1 inch tubes on an enamel plate until 2 p.m., were transferred to jars of dry soil. The temperature was 27° C. One produced its larva almost immediately and the second within 2½ minutes. Two other black-lobed females were transferred at 2 p.m. from tubes to wet soil, but without result. These were then changed from their wet soil jars to dry. Both remained motionless as soon as they touched the dry soil and one produced a larva three minutes later. The fourth did nothing within ten minutes, so she was put back to her wet soil pot, where she gave birth about 6 p.m. the same day. These observations suggest that dry soil and warm conditions are what the female fly prefers, and that in their absence (see Table 6) she can postpone larviposition to some extent. Accordingly, for comparison with previous data, I recorded 56 observations of the time when *G. swynnertoni* larviposited on dry soil. The flies (captured in Block 9) were maintained as before, singly in 3 × 1 inch tubes, until the black lobes of the larva could be seen, after which they were placed singly in glass jars containing earth obtained from a breeding site in Block 9. The past results obtained for *G. morsitans* and *G. swynnertoni* are shown in Table 9, along with the results on *G. swynnertoni* when placed on dry soil.

Both with *G. morsitans* and *G. swynnertoni,* which larviposited in 3 × 1 inch tubes, the peak time was from 4 p.m. to dark: nineteen of the 64 "night" observations in the case of *G. swynnertoni* were close on 7 p.m., just as darkness sets in, and of course the remainder may have been spread over several hours. The results for *G. swynnertoni* on dry soil are more or less evenly scattered through the hot hours of the day, from 11 a.m. to 5 p.m. The indication again is therefore that the female is able to hold up larviposition for a few hours if she is not satisfied with

TABLE 9.

The times of larviposition, at ordinary laboratory temperature, of G. morsitans *and* G. swynnertoni *contained singly in tubes and the times for* G. swynnertoni *on dry soil.*

Time of larviposition at normal laboratory temperatures	3" x 1" glass tubes		Dry soil in glass jars (*G. swynnertoni*)
	G. morsitans	*G. swynnertoni*	
Dawn to 9 a.m.	NIL	NIL	NIL
9-10 a.m.	1	1	1
10-11 a.m.	1	0	0
11-12 a.m.	2	2	5
12-1 p.m.	2	4	10
1-2 p.m.	4	18	14
2-3 p.m.	1	29	10
3-4 p.m.	16	52	4
4-5 p.m.	8	81	9
5-6 p.m.	19	78	1
6-7 p.m.	24	55	1
Night	21	64	1
Total observations	99	384	56

her environment. There were no depositions before 9 a.m. when flies were kept in day-light, but Table 7 shows there were two such occurrences out of ten flies kept in total darkness.

The fact that the female holds up larviposition if kept in 3 × 1 inch tube affords a fairly ready means of obtaining a tsetse larva within a few minutes when one is needed, by merely transferring the fly from the tube to dry soil under warm conditions. I have exploited this successfully on many occasions to study the act of larviposition.

The act of larviposition.

The act of larviposition in *G. swynnertoni* takes place in four stages:

1. The abdomen of the fly remains straight and motionless, but the black lobes of the larva can be seen just protruding from the tip. This stage is difficult to detect and lasts for about 30 seconds.

2. With the body of the fly still straight, the posterior part of the larva bulges out until it touches the ground.

3. The female now takes a step forward and at the same time curls her abdomen down, with the result that she draws away from the larva and becomes free of it. For a moment the larva is greatly attenuated. Stages (2) and (3) are usually completed within three seconds. Sometimes birth stops at stage (2) and the hind end of the larva is left protruding from the vaginal opening. This has never occurred in my experience, the nearest approach I have witnessed being No. 12 in Table 6 when conditions were cold and inclement.

4. With the larva born, the female continues motionless with the abdomen curled down. After about 30 seconds she starts to emit a plaintive, sizzling noise and she may continue thus for five minutes or more.

It so happened that my earlier observation on times of larviposition were made on flies kept singly in 3 × 1 inch tubes resting on bare enamel plates. Under these circumstances this characteristic note (in *G. morsitans* and *G. swynnertoni*) could be heard at a distance of several yards and afforded a most valuable index that a larva had just been born. Later I found that if the plate contained soil, the sound was considerably deadened and it was inaudible from a fly in a closed vessel. It thus appears that the practice initially adopted served to amplify the note.

Prediction of larviposition.

As mentioned above larviposition may be held up for a few hours, irrespective of temperature, merely because the female is not satisfied with her environment. In 3 × 1 inch tubes the majority do not give birth until the day following that on which the larval lobes blacken. The best chance of getting a larva without an undue amount of waiting is to transfer such an individual after the lapse of about 30 hours to dry soil at 25-27° C. I was quite unable to predict, from the degree of blackness of the lobes seen through the abdomen of the fly, whether she would deposit that day, or the next. It sometimes happened that individuals in which the lobes were less evident produced a larva before one in which they were prominent. Probably in such cases the true degree of blackness is obscured by the presence of an intervening layer of fat.

The inevitability of larviposition and pupation.

However unfavourable the circumstances the black-lobed fly *must* give birth to the larva if she is to live. Similarly, if the larva is to remain viable, pupation is inevitable. During the heat of the day a larva on a hard surface generally pupated after 40 minutes, but in the cool of the evening examples remained active for 1¼ hours.

Phototaxis of the larva.

MELLANBY (1936) found that the larva of *G. palpalis* did not respond to a beam of light. My experience with the larva of *G. swynnertoni* observed in a dark room with the beam from an electric torch was similar, provided the beam was directed on the larva anteriorly. In ordinary daylight in the laboratory, however, the behaviour of *G. morsitans* and *G. swynnertoni* larvae was quite different. The larva always moved away from the window (negative phototaxis), directly away when the light from the sky was uniform, obliquely when the most intense light (as reflected off a cloud) was coming in at a slant. If a small opaque object a few inches square were interposed so that the larva was left within the small umbra of denser shadow it would not leave this zone of deeper shade and enter the penumbra of lighter shadow bordering it. The larva is negatively phototactic both in the dim light of evening and at hours when light is intense [1]: its course was not affected by the colour (white or black) of the background on which it moved, but there was a tendency for it to pupate on a dark coloured spot.

The behaviour of the larva was such as to suggest strongly that it perceives differences of light intensity at its posterior end, probably down between the lobes. This would help to explain why the direction is unaffected by a beam of light directed from the front. It is a subject which evidently calls for further investigation. My own trials with artificial light were not conclusive, and a larva so treated no longer behaved normally in daylight.

The observations show that the larva is equipped with a mechanism that is sensitive to daylight and results in the creature moving away from high light intensities, as well as serving to keep it within the densest shade of the place where it was deposited.

Behaviour of female flies.

The role played by the "perching place", which is such a feature in breeding sites, was not discovered and further study is needed to explain the evident association between the occurrence of pupae and such places. No case was encountered in the laboratory wherein a larva was dropped with the parent vertical, except for No. 12 in Table 6, wherein the birth was abnormal and the pupa non-viable. The fly always rests on the floor of the receptacle.

Newly engorged flies which escaped in the laboratory never flew to the window, but could be recovered shortly afterwards from the ceiling. To a lesser degree black-lobed females tended to do the same. On dry soil at ordinary laboratory temperatures, such flies usually rest flat and motionless for several hours before the larva is born. I have not confirmed that this takes place in the field. The nearest approach to it was a non-hungry, pregnant female caught on the soil at site No. 394 (fig. 4) on 22. 4. 52. She engorged fully on me that evening, that being the last meal before she larviposited about noon on 25th, having scarcely moved for 2½ days on bare soil before then. The observation suggests that

[1] At first (see *Jackson*, 1952) it was thought that the larvae did not respond to light about noon. Further observations have, however, confirmed that at this time of day, also, larvae are strongly negatively phototactic.

this fly was exploring a suitable breeding site *before* she got too heavy with pregnancy. In the laboratory, if deposition has not taken place before nightfall the female adopts a vertical position until the following day when she again resumes her placid waiting on the soil. If kept in 3 × 1 inch tubes, the flies are much more restless, presumably because they seek a more favourable place for the larva.

Comment.

Obviously the answers to several questions arising particularly during the later part of this investigation are very incomplete, and call for further study, not only of *G. swynnertoni* but of other species as well. Even for *G. swynnertoni*, although wet season pupae can now be found far more readily than ever before, the method was developed only near the end of the last rainy season, and the several implications need further study.

Zusammenfassung.

Die Tsetsefliege *Glossina swynnertoni* Austen verpuppt sich in Gestrüppformationen unter Fallholz, Bäumen und Felsen. Es war jedoch, abgesehen von sehr trockenen Jahren, bisher unmöglich, während der Regenzeit an solchen Stellen Puppen zu finden. Bald nach Ende der Regenzeit können Puppen ebenfalls in hohlen Bäumen gefunden werden, zahlreicher jedoch erst nach Erlöschen der Steppenbrände. Es sind auch Puppen in Baumlöchern bis zu 6 m über dem Boden gefunden worden. Während der frühen Trockenzeit sind sie zahlreich unter kleinen, laubabwerfenden Gebüschen zu finden.

Die normale Puppensuchtechnik bestand zunächst darin, die Erdoberfläche vom darüberliegenden lockeren Blatt- und Holzmaterial zu säubern und dann den Boden aufzugraben. Früh im Jahre 1952, anläßlich einer sehr feuchten Periode, ging man dazu über, die oberflächliche Bodenschicht nicht mehr aufzugraben, sondern nur vorsichtig wegzukratzen; mit dieser neuen Methode gelang es, die Zahl der Puppenfunde wesentlich zu steigern. Sowohl damals wie auch in der darauffolgenden frühen Trockenzeit waren ergiebige Puppenplätze charakterisiert durch nackten Boden unter großen Fallholzstücken oder überhängenden Gebüschen, die den Fliegenweibchen offenbar Sitzgelegenheiten boten.

Der Unterschied zwischen Regen- und beginnender Trockenzeit drückt sich weniger in der Art und Beschaffenheit der Plätze als in der jeweiligen Lage der Puppen im Boden aus. Laboratoriumsversuche haben gezeigt, daß von natürlichem Regen benetzte Larven sich nicht eingraben können, und daß dann die Verpuppung an der Oberfläche stattfindet; jedoch war es in solchen Fällen unmöglich, die Puppen optisch wahrzunehmen, bis die Erdoberfläche etwas ausgetrocknet war. Solche «Oberflächenpuppen» waren in der Regel lebensfähig, jedoch verzögerte sich die Larven-Ablage auf kalten, nassen Böden zuweilen beträchtlich, und die normale Verpuppung blieb aus oder die Puppen gingen ein.

In Glastuben werden die Larven gewöhnlich am späten Nachmittag deponiert, über trockenem Boden dagegen etwa drei Stunden früher, und trächtige Fliegen, die aus Glastuben über warmen (26° C), trockenen Boden gebracht werden, legen ihre Larven oft innerhalb weniger Minuten ab. Es konnte bis jetzt nicht abgeklärt werden, ob das Vorhandensein von «Sitzgelegenheiten» über den Brutplätzen von Bedeutung ist: im Laboratorium bleiben trächtige

Fliegen bewegungslos auf dem trockenen Boden sitzen, bis die Larve geboren ist. Allerdings, wenn sie am gleichen Tage nicht geboren wird, können die Weibchen die Nacht senkrecht an der Wand verbringen. In normalem Tageslicht verhält sich die Larve stark negativ phototaktisch, und es macht den Anschein, als ob sich die lichtempfindliche Stelle an ihrem Hinterende befinde. Allerdings ist die negative Phototaxis nicht entscheidend, denn die Larven graben sich sogar bei vollständiger Finsternis ein, wenn auch etwas weniger tief. Auch bei Kälte vergraben sich die Larven häufig weniger tief oder überhaupt nicht. Auf harter Oberfläche verpuppen sich die Larven gewöhnlich nach etwa 40 Minuten. In der freien Natur werden die Puppen meist nahe beieinander gefunden; unter einem einzigen Fallholz können oft mehr als eine solche Puppenansammlung angetroffen werden. Die Topographie der Brutgebiete kann von Jahr zu Jahr wechseln und scheint mitbedingt zu sein durch das regelmäßige Vorkommen von Warzenschweinen (Phacochoerus).

Eine Reihe von Fragen, die sich besonders im letzten Teil dieser Untersuchungen gestellt haben, können noch nicht restlos beantwortet werden. So können z. B. jetzt in der feuchten Periode Puppen viel leichter als je gefunden werden, denn die neue Suchmethode wurde erst gegen Ende der Regenzeit entwickelt, und verschiedene Zusammenhänge müssen noch weiterhin untersucht werden.

Résumé.

La pupaison de la mouche tsétsé, *Glossina swynnertoni* Austen, a lieu dans des bosquets de broussaille sous du bois mort, au pied d'arbres ou sous des rochers. Sauf dans des années particulièrement sèches il fut jusqu'à présent impossible de trouver des pupes dans ces gîtes durant la saison des pluies. Bientôt après cette saison on peut également rencontrer des pupes dans des creux d'arbres, en plus grand nombre seulement après les feux de brousse ; on a également découvert des pupes dans des trous d'arbres se trouvant jusqu'à 6 m. au-dessus du sol. Pendant la première partie de la saison sèche, on peut récolter de nombreuses pupes sous des buissons à feuilles caduques.

La technique habituelle pour récupérer des pupes consistait à débarrasser d'abord le sol de matières organiques qui le recouvrent, puis à creuser la terre. Tôt en 1952, lors d'une période très humide, on a commencé à changer de technique en grattant dorénavant la surface du sol et en le fouillant délicatement couche par couche ; les récoltes en pupes furent alors beaucoup plus riches. Aussi bien à cette époque que pendant le début de la saison sèche qui y faisait suite, les gîtes riches en pupes se trouvaient dans du sol nu, recouvert de grosses pièces de bois mort ou de buissons, servant éventuellement de perchoirs aux mouches prégnantes.

La différence entre la saison des pluies et le début de la saison sèche s'exprime moins par le caractère des gîtes que par la disposition des pupes dans le sol. Des observations en laboratoire ont montré que des pupes mouillées par la pluie naturelle étaient incapables de s'enterrer et qu'alors la mise en pupe avait lieu à la surface, mais il était impossible d'y reconnaître les pupariums avant que le sol fût ressuyé. Ces « pupes de surface » étaient généralement viables, mais souvent leur dépôt sur le sol froid et humide fut considérablement retardé, parfois la pupaison ne s'achevait pas normalement ou les pupes dépérissaient.

Les femelles portantes, conservées dans des tubes de verre nus, déposent leurs larves tard dans l'après-midi ; placées sur du sable, elles déposent environ trois heures plus tôt. Des femelles prégnantes très avancées déposent souvent dans l'espace de quelques minutes lorsqu'on les transfère des tubes de verre sur du sol chaud (26^0 C.) et sec. On n'a pas encore réussi à élucider la question si la présence de « perchoirs » au-dessus des gîtes est d'une certaine importance : En laboratoire les mouches portantes restent immobiles sur le sol

sec jusqu'à l'accouchement de la larve. Cependant, si la larve ne naît pas ce même jour, les femelles peuvent passer la nuit posées verticalement sur la paroi du récipient. Dans la lumière naturelle du jour la larve montre un phototactisme négatif et il semble que c'est sa partie postérieure qui est sensible à la lumière. Ce phototactisme négatif n'est cependant pas indispensable pour l'enfouissement de la larve, car ce dernier a lieu aussi, un peu moins profondément, il est vrai, en pleine obscurité. Le froid peut également empêcher ou entraver l'enfouissement de la larve. Posée sur une surface dure, la larve se met généralement en pupe en 40 minutes environ. Dans les gîtes naturels on trouve souvent un certain nombre de pupes rassemblées en un espace limité ; sous un même bois mort on peut trouver plusieurs de ces assemblages de pupes. La topographie des gîtes peut changer d'année en année et semble dépendre dans une certaine mesure de la présence régulière de phacochères dans ces parages.

Il est impossible pour le moment de répondre à un certain nombre de questions qui se sont posées surtout vers la fin des investigations en cours. Ainsi la nouvelle technique de récupération, développée seulement en fin de saison des pluies, permet actuellement de détecter beaucoup plus aisément les pupes pendant la période humide. D'autres recherches aboutiront peut-être à la solution de ces problèmes.

Acknowledgments.

It will be apparent to the reader that certain key observations, vital to the theme of this paper, were made by an African and when this has been the case I have made acknowledgment to him in the text. The photographs were kindly taken by Dr. *P. E. Glover* and Mr. *C. J. Webb.* The investigation came to a head so rapidly in its later stages that I have been forced to leave many channels imperfectly exposed, or not explored at all. I tender my thanks to Dr. *C. H. N. Jackson,* Chief Entomologist of this organisation, for the stimulating interest he has shown and the very considerable help he has given to me. The work owes much to Dr. *Jackson*'s helpful criticism, without which I should not have been led to make the 1952 laboratory observations.

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