Training Manual
for
TSETSE CONTROL PERSONNEL

VOLUME 2

Ecology and behaviour of tsetse

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TABLE OF CONTENTS

CHAPTER 1

ECOLOGY AND BEHAVIOUR OF TSETSE

1.1 ENVIRONMENT

1.1.1 Introduction The conditions under which the tsetse lives make up its environment. It includes conditions of climate, vegetation, animal life, soil, and the effects of human activity. All these may be called environmental conditions or environmental factors.

The study of the tsetse in its environment is called ecology.

The particular place where the tsetse lives is called its habitat. For example, gallery forest, thicket, miombo woodland, and mopane woodland are different kinds of tsetse habitat.

Where one type of vegetation gives way gradually to another, that is called an ecotone. For example, as one passes from thick woodland to open grassland, one may walk through an area of smaller, more scattered trees. This area is an ecotone.

1.1.2 Climate (see also Volume I, 10.2) Sunshine, rainfall and humidity, temperature, atmospheric pressure and wind make up the climate of a particular area. Temperature and humidity are the most important of these for tsetse, and light can also be important.

Very restricted areas in the habitat may have a special climate of their own, called the microclimate (see 1.1.2.3).

1.1.2.1 Temperature Glossina lives well at 25-26°C and most laboratory colonies are kept at that temperature. If the temperature goes much higher or much lower than that, there may be some damage to the fly. Here are some examples:

- death occurs rapidly (in 5 minutes) if G. morsitans adults are kept at 460c
- death occurs if G. tachinoides adults are kept at 44OC for 1 hour
- death occurs if G. morsitans adults are kept at 40°C for 1 hour
- death occurs if G. fuscipes adults are kept at 40°C for 3 hours
- around 14°C and below, Glossina adults cannot fly
- death occurs if G. morsitans adults are kept at -4°C for 6 hours.

In general, a temperature above 38°C is damaging to the adults; and a temperature below about 17°C will not allow the adult to live a normal active life.

For pupae, 32°C is the upper limit for normal development, and 16°C is the lower limit.

At the northern limit of tsetse distribution, high temperature and dryness limit the spread of the fly.

In the south of the continent, the limits of tsetse distribution may also be set by high temperatures and dryness (in the hot dry season). But in some areas, seasonal low temperatures are more important. Gold winter months may delay the development of tsetse pupae for so long, that they cannot produce adults successfully.

Temperature also affects the rate at which the fly lives.

High temperatures:

- shorten the time from emergency to the production of the first larva

- shorten the time from the production of one larva to the production of the next (interlarval period)

- shorten the period spent as a pupa (pupal period)
- shorten the life of the adult
- shorten the period the adult can last without a blood meal.

Low temperatures have the opposite effect in each case.

1.1.2.2 Rainfall and humidity Rainfall probably does not have any direct effect on tsetse, but does so indirectly by:

(a) affecting the humidity
(b) causing local flooding which may drown many pupae
(c) maintaining different vegetation zones, according to how much rain falls and how long the rainy season lasts (see 1.1.3).

A humid atmosphere allows tsetse to spread away from sheltered habitats, so long as the temperature is not too high. So in the wet season G. morsitans disperses away from its dry season home (riverside woodland) into more open country, in the northern savanna areas.

In the southern parts of its range, G. palpalis can live away from free water, probably because of the humid atmosphere.

In high rainfall areas, G. tachinoides is also able to live away from free water.

Both G. pallidipes and G. longipalpis have dry season habitats in well-sheltered thickets, but wet season dispersal areas in less densely wooded country.

Humidity of the soil is important to the survival of tsetse pupae.

- Glossina longipennis, G. morsitans morsitans and G. swynnertoni pupae can develop in very dry soils (0-10% R.H.).
- Glossina morsitans submorsitans, G. pallidipes and G. tachinoides pupae can develop in fairly dry soils (30-40% R.H.)
- Glossina austeni and G. fuscipes pupae require rather mare humid soils (40-50% R.H.)
- Glossina palpalis, G. brevipalpis and G. fuscipleuris require very humid soils (about 70% R.H.).

The humidity is affected by wind, especially in West Africa. Here, humid winds blow during the rainy season from the south-west; during part of the dry season a dry dusty wind (Harmattan) blows from the north-east.

1.1.2.3 Microclimate Meteorological instruments (see Volume I, 10.2.6) are usually placed in rather open places, to give information about the general climate of the area, but the local climate (microclimate) of small sheltered parts of the habitat (microhabitats)may be very different.

The following are some of these microhabitats:

- At the river bank, especially under an overhanging bank. Here the air remains very humid even in the dry season, and it is a favourite resting place for palpalis group flies, in the far northern limit of their distribution. In this area, nearly all the palpalis group flies are found within 5 m. of the river bank.
- In rot holes, or in hollow trees, or in animal burrows. For example, in the Zambesi valley Glossina pallidipes enters rot holes in trees in the daytime, during the hottest season. Here it is cooler and more humid than outside.
- On a tree trunk, especially low down and in cracks in the bark, or between buttress roots. In the day it is cooler and more humid here than in the more exposed parts of the habitat.

- At the top of trees, at night. Here it can be wanner than nearer the ground, because the ground may lose much heat by radiation at night, especially in the cold season and when there is no cloud.

The fly's behaviour (see 1.2) can bring it into these places where it can survive better than if it had to suffer the general climatic conditions of the area.

1.1.3 Vegetation zones and tsetse habitats

1.1.3.1 In West Africa The following are some of the main vegetation zones in West Africa starting from the coast and working inland, and some of the tsetse species to be found in these zones.

- Mangrove swamps. These are found along some parts of the coast especially in the river mouths, where the water is brackish (part river water, part see water). They are habitats of Glossina palpalis and G. caliginea (in Nigeria).
- Fresh water swamp forest. Some G. palpalis and G. caliginea are found here also.
- Rain forest. An area of very high rain fall, very tall trees, high humidity and dense shade at ground level. Where this forest is well-developed, these species may be found: G. tabaniformis, G. haningtoni, G. fusca and (for instance in Nigeria) G. nigrofusca, as well as other less cannon fusca group flies. Glossina pallioera and G. palpalis are also found here. Further north, where the forest is slightly drier, the trees are less tall and more often lose their leaves in the dry season, the forest edge species G. medicorum and G. nigrofusca (in Ghana) live.
- Derived savanna. This is a forest zone that has been largely cut down and burned to make farms. It is sometimes called farm

bush, especially where there has been re-growth of trees. It is therefore country that has patches of forest on poor land, with farms and savanna areas in between. The forest patches have G. medicorum, G. fusca, G. longipalpis and G. palpalis. Of these, G. longipalpis may spread out into savanna areas, especially in the wet season.

- Southern Guinea savanna. This has a dry season of 3-4 months. The trees are 15-18 m. (40-50 ft) high, sometimes taller, broad leafed, and forming an open woodland with tall grass. Glossina longipalpis lives in the southern parts of this zone. Further north, G. morsitans replaces it. Rivers and streams along which evergreen trees grow form the habitat of G. palpalis and G. tachinoides.
- Northern Guinea savanna. This has a dry season of 4-5 months, and an annual rainfall of about 1000 mm. (approx. 40 inches) and over. The dominant trees are doka (Isoberlinia doka, I. dalzielii), members of the family Caesalpinaceae. The trees in this zone are about 13 m. (40 ft) high, and the woodland has a very uniform appearance. Grass is shorter than in the southern Guinea savanna. The zone is infested with G. morsitans.Along rivers and streams, G. palpalis and G. tachinoides are found. Glossina medicorum inhabits vegetation along the Komoe and the Black Volta rivers.
- Sudan zone. The dry season here lasts about 7 months. Annual rainfall is 500-1000 mm. (20-40 inches). It can become very hot. Characteristic trees are Acacia, baobab (Adansonia. digitata), doum palm (Hyphaene thebaica); there are also thorny thickets. This zone is inhabited by *G.* morsitans, but the species is based mainly cm patches of forest, dispersing a little in the milder rainy season. Glossina tachinoides and G.p. gambiensis can live here, but only

along river banks. For this zone, G.p. gambiensis is limited to the area Senegal to Togo.

1.1.3.2 Other vegetation zones The vegetation of East and Central Africa is not set out in such a clear manner as that of West Africa. Some extensive vegetation types are:

- Miombo woodland. This closely corresponds to the northern Guinea zone of West Africa. The dominant trees are Brachystegia and Isoberlinia (Caesalpinaceae) of which there are several species. It is one of the main habitat of G. morsitans.
- Mopane woodland. This occurs along the valleys of Zambesi, Limpopo and Luangwa rivers. The dominant tree is mopane, Colophospermum mopane (Caesalpinaceae). It forms an important habitat for G. morsitans in the Luangwa and parts of the Zambesi valleys.
- Baikiaea woodland on Kalahari sands (gusu woodland). This occupies a large area of western Zimbabwe, Zambia (much of Western Province) and part of Botswana. It is not much used by tsetse, probably because the sandy soil becomes too cold for too long a period in the winter months. It is also a dry soil.
- Manga woodland. This contains much Acacia, Albizia, Combretum and Terminalia. It forms only a marginal tsetse habitat in Zambia.
- Dry thorn bush (nyika) is a drier type of Acacia dominated woodland, with Commiphora and Combretum, and occupies much of Somalia, Sudan, Kenya, Uganda and northern Tanzania. It is the home of Glossina swinnertoni and G. pallidipes.
- Patches of evergreen forest, not as extensive in East Africa as the other vegetation types mentioned, are the habitat of G. brevipalpis and G. austeni.

- Itigi thicket is not favoured by tsetse.

1.1.3.3 Less typical habitats Under 1.1.3.1 and in Chapters 2, 3 and 4, descriptions are given of the typical habitats in which various Glossina species may be found. But these may not include all the places where a particular species occurs. If a spraying programme misses out these unusual habitats, then the sprayed areas will quickly be re-infested.

Many of the less typical habitats are man-made ones, for example in and around villages, especially in the rain forest belt of West Africa, where the original vegetation has been cut down to make farms and plantations.

From these places, flies can attack man and village livestock, especially pigs and to a lesser extent cattle, so that these populations of flies can be very important from the point of view of disease transmission.

Because they are around places where people live, these tsetse populations have been called peridomestic ('around the home').

1.1.4 Effect of other animal life on tsetse

1.1.4.1 Host animals Lists of the hosts that are used by different species of tsetse are given in Volume I, Chapter 6. Some additional information will be found in the following chapters of the present volume.

Although the tsetse is completely dependent on the host animals for their food, these animals are the most difficult environmental factor to study in tsetse ecology. When a worker goes out into the field, he may at once frighten away the host animals and may attract a few of the tsetses to himself. Therefore, the natural situation is completely altered. The field worker should remind himself of the dependence of tsetse on host animals, even where these seen to be scaroe.

The dependence of tsetse on wild game animals is also shown by:

(a) the effect of the rinderpest outbreak
(b) the success of some game elimination schemes in removing tsetse.

Rinderpest is a disease affecting many kinds of wild animals. It particularly affects buffalo, giraffe, eland, bushpig and warthog, but also to a lesser extent affects reedbuck, wildebeest, kudu and giant forest hog. Wild animals that are very much affected by rinderpest provide 80-90% of tsetse feeds in East Africa. When the disease killed off many of the African animals in the period 1889-1896, the tsetses were greatly reduced in numbers, and their distribution became restricted to quite small areas.

When the main outbreak was over, the game animals recovered in numbers and the fly belts expanded, eventually to reach their present size.

Examples of game control to eradicate tsetse are given in Volume III, 2.2.

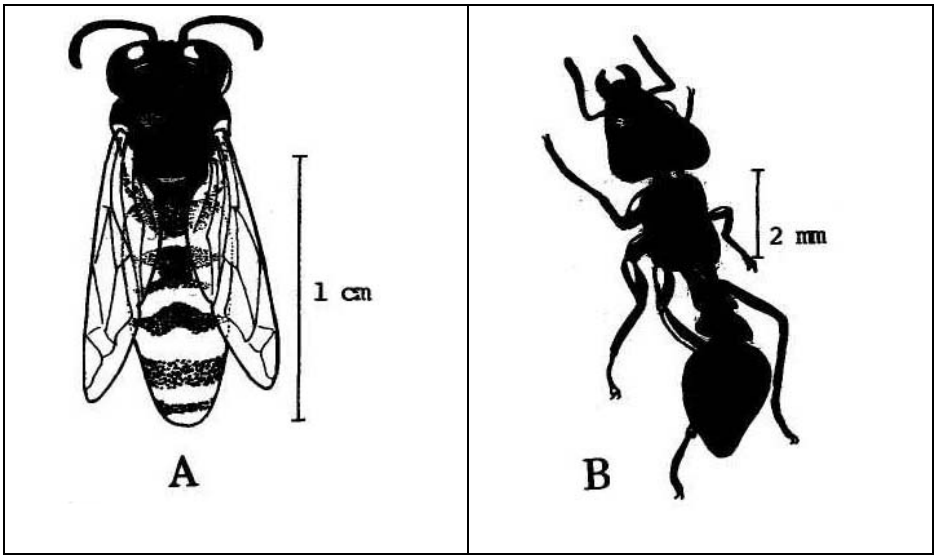
Sometimes, tsetses use domestic cattle for the food supply, rather than wild animals (for example, in the Koalib Hills, Sudan, where an isolated belt of G. morsitans used to live). In other places, such as at the northern fringes of G. palpalis distribution, populations of flies may depend for their food on people visiting a water hole.

1.1.4.2 Predators and parasites

(a) Predators Figure 1.1 illustrates some of the predators known or believed to feed on tsetse adults and pupae.

The most important predators are probably ants feeding on tsetse pupae, and asilids (robber flies), waspes and spiders feeding on the adults.

(b) Insect parasites Included here are insects that attack the pupa of Glossina from within.



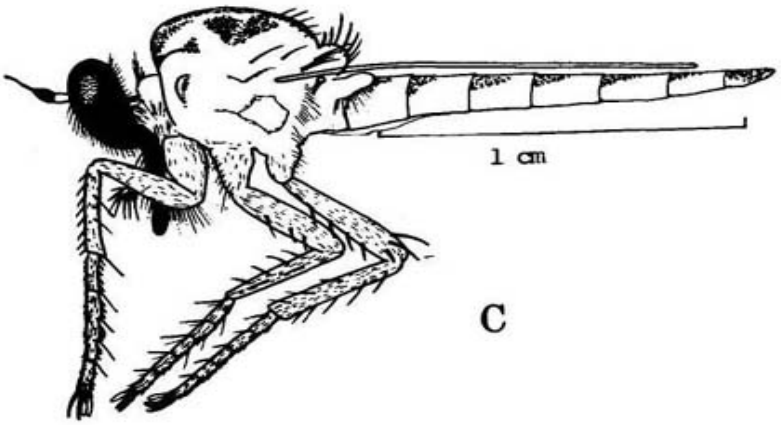


Fig. 1.1 Predators of tsetse A. <u>Bembex</u> wasp; B. Ant; C. Asilid (robber fly)

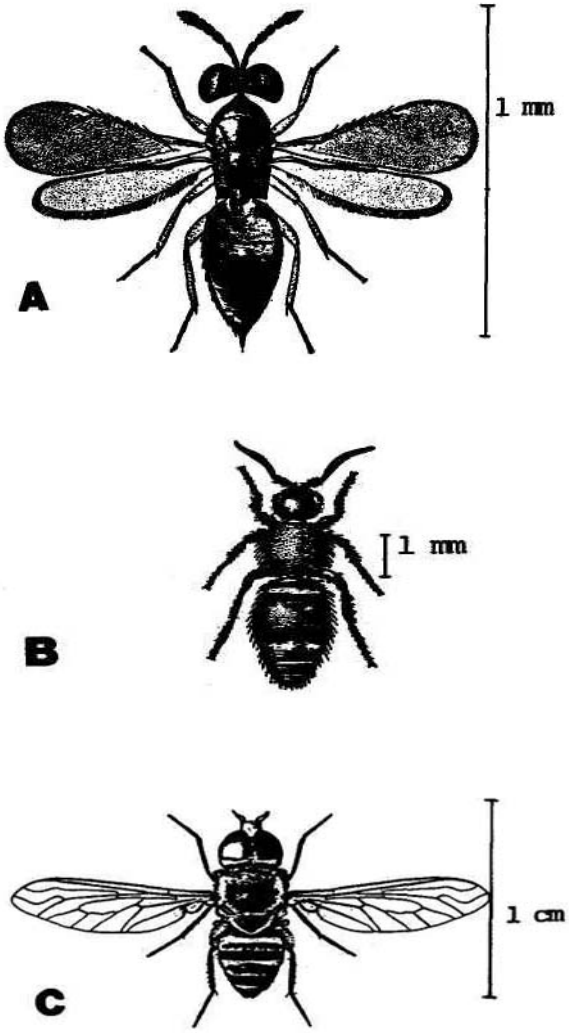


Fig. 1.2 Parasites of tsetse pupae A. Syntomasphyrun (Hymenoptera); B. Mutilla (Hymenoptera) ; C. Thyridanthrax (Diptera)

- Syntomosphyrum (Hymenoptera) (Figure l.2 A)
  This is a tiny black wasp about 1 ran. long. It is easily reared in the *pupae* of various fly species, and millions of the adults have been released into the field in various control attempts which, however, have had no lasting effect. The female wasp lays its eggs inside the tsetse puparium. Several or many of these wasps emerge from each infected tsetse pupa. Natural rates of infection are normally about 0.2% or less.
- Mutilla (Hymenoptera) (Figure 1.2 B)
  Ihis is a larger insect, about 4 mm. long. The male is winged but the female is wingless. The female lays only about three eggs in each tsetse pupa, and of these only one developes all the way to become a wasp. Six times as many females emerge as males. Natural rates of infection may be as high as 40% in the warmer seasons (G. morsitans). But the period spent in the tsetse pupa is much longer than pupal period of the healthy tsetse, so that infection rates can be overestimated. The parasite is not easy to rear in large numbers, and it has not been used for attempts at control.
- Thyridanthrax (Diptera) (Figure 1.2 C) This is a fly, slightly smaller than the tsetse it parasitises. Eggs are laid on the soil surface, and the tiny larvae burrow searching for pupae. Only one fly emerges from each parasitised tsetse pupa. Locally, rates of parasitism may be as much as 20% or more, and it is probably one of the most important of the tsetse parasites. The pupal period may last much longer than the 4-5 weeks that is normal for tsetse or it may be shorter. It is a difficult insect to breed and no field releases have been made.

There are many other species, particularly Hymenoptera, that have been recorded as emerging from tsetse pupae. So far as is known, they are not as

important as the ones described above.

(c) Other parasitic organisms Other types of organisms that have been known to attack tsetse (pupa or adult) include bacteria, fungi, protozoa, viruses and nematode worms. Their relative importance is not yet clear and more work has to be done on them.

For both predators and parasites of tsetse, it is not yet known how important they are in keeping down the numbers of tsetse in the field.

1.1.5 Human activity (see also Volume II, Chapter 2) Human settlements, with crop farming and tree-felling, may locally prevent tsetse from existing in an area, at least in large numbers. The reasons are that

(a) the tree cover that the tsetse require is reduced
(b) game animals are hunted out or frightened away.

One of the most important results of human activity is fire. Fires late in the dry season change the environment by destroying young trees and bushes and thus encouraging vigorous grass growth. Fire also makes the area drier, and tsetse are therefore pushed into places of shadier, thicker vegetation where the air is moister.

Fires early in the dry season may have the effect of making the habitat more wooded, but this change is brought about very slowly, over many years.

1.2 TSETSE BEHAVIOUR

1.2.1 Flight Only about 15-30 minutes of each day is spent in active flight. A single flight does not last longer than about 1 1/2 - 2 1/2 minutes. The speed of flight may be 3-6 m/sec (11-24 km/h = 7-15 miles/h), but it is much slower immediately after a meal.

After taking in a large blood meal a short, slow flight is made away from the host animal to a resting place such as a tree trunk. Here, the weight of the fly is quickly reduced by primary excretion (some drops of water are passed out through the anus). More short flights may then follow, taking the fly to a safer place.

1.2.2 Best and resting sites Tsetses spend most of the day settled. The places where they remain settled for long periods are called resting sites. These are different from the places where flies may perch temporarily, for example when they settle out from a following swarm, or when they are looking out for the next meal.

It is important to know about resting sites (sometimes called 'true resting sites') because these are the best places for spraying persistent insecticides for killing the tsetse. Insecticides placed at the resting sites and only at the resting sites will have the maximum effect against tsetse and minimum effect against other animal life.

Resting sites have been investigated (see Vol. I, 7.4):

- by searching the vegetation carefully for resting flies
- by enclosing whole trees and bushes in a net cage and releasing fed flies within the cage to see where they rest
- by marking ('tagging') flies with fluorescent or reflecting paint and looking for them at night using lamps.

Flies have also been tagged with radio-active materials and searched for later in the bush. This technique is not described in the Manual because it requires very specialised instruments and safety precautions in which the research chief will give training.

Besting sites may vary according to:

- the time of day or night
- the climate: and season
- the species of tsetse fly
- the vegetation
- the resting places of host animals (e.g. bushbuck).

During the hottest part of the day (visually early to mid-afternoon), the true resting sites are lowest down on tree trunks, and on the underside of shaded, fallen logs. At copier times of the day, and in cooler seasons, the flies rest higher up tree trunks, and on the underside of branches. At night, some flies go up into the canopy of trees and rest on the leaves or twigs.

Woody living parts of the vegetation are often chosen for day time resting, but some species (e.g. Glossina palpalis gambiensis) may prefer leaves.

The resting habits of different species are described in Chapters 2, 3 and 4.

1.2.3 Response to host animals Usually a fly detects a host animal by its sense of smell, from up to 100 m away. Larger host animals or more of them, are more attractive to tsetse than smaller host animals, or single individuals.

When it smells the host, the fly moves up-wind, which brings it closer to the host animal. Then the fly is able to see the host (at 50 m or more).

Flies may land on a greater variety of host species than is indicated by the blood meal list. However, some hosts prevent flies from feeding by flicking their tails and twitching the skin.

Many flies, especially non-hungry males, are attracted to hosts even though they are not going to feed. They make up the 'following swarm', a party of males that settles on the ground or low vegetation close to a moving host. A male in a following swarm may fly on to a virgin female as she comes for her first meal, and mate with her.

1.2.4 Daily activity Under average conditions most activity is in the early to mid-morning, and in the late afternoon.

Under very hot conditions, activity during the middle of the day may be stopped almost completely, with flies finding the cool places in which to shelter from the great heat.

Under cool conditions, there may be one period near the middle of the day when tsetses are most active in the field.

1.3 TSETSE POPULATIONS

Some facts concerning the life of tsetse cannot be described for individual flies, but only for a group or sample of flies. Examples are the percentage of females caught by a trap, the density of tsetse living in an area, and the distribution of resting sites.

When gathering this information we are usually trying to learn more about the population of the flies living in an area.

1.3.1 Pupal population

1.3.1.1 Importance of the pupal population In general, more than half of the total population of tsetse in an area are present below ground, as pupae.

Experience shows that in some seasons particularly in the rains) pupae are very difficult to find.

It is therefore impossible to work out what number of tsetse are living in a given area, from the number of pupae found there.

But the collection of pupae can give information about:

- the changes in the breeding areas according to season
- what parasites the pupae suffer from
- where tsetse are living.

1.3.1.2 Breeding sites (larval deposition sites) Ways to search for pupae are given in Volume I, 7.1.

The following table shows the sort of places in which tsetse pupae might be found. These are called breeding sites.

Table 1.1

Sites	Species
1. In soil under fallen logs and under leaning trees in deciduous woodland	G. morsitans, G. brevipalpis
2. In soil under fallen logs in open country	G. longipennis
3. Under fallen logs but on the soil surface	G. swynnertoni (wet season)
4. Under overhanging rocks	G. morsitans, G. austeni, G. palpalis/fuscipes
5. Under leaf litter in (a) thickets; (b) gallery forest	G. pallidipes, G. palpalis gambiensis
6. In dry sandy beaches or river beds where shaded by dense vegetation	G. morsitans (dry season) G. palpalis/fuscipes (dry season)
7. Where there is high canopy cover as well as lower level cover given b low branches and creepers immediately over the site	G. palpalis/fuscipes

8.	At sandy spots, where there is high canopy cover	G. tachinoides
9.	Around the base of oil palms (Elaeis), where shelter is given by broken frond stems	G. palpalis/fuscipes G. longipalpis
10.	In rot holes in trees	G. palpalis/fuscipes, G. morsitans, G. swynnertoni (dry season)
11.	In animal holes in the ground	G. morsitans (dry season)
12.	Under Lantana and Euphorbia hedges locally in Western Kenya	G. fuscipes
13.	In plantations of mangoes, etc.	G. tachinoides

Breeding areas are zones in which breeding sites may be found. They are more concentrated in the dry season (especially in deciduous woodland) and more widespread in the wet season.

1.3.2 Adult populations

1.3.2.1 Sex ratio The proportion of females amongst flies emerging from a collection of pupae is normally close to 50%.

Females usually live longer than males, so that a field population of flies will normally have more females than males.

But hand net samples taken on a fly round usually contain a low proportion of females, because the flies that come within reach of the nets are mainly males,

Samples taken in traps have a higher proportion of females, often in the range of 60-70%. This figure
can vary according to location, time of day and year, and according to the species.

1.3.2.2 Age The fly that emerges from the pupa is hungry. After spreading and hardening its wings, its main problem is where to get its first meal. During this time, from emergence to taking the first blood meal, the fly is called a 'teneral' fly.

Ihe food obtained at the first meal is used to build up the flight muscles of the thorax, which are poorly developed at emergence.

In this way the fly gradually becomes a stronger flier. In the case of the female this is necessary for the later task of carrying the larva in the abdomen. In the case of the male it is necessary for catching and mating with virgin females, in competition with other males.

At each feed, there is a chance of the fly becoming infected with trypanosomes (this chance is greater with the earlier meals). Any trypanosomes picked up have to go through a cycle of development before the fly is permanently infective.

It follows that older flies are more important as disease vectors than younger flies.

Traps are able to catch older flies, especially older females, compared with other methods (e.g. hand nets used with men, vehicles or ox).

Males may live about 3 weeks in the field.

Females certainly live longer than males. Glossina pallidipes females in one population were estimated to live an average of 35 days or more.

Flies live for longer periods

- when it is cool (rather than hot)
- when it is humid (rather than dry)
- when there are many hosts available (rather than only a few).

1.3.2.3 Physiological state

(a) Hunger *The* idea we gain of the hunger state of a population also depends on the type of sample examined.

Most flies taken during a normal fly round are non-hungry males.

Nearly all flies (G. morsitans and G. pallidipes) attracted to a stationary bait (live animal or animal model) are hungry, but 10-25% of flies visiting moving baits are not hungry.

With a man and an ox being used as bait together, the flies (G. morsitans) coming to feed on man are fewer and hungrier than those visiting the ox.

(b) Mated status and pregnancy Nearly all non-teneral female flies are mated (but not in G. pallidipes; see 2.4.7).

Under the best conditions, the uterus of a female fly is seldom empty once ovulation has started. This is because very soon after the deposition of the mature larva, the next egg passes into the uterus and begins its development.

Pregnancy rates may differ according to whether the flies are caught as they come to a party of men, to a bait animal or in a trap.

1.3.2.4 Density The density of a tsetse population in a given area is never very accurately known unless all the flies are caught. This could only be done on an island or in a very isolated woodland or thicket.

Usually the density is estimated by a mark-release-recapture method (see Volume I, 7.7).

The terms Apparent Density and True Density are sometimes used. 'Apparent density' is taken as the number of non-teneral males (savanna flies) caught in 9000 m. (10,000 yards). It is a figure obtained from fly-round results. It does not necessarily give information about the 'true density', which is simply the number of flies per unit area. For instance, a high catch may indicate a hungry population, rather than a dense one.

When traps are used, apparent density is defined as the number of flies/trap/day (F.T.D.).

CHAPTER 2

ECOLOGY OF MORSITANS GROUP SPECIES

2.1 ECOLOGY OF GLOSSINA MORSITANS 2.1.1 Environment

2.1.1.1 Climate Glossina morsitans occurs in regions of tropical Africa having a mean annual temperature of from 19-28°C, and where it is neither very humid nor very dry.

The species is divided into three subspecies:

(a) Glossina morsitans submorsitans This is distributed as a broken belt across Africa from Gambia and Senegal, extending eastwards as far as Ethiopia and Uganda. It lives best at 24-26OC.

(b) Glossina morsitans morsitans This is widely distributed in East Africa as far south as Mozambique, and as far north as northern Tanzania. It lives best at 21.5-24OC.

(c) Glossina morsitans oentralis This is distributed in Central Africa, covering parts of Botswana, Angola, Zaire, Zambia, Rwanda, Burundi, Uganda and Tanzania. Since it is separated from G.m. morsitans by a relatively narrow watershed, it probably needs the same climatic conditions as that subspecies.

At the edges of its distribution, the fly population concentrates into the cooler and moister parts of its habitat to escape the worst effects of the hot season. In these areas therefore it can behave as a riverine fly in the hot dry season.

2.1.1.2 Vegetation

(a) Typical habitats.

The typical habitat of G. morsitans is open woodland and woodland savanna with plenty of game animals living in the area.

In West Africa G. morsitans lives in 'doka' woodland, in which the main (dominant) tree is Isoberlinia doka (or its close relatives).

In East and Central Africa the same kind of woodland is miombo, dominated by trees such as Isoberlinia, Brachystegia and Julbernardia.

In addition, the species occupies dry thorn bush of Uganda and Ethiopia, for instance.

More northerly parts of West Africa, in the Sudan vegetation zone, also contain G. morsitans. Here the dominant trees are Anogeissus, Balanites, Lannea, Combretum and certain Acacia species.

In more southerly parts of East and Central Africa, the Zambezi-Luangwa river valleys are dominated by mopane, Colophospermum mopane; here G. morsitans can live in large numbers, and yet be absent from the hills next to the valleys.

In West Africa, the zone to the south of doka woodlands is the southern Guinea and derived savanna. It contains G. morsitans, and the vegetation is dominated by Daniella, Hymenocardia, Detarium, Afzelia, Lophira, and Terminalia trees. There is not very much south of the equator to correspond with this vegetation zone.

(b) Other habitats.

Glossina morsitans can change its visual behaviour and live off domestic animals, especially cattle, in the absence of game animals. This has occurred in Sudan (Koalib Hills pocket, now exterminated, where practically the only game is baboons, monkeys and hyrax); and in Nigeria the species used to live along a busy cattle trekking route passing through a densely populated and heavily cultivated area, well outside its usual range.

The same dependence on cattle may be developing in other areas where game is absent, but where there are plenty of cattle with some trypanosomiasis.

(c) Vegetation areas not used by G. morsitans

- 'Gusu' woodland (dominated by Baikiaea trees) in parts of Botswana, Zambia and Zimbabwe. The dry sandy soil and cold winter months may kill off any pupae placed in this area.
- Unbroken thicket in which the canopies of trees and bushes touch and give so much shade that there is no grass growth (but small thickets may be lived in, and some pupae deposited there).
- Very high rainfall areas such as rain forest and mangroves.

2.1.1.3 Effect of other animal life on G. morsitans

(a) Host animals (see also Volume I, Chapter 6).

Glossina morsitans gets from one-third to nearly a half of its food from warthog.

Bovids are very important also, especially kudu, buffalo, bushbuck and eland. Other species may be important locally.

The fly feeds on cattle when available, and this is the reason for its great economic importance as a vector of trypanosomiasis.

Some animals are hardly ever used as hosts, for example zebra, impala, gazelles and wildebeest (see Volume I, 6.1.2).

(b) Predators and parasites.

Glossina morsitans is eaten by many predator species, from small mammals and birds to other insects. Both puparia and adults are taken.

The morsitans group is attacked by more parasites than are the other tsetse groups. Glossina morsitans has more than 30 recorded insect parasites. Those of Mutillidae (Hymenoptera) and Bombuliidae (Diptera) are probably the most important.

Another parasite, Syntomosphyrum (Eulophidae, Hymenoptera) has been bred in large numbers for field release, in an attempt at biological control, but without any lasting success.

2.1.1.4 Effect of human activity When natural habitats are affected by man there is often a reduction in the wildlife. Glossina morsitans does not easily change its habits to feed on man and his domestic animals, and is generally one of the first species to disappear when the human population in an area grows.

Peri-domestic habits as seen in some palpalis group species are not often found (but see 2.1.1.2 (b)).

2.1.2 Behaviour of Glossina morsitans

2.1.2.1 Flight Most of the information in 1.2.1 cones from the study of G. morsitans.

2.1.2.2 Resting sites As with other species, the fly rests at higher levels in the vegetation

(a) when the weather is cooler
(b) when the air is more humid
(c) in the evening.

Towards mid-day, as the temperature rises and the humidity falls, flies move to large shaded tree trunks and rest up to about 3 m from the ground.

In the late afternoon, as the temperature falls and the humidity rises, flies move to the underside of horizontal (or nearly horizontal) branches up to 30 cm thick and from 1-6 m above the ground.

At night flies rest on the upper surface of leaves up to 9 m from ground level.

Females rest at slightly higher levels than males, and hide themselves more carefully in the cracks of tree bark, and in similar places. Ihey are therefore more difficult to find than males.

Tsetse behaviour may vary from place to place, so that special studies have to be made on resting places for each area.

(a) During the day. Newly emerged flies perched on the underside of small branches, 2 to 4 m above the ground (Tanzania).

In the dry season (Zambia) flies were not found above 3.6 m, with most flies concentrated on the lower part of tree trunks; bushes and fallen logs were also most used. In the rainy season (Zambia) tree trunks and grassy undergrowth were used more than branches or canopies.

In Sudan savanna (Nigeria) flies vised only the trunks of large trees, and settled up to 1.5 m above ground.

In Northern Guinea savanna (Nigeria) flies rested on the underside of branches up to 5 m above ground. As temperature increased, more flies rested on trunks, and the height above ground decreased (to about 1 m at 38OC).

(b) At night. Most flies rested on leaves up to 6 m or more, in teak woodland (Zambia).

Flies moved rapidly at the approach of dusk, to settle on the upper foliage (Nigeria), or twigs, leaves and small creepers at 0.3-4.6 m (Nigeria).

2.1.2.3 Response to host animals Much of the information in 1.2.3 comes from the study of G. morsitans.

2.1.2.4 Daily activity The normal daily behaviour pattern shows greatest activity just after dawn, and another period of high activity in the late afternoon.

This pattern is altered by climatic conditions.

When the average temperature is low, general activity is low. In the cool season the morning activity is reduced, and most activity is in the afternoon when the area has become warmed up.

When the average temperature is high, general activity is high. But during the times of day when the temperature is very high, then activity is greatly reduced because it becomes too high for. the tsetse to survive without shelter. Therefore in the hot season the afternoon activity is reduced.

Flies move away from regions of very bright light and will not feed in bright light. At very high

temperature flies start to move towards dark places (which are cooler).

Flies are not active just after they have fed. Daily activity increases each day after feeding.

2.1.3 Populations

2.1.3.1 Pupal populations and breeding sites It is difficult to find many pupae, in comparison with the flies that can be caught.

In some areas practically all the pupae found will give rise to adult flies successfully. In other places as many as half of the pupae collected will be dead.

Rates of parasitism have been mentioned under 1.1.4.

The site chosen by the female for depositing the larva varies from season to season.

In the wet season pupae can be found under logs in open woodland.

In the hot dry season pupae can be found in patches of forest or under banks along river beds. Here, areas of loose soil with shady perching places above are often chosen. Beneath logs and in the soil shaded by leaning trees are favourite pupal sites of G. morsitans.

But there must be many other pupae sites that are more difficult to find.

2.1.3.2 Mult populations

(a) Sex ratio. Fly round catch few teneral flies and few females. But with catches using bait oxen, the proportion of females is higher.

The proportion of females caught from resting sites may be slightly lower than the proportion of females in the area as a whole, because they select more sheltered places and slightly higher places as resting sites, than males.

(b) Age. Male G. morsitans live on average about 30 days, and females for about twice as long. Both these figures are very variable. Many flies live for much' longer.

Techniques for estimating age are described in Volume I, Chapter 8.

(c) Physiological state. The female is nearly always mated before or while she takes her first meal. It is rare to find a female that has fed but has not mated.

Flies landing on man in the 'head up' position are generally hungry flies.

Flies landing on man rather than on a bait ox nearby, are hungrier than those on the bait ox.

Fully engorged flies are often found rather low down on the resting sites. They are very inactive.

Ihe time from one blood meal to the next is called the feeding cycle or hunger cycle (see Volume I, 7.6). For G. morsitans this lasts about 2-3 days in the dry season and about 3-5 days during the rains.

(d) Density and dispersal. Glossina morsitans populations vary around an average level which is surprisingly steady. Seasonal variation is most obvious near the edges of the species' distribution rather than in the middle of fly belts.

Near the hot limits of the distribution of G. morsitans (e.g. in the Sudan vegetation zone of West Africa) the greatest fly round catches are made at the end of the rains. Ihis is also true of East Africa. Near the cold limits (in southern Africa) they are made during or at the end of the dry season.

Estimates of population density give results varying from 40 (or less) to 400 (or more) males per square kilometer. There are more females than males, but they are more difficult to catch and therefore more difficult to count.

During each year there are movements of G. morsitans populations according to season, especially in West Africa at the edge of the species' distribution. In West Africa the dry season habitats are within the thicker vegetation along water courses, and in the wet season flies spread out into the surrounding savanna woodland.

Within the main areas of distribution away from the edges, G. morsitans spends more time in savanna woodlands which may be all-season habitats, especially if there are patches of thicker vegetation present. In the dry season of southern central Africa, dambo edges are fly concentration areas.

In the southern Guinea zone of West Africa G. morsitans in the dry season concentrates around the headwaters of streams, between the thick fringing forests and the surrounding savanna woodlands.

Certain areas are well known as places in which tsetse and trypanosomiasis are always present. These are known as 'persistent foci' (singular, focus).

Other places may show a spread (advance) of fly, or its retreat (recession). There may be several possible causes of such advances or recessions:

- if cultivated land is abandoned, fly may be able to move in as the bushes and trees grow up
- if wild hosts increase in numbers because of protection from hunting or because of recovery from animal diseases, then more flies will be able to live in the area. The introduction of herds of domestic cattle might have the same effect
- if the climate is favourable for a number of years this will encourage the fly to spread and perhaps to reach areas (e.g. other river systems) where it can live permanently even after the return of less suitable climatic conditions.

Fly recessions may be caused by the reverse of these changes. Advances and recessions may occur without any very obvious cause; they are sometimes called 'spontaneous advances' and 'spontaneous recessions'.

Some flies, especially males, may be carried for several kilometers by animals or man (and traffic). But the proportion of flies that get carried in this way is very small.

2.1.4 Epidemiology and control Glossina morsitans is the most important vector of cattle trypanosomiasis. It is also an important vector of Trypanosoma rhodesiense, causing sleeping sickness in East and Central Africa.

It is easily infected with trypanosomes and shows high levels of infection. Average rates (all infections) are around 12%, but locally this might rise to as much as 90% (along trade cattle routes).

Fly infections with T. vivax are commoner than those with T. congolense, and these are commoner than those with T. brucei (see Volume I, 6.5.1).

Warthog (and other pigs) do not support T. vivax, so that where G. morsitans does most of its feeding on these animals, the proportion of T. vivax infections in the fly is low, and may be less than the T. conqolense infection rate.

Drug treatment of cattle leading to the quick suppression of T. vivax can lead to the same situation.

A method of G. morsitans control that was widely used in the past was discriminative clearing (see Volume III, Chapter 2). Sometimes it worked and sometimes it did not. It was based on the idea that removal of woody vegetation from certain limited areas (concentration areas) would destroy the fly population. It is now believed that in at least some parts of the distribution of G. morsitans, the fly population is much more evenly distributed in the different vegetation . types, than has been thought in the past. In other words, the concentration area need not be the only place that the tsetse lives in. This could explain the failures of some discriminative clearing exercises in the past.

2.2 ECOLOGY OF GLOSSINA SWYNNERTONI

2.2.1 Environment Glossina swynnertoni is distributed in belts in northern Tanzania, and across the border in Kenya. It does not extend further probably because of competition from G. morsitans,which it closely resembles. However, when G. morsitans was released into G. swynnertoni- areas, both species were able to live because G. morsitans took up a slightly different part of the habitat.

The environment of the area is dry. There are thickets and large areas of mbuga, with Acacia. The miombo of the area is not inhabited by G. swynnertoni.

2.2.2 Resting sites By day in the wet season
G. swynnertoni rests on the underside of branches of small trees, 1-4.5 m above the ground.

Sliqhly more than half of the flies rest on branches 2.5-10 cm in diameter 1.25-3.75 m above the ground.

As night comes, the flies move to rest on the upper surface of leaves, mainly 0.5-3 m above the ground.

2.2.3 Host animals Like G. morsitans,
G. swynnertoni relies heavily upon the warthog for its blood meals. Between 60-70% of the food of the species cones from this host animal. Other important host animals are giraffe and buffalo.

2.2.4 Predators and parasites Ants (Pheidole sp)
are thought to be the roost important predators of pupae,
and they have been seen carrying off tsetse pupae.

Predators were more effective in destroying pupae in unburnt bush than in burnt bush. The reason is not certain.

Spiders (Hersilia setifrons) were seen to catch many G. swynnertoni adults, on tree trunks. In one area up to 17% of the tsetse population were caught each week by spiders.

Thyridanthrax has been recorded as parasitising G. swynnertoni pupae.

2.2.5 Behaviour Male flies are more often caught
by men on fly rounds during the second and third week
of life. This probably indicates that teneral.males
are rather inactive compared with other males.

Man is not favoured as a host animal, but flies do form following swarms behind him.

The feeding cycle (interval between feeds) of G. swynnertoni is 4-5 days in the dry season.

The method of judging the hunger state of adult males can be used on G. swynnertoni (see Volume I, Chapter 7).

Oxen moving 140 m (450 ft.) away can be seen by G. swynnertoni in a good light, but at 180 m (600 ft.) they cannot. A calf hidden behind a screen attracts more flies than a screen by itself.

2.2.6 Breeding sites Pupae are found especially in open thickets. The spot chosen for depositing a larva is often immediately below a horizontal branch. Holes in trees are also used, for example in baobab.

Breeding goes on throughout the year (tenerals can always be found) but wet season breeding sites are difficult to discover.

2.2.7 Insemination rates Non-teneral females are nearly always inseminated (mated).

2.2.8 Age of population The wing fray method of estimating the age of male flies can be used on G. swynnertoni.

One study showed that the average life of a male lasted between 2 and 4 1/2 weeks.

2.2.9 Seasonal movements Like G. morsitans, G. swynnertoni increases its range in the wet season, and becomes more concentrated in smaller areas in the dry season. For example, open mbuga with stands of Acacia drepanolobium forms a temporary dry season habitat for G. swynnertoni, but thorn bush on slightly higher ground acts as the permanent breeding area. Locally, a very thin tree cover may allow tsetse breeding, if the air is humid (as it is, close to Lake Victoria) and if game animals are abundant.

2.2.10 Epidemiology and control From 1922 to 1935 there was a local outbreak of Rhodesian sleeping sick ness in Tanzania, in which G. swynnertoni was the vector. The fly is also an effective vector of cattle trypanosomiasis.

Areas of G. swynnertoni have been cleared, experimentally, by the destruction of game animals, but this is not a method in use at present.

Insecticide spray has been applied to resting places of G. swynnertoni in open bushland in Tanzania, concentrating on the underside of brandies 1.2-2.8 m above the ground, the branches being 2.5-10 cm in diameter and sloping at less than 35° from the horizontal.

2.3 ECOLOGY OF GLOSSINA LONGIPALPIS

2.3.1 The environment Glossina longipalpis extends from Senegal in the west to north-west Zaire in the east. There are large gaps in the distribution of the species, especially between east Nigeria and north-west Zaire.

It inhabits savanna woodland immediately north of the blocks of rain forest. Its north-south distribution is very limited. Near its northern limit it overlaps in some areas with the southern limit of G. morsitans submorsitans.

It does not occur in rain forest or in dry open woodland savanna. Vegetation between these two types seems to be more suitable. Such vegetation has been called forest-savanna mosaic, forest-island vegetation or derived savanna. Much of this vegetation has grown up following shifting agriculture by man.

Further north it also occurs in moist savanna (southern Guinea savanna) mainly in riverine gallery forest vegetation. The same areas are often also inhabited by G. palpalis.

During the dry season it concentrates in gallery forests and forest islands but seasonal movements are less than those made by G. morsitans.

2.3.2 Behaviour Glossina longipalpis feeds mostly on species of Bovidae, especially the bushbuck, if these hosts are available. It will also feed on wild pigs (Suidae).

Flies are most active at temperatures of about 25°C and at relative humidities of about 85%.

Little is known about the resting sites of G. longipalpis. Male flies particularly are attracted to the vicinity of man, although they do not often land on him. They are often seen resting on twigs, leaves and blades of grass, especially in dappled sunlight in clearings. They fly rapidly front one site to another.

2.3.3 Populations Puparia of G. longipalpis have been found under logs in forest islands during the dry season and early rains. The wet season breeding sites are unknown.

When man is the bait, most flies are caught from nearby twigs, leaves and blades of grass. Most (often about 98%) of these flies are males from the following swarm.

The percentage of females in the catch from man increases in the early morning and late evening. It is also higher at the end of the dry season.

With an ox as bait many more flies are caught. The female percentage is then 40-50%.

More hungry flies are caught when an ox is the bait. This is probably because ox is an attractive host for feeding purposes, whereas male flies are mainly attracted to man simply as a moving object, to which females may also be attracted, rather than to feed.

Numbers of flies caught decline throughout the dry season and are lowest in the early rains. Numbers rapidly increase during the wet season and are highest early in the dry season.

Populations of G. longipalpis are generally heavily infected with trypanosomes. The infection rate in a large sample of* flies from southern Nigeria was 21.5%.

Glossina longipalpis could become important as a vector of animal trypanosomiasis if cattle were to come within range, and the fly does prevent the keeping of cattle in some good grazing areas. No attempts have been made to control this species, although plans to do so have been made in the past, for instance in Ghana.

2.4 ECOLOGY OF GLOSSINA PALLIDIPES

2.4.1 Environment Glossina pallidipes is patchily distributed throughout eastern Africa, from Ethiopia, Sudan and Somalia in the north, to Zinbabwe and Mozambique to the south. Parts of eastern Zaire and Zambia are also infested. The species used to live in parts of South Africa, but it has been eradicated from there.

Glossina pallidipes requires thickets and does not occur above 2000 m (6000 ft.). Under mild climatic conditions this species can spread through areas of scattered thickets, woodland and even open country. Rarest edges along the Kenya coast are infested with G. pallidipes.

Untrimmed hedges and tree crops can encourage G. pallidipes infestation.

Like its close relative G. longipalpis, G. pallidipes depends cm bushbuck for most of its food.

2.4.2 Resting sites Day time: at temperatures between 20o and 30O (Zimbabwe) flies rest on the under side of horizontal or nearly horizontal branches, up to 12 m above ground. At higher temperatures, flies move to lower cooler resting sites, such as tree trunks near ground level, the underside of fallen logs, the cracks in bark, and rot holes in trees.

Night time: flies move to rest on leaves 2.5 m to 4 m above the ground.

2.4.3 Host animals This species depends very heavily on bushbuck for its food. Warthog, bushpig and buffalo are also important. Roan antelope is readily fed upon when available.

In particular areas, other hosts may replace buchbuck as the main source of food. For example, in Masai Mara (Kenya) buffalo is the main host.

For one G. pallidipes population, it was estimated that on average each host animal (usually bushpig or bushbuck) supported 1163 tsetses, and gave 291 blood meals each day.

2.4.4 Parasites Mutillids, Ihyridanthrax (Bombyliidae) and various parasitic wasps have been reported as parasites of G. pallidipes.

In Kiboko (Kenya) and Mwalewa *(Kenya)* a high rate of parasitism by Thyridanthrax was found.

2.4.5 Behaviour Daily activity of G. pallidipes, as measured by the netting of flies coming to bait cattle at Lugala (Uganda) was different in the two sexes. Male catches increased throughout the day (whatever the season) until just before sunset, when the catch quickly dropped to zero. Female catches rose to reach a moderate level at about midday, which continued until sunset, when the catch dropped.

But in some places in Kenya the catch showed a morning maximum and another smaller afternoon maximum, the two being separated by a rather inactive midday period.

The reasons for these differences are not understood.

In Zimbabwe in the hot dry season, there was a slight morning peak in feeding activity, but feeding was greatest in the afternoon, stopping suddenly at 18.45-19.00 hours. In the rains there was no morning maximum.

There may be some activity and feeding at night.

2.4.6 Breeding sites Along the Lambwe Valley (Kenya) breeding sites were found mostly along the well-drained sheltered banks of the river courses with Sansevieria as the ground layer vegetation. At Kilifi (Kenya) pupae were found scattered at random over the thicket and

forest floor. At Mwalewa and Nkruman (Kenya) pupae were found mainly under shrubs giving the darkest shade,
especially where there low overhanging branches.

In Zimbabwe, G. pallidipes uses sandy river beds in the cool dry season, and animal burrows in the hot dry season. Some pupae have been found under fallen logs in the wet season, but few pupae are found.

2.4.7 Adult populations Very few teneral females are inseminated, so it is believed that mating takes place after the first blood meal has been taken by the female.

In a sample of flies collected from bait oxen, the flies taken during the middle hours of the day were older than the flies taken in the early morning and in the evening (Lugala, Uganda).

Glossina pallidipes is easily caught by trapping. Mare females than males are caught in traps. The Langridge, Moloo and Challier-Laveissiere traps are more effective in catching G. pallidipes, than fly-round patrols.

Different methods of sampling catch different parts of the fly population (see Volume I, 7.10.1). Flies caught on a fly-round are younger than flies caught at a tethered ox, and these are younger than flies caught in traps. While traps catch more females than males, many more males than females come to a fly-round patrol.

A trap that is left for months in the same position catches fewer flies as the weeks pass by, even if the traps are remade using new material. But on placing the traps in new positions, the catch increases greatly.

A rate of dispersal of about 140 m per week within a G. pallidipes fly belt has been estimated.

2.4.8 Epidemiology and control Glossina pallidipes is a very important vector of animal trypanosomiasis.

Glossina pallidipes can also be important in spreading Rhodesian sleeping sickness. Sometimes it is the only vector infesting a sleeping sickness area, but even when it lives together with greater numbers of G. morsitans it may still be important because:

(a) Glossina pallidipes depends heavily on the bushbuck for its food

(b) Bushbuck is known to be a reservoir for T. rhodesiense

(c) Bushbuck often lives in fairly close association with man.

Cattle can also be very important as a reservoir of T. rhodesiense, in G. pallidipes areas (Alego, Kenya).

In Lambwe Valley (Kenya) it was thought that G. pallidipes feeding on game animals, especially bushbuck in thickets, kept T. rhodesiense transmitted to natural hosts. Contact between man and cattle on the one hand, and the tsetse and wild host on the other, could cause outbreaks of sleeping sickness.

Total trypanosome infection rates in G. pallidipes vary according to area but not significantly to season.

At Lugala (Uganda), congolense and vivax mature infections began to appear in flies about 11-15 days old and reached a high level (17% and 6% respectively) in flies about 40 days old. Brucei infections did not appear until flies were about 43 days old.

Insecticidal control schemes directed against G. pallidipes (Kenya) have included: ground spraying of dieldrin in the Lambwe valley outside the game reserve, in the Lake Victoria basin; and experimental aerial spraying (both by helicopter and fixed-wing aircraft) using dieldrin.

Deliberate bush clearing as well as human settlement has greatly assisted the eradication of G. pallidipes from very large areas of Kenya.

2.5 ECOLOGY OF GLOSSINA AUSTENI

2.5.1 Environment The species is distributed along the eastern side of Africa from Somalia to South Africa. It is limited mainly to regions within about 200 km of the coast, and up to altitudes of 900 m.

The main habitat is evergreen thicket. Dense secondary forest and sacred groves (Kenya) are also used. Abandoned plantations, for example of rubber, cloves and teak, may contain G. austeni.

2.5.2 Resting sites In Kenya, the fly uses the densest shade that is available in hot dry weather. It rests on the underside of horizontal branches, up to 1 m from ground level.

It also rests under curled-up dead leaves on the ground, in the forest.

2.5.3 Host animals The host animal most often fed upon by G. austeni is the bushpig. Nearly 60% of feeds are taken from this one species. Also important are man, cattle and duiker. The bushpig and duiker are selected because of their habit of sheltering in the same thickets as G. austeni.

2.5.4 Predators and parasites The elephant shrew (Petrodomus tetradactylus) may find and eat pupae of G. austeni.

Thyridanthrax (Bombyliidae), mutillid wasps and certain other parasitic wasps have been bred from G. austeni pupae, but at very low rates (0.7%).

2.5.5 Behaviour This species attacks man silently, settling just behind the knee. However, it is not particularly attracted to man, which may make it

difficult to survey even when it is thought to be present in an area. Using a bait ox gives much better results than using man alone.

Early morning and late afternoon times for surveys are recommended.

Flies may sometimes feed at night, especially in the hot dry season. This is unusual behaviour for tsetse.

2.5.6 Breeding sites Pupae may be found in the dry earth beneath overhanging rocks, as well as under fallen logs and under horizontal tree trunks. Pupae are commonly found around the base of cycads.

2.5.7 Epidemiology and control Glossina austeni can transmit cattle trypanosomiasis. Trypanosome infection rates may be quite high. In one area over 12% of G. austeni were infected with vivax group and congolense group; this was a rate higher than that found in G. morsitans, G. pallidipes or G. brevipalpis living in the same district (Sitatonga, Mozambique).

Where the local distribution of G. austeni is limited to waterside thickets, clearing has helped in control in the past.

Glossina austeni was exterminated (along with the more abundant G. pallidipes) from a game park in Zululand, South Africa, by means of an aerial insecticide campaign starting August 1946 and ending successfully two years later.

CHAPTER 3

ECOLOGY OF PALPALIS GROUP SPECIES

3.1 ECOLOGY OF GLOSSINA PALPALIS GAMBIENSIS 3.1.1 Environment

3.1.1.1 Climate The northern limit of distribution of Glossina palpalis gambiensis follows closely the 1000 mm rainfall limit from Mali to Togo. In the region of Dakar, Senegal, the fly lives in an area of low rainfall and high humidity, due to humid winds coming from the sea.

The southern limit of distribution is set by thicker vegetation, in which G.p. gambiensis is replaced by the very similar G.p. palpalis.

The distribution area of G.p. gambiensis covers different climatic zones with large variations in

- rainfall (1000-2000 mm)
- temperatures (mean temperature of the coldest month more than 2Co and the daily maximum temperature may reach 40°)
- relative humidity (5-100% according to season and latitude)
- winds (in the rainy season wind blows from south-west and in the dry season the Harmattan blows from the north-east).

Species of the palpalis group need high humidity and deep shade. The best conditions are about 25° and 80-85% R.H.

Glossina palpalis gambiensis living in a wide range of climates in the savanna zone of West Africa is able to find suitable microclimates in dense vegetation along watersides with a closed canopy. A thick mat of

vegetation to each side prevents dry winds from penetrating the gallery forest. Shade allows temperatures to remain lower in the daytime and higher during night time than in the surrounding savanna. The presence of water nearby (either free or underground) provides the required high humidity.

During the host dry season maximum temperatures are very high but flies find resting places close to water, where conditions are more suitable than in the gallery forest as a whole.

3.1.1.2 Typical habitats Glossina palpalis gambiensis is distributed along gallery forests of the dry Sudan savanna zone and the more humid Guinea savanna zone.

In the dry season most small streams dry up especially in the Sudan savanna, but in some streams a few waterholes remain. In others with a deep riverbed, humidity remains quite high because of underground water. When small open gallery forests become too dry, tsetses leave and concentrate along the remaining humid areas.

3.1.1.3 Other habitats

- Sacred groves. These are small patches of vegetation consisting of large old trees, dense creepers and shrubs, often around a water hole or flooded area. They are often very close to villages and are protected by the villagers. Vegetation is very dense and provides suitable shelter for tsetse.

- Niayes. This Wolof word is used for land scape typical of the Dakar region, Senegal. The dominant tree is the oil palm (Elaeis guineensis). Rainfall is low (600 mm) but humidity is high due to sea winds and underground water.

- Mangrove swamps. The seashore of West Africa, from Senegal to Liberia (at the western limit of G.p. gambiensis) is lined with mangroves,

especially at the mouths of rivers. In Senegal this vegetation (dominated by Rhizophora and Avicennia) is occupied by tsetses, but not as a breeding area.

- Lakeshores. If there is dense vegetation there, the lakeshore provides tsetse with the same sort of shelter as the gallery forest.

3.1.1.4 Effect of animal life on G.p. gambiensis

(a) the host animals available to G.p. gambiensis are

- species always available: monitor lizard (Varanus) and crocodile, that live permanently at watersides
- species sometimes available: bovids (especially bushbuck), warthog, when these animals come to drink
- man, when visiting the habitat for fishing, washing, cutting wood and cultivating gardens near rivers.

Blood meal identifications from G.p. gambiensis at Kou Forest (near Bobo-Dioulasso, Upper Volta) gave the following results: reptiles 58%, man 24%, other primates 2%, bushbuck 2%, other bovids 12%, other mammals 2%.

(b) Predators. The predators of G.p. gambiensis are the same as those of other tsetse species. In Poa Forest (near Bobo-Dioulasso, Upper Volta) spiders (Theriidae and Clubionidae) have been seen holding tsetses.

The action of predators appears to be greatest in the rains, especially in May.

(c) Parasites. In the rainy season some nematode worms live inside a few tsetse flies, but seem to do the flies no harm. No pupal parasites have been found so far.

3.1.1.5 Action of man on the environment

(a) Man-made habitats.

- Dams. These are being built in West Africa, but it is still too early to judge for certain their effect on vegetation, but probably the artificial lakes that are formed will encourage vegetation growth favourable to tsetses.

- Plantation. Many mango plantations are grown along riversides. These provide tsetse flies with suitable shelter, particularly so in the case of old trees with low branches.

- Hedges. The soil beneath hedges of Euphorbia balsamifera planted for fencing off gardens, is used as tsetse breeding sites.

(b) Bush clearing.

There was an important campaign in 1938-1939 clearing bush from 500 localities from Senegal to Niger. This resulted in a retreat of G.p. gambiensis from its original northern limit.

Settlement and farming along river banks has resulted in the progressive destruction of gallery forest, for firewood.

3.1.2 Behaviour

3.1.2.1 Choice of breeding site Females deposit their larvae in shaded places. Pupae are found at 3-4 cm depth

- in sandy soils
- in humus with coarse particles

- voider logs
- at the foot of large trees with buttress roots
- under culverts
- between aerial roots
- under dry leaves on the ground
- in soil under low overhanging branches

In the dry season breeding sites are concentrated along dried-up river beds. These may be flooded at the first heavy rains; if so, many pupae are destroyed.

3.1.2.2 Resting sites (as at Poa Forest, Bobo-Dioulasso, Upper Volta).

(a) Day resting sites (December).

These have been studied by tagging flies with radioactive materials (a special technique not described in this Manual). 95% of flies prefer the underside of the long woody parts of plants such as branches, twigs, roots and trunks; very few rest on leaves.

85% of flies select twigs, branches and trunks with a diameter less than 10 cm, as resting sites; just over half of the flies (51%) prefer twigs and branches 1-2 cm in diameter.

Flies often choose resting sites in the river bed close to water (29%) or within 0.50 m from the river bank (40%). Hardly any flies are found more than 3.5 m away from the edge of the stream.

Flies rest near the ground: 80% rest lower than 0.50 m and none rest higher than 1 m from ground level.

(b) Night resting sites.

Most (90-95%) of the flies choose leaves as places on which to rest, especially green leaves of small plants (79-80%).

Other resting sites are grass stems, branches, twigs and exposed roots. Very few flies (less than 0.1%) rest on the ground.

In the early dry season (May-June) 96% of males rest less than 3 m away from the river bank; 93% rest below 0.50 m; 60% rest below 0.20 m.

During the hot dry season (March) flies are seldom found higher than 0.50 m, and none more than 2 m from the river bed.

Nearly 50% of flies rest vertically, and most of the remainder rest horizontally. The usual habit is to rest on the tip of a leaf or on the end third of the leaf blade. The fly lies parallel to the main vein of the leaf with its head towards the stem. On dry twigs fallen to the ground the fly stands on the highest point.

3.1.2.3 Activity In Glossina palpalis gambiensis the daily activity pattern depends on temperature and light intensity.

Activity starts shortly before dawn, at a temperature of about 16°.

Males show a high activity level in the morning (10.00-11.00 hours), low activity at midday (12.00-13.00 hours), followed by a second smaller increase in activity in the afternoon. Female activity is similar except that greatest activity is generally in the afternoon (13.00-15.00 hours).

Activity declines rapidly from 16.00 hours and ceases altogether at sunset (18.00 hours in the dry season).

The activity pattern varies according to season.

During the cold season (December-February) activity starts from 08.00 to 09.00 hours, increases rapidly, and stays at a high level for six hours before decreasing.

At other seasons activity starts at sunrise then rapidly increases; but the early afternoon decrease varies according to the season.

In the hot dry period (late February-March) there is an obvious early afternoon drop followed by a second peak.

In April-May there is a rather steady activity.

In the rainy season, for both sexes the morning high activity level slowly decreases until at 17.00 hours it decreases more rapidly.

3.1.2.4 Dispersal Glossina palpalis gambiensis generally disperses along the river line, following river beds or the edges of gallery forests, exceptionally covering up to 4 km in one day. It can also cross open spaces without vegetation and can even cross from one river system to another (across a watershed).

In the rainy season, this subspecies can also disperse through savanna. In the dry season, it concentrates along parts of gallery forests only where flowing, still or underground water occurs. These are the permanent habitats.

3.1.3 Populations

3.1.3.1 Breeding sites Breeding sites may dry out in the dry season, causing death of pupae placed there. In the early rainy season breeding sites along river beds are often flooded (see also 3.1.2.1).

3.1.3.2 Physiological state Males are active not only when hungry but also when they have partly digested the bloodmeal in their gut. Very few fully engorged flies are caught. Hungry flies are caught in hand nets in greater numbers in the middle of the day whereas flies in intermediate hunger stages are caught throughout the day.

Soon after larviposition females urgently need to take a blood meal. A second meal is taken when females bear a first or second instar larva. Females carrying a third instar larva rarely need to feed.

Teneral flies generally rest at the breeding sites for one or two days before taking their first blood meal.

3.1.3.3 Density and distribution In the dry season, particularly in March, low humidity and very high temperatures are unfavourable to tsetse. At this period of the year vegetation is not dense enough to provide adequate shelter and adult flies die from excessive water loss.

After the recent drought in the Sahel zone the northern limit of G.p. gambiensis in Niger and Upper Volta is now 50-100 km further south of that in 1953.

3.1.4 Epidemiology and control

3.1.4.1 Epidemiology With respect to human trypanosomiasis (Gambian sleeping sickness), G.p. gambiensjs is the most important vector in West Africa because of its wide distribution over the savanna zones.

Most villages lie near water courses. Man-fly contact is very close in the dry season when flies concentrate at waterholes or in the moist parts of riverine vegetation. Thus places such as bridges, fords, watering sites, riverine fields and gardens are important points where the disease might be picked up.

The subspecies is also an important vector of animal trypanosomiasis. Cattle going to streams and rivers to drink come in close contact with tsetse at such places.

3.1.4.2 Control Work carried out in the past to control tsetse by riverine bush clearing has already been mentioned (3.1.1.5).

The fact that G.p. gambiensis is a riverine species resting near the ground and near water helps in the selective application of residual insecticides.

Only a narrow and low strip of riverine vegetation has to be treated. Also, the dry season is long enough (4-5 months) for a single application of insecticide to be sufficient.

3.2 ECOLOGY OF GLOSSINA PALPALIS PALPALIS

3.2.1 Environment In savanna areas the ecology of G.p. palpalis is very similar to that of G.p. qambiensis and will not be redescribed in detail.

Glossina palpalis palpalis extends from Ghana in the west to Nigeria in the east, then continues to the south as far as Angola.

Forms transitional between this subspecies G.p. gambiensis occur in southern Ghana, Ivory Coast and Liberia.

Glossina palpalis palpalis occurs in a wide range of vegetation zones. In the north, in the Sudan savanna vegetation zone, it occurs in vegetation closely associated with rivers and streams. In the Guinea

savanna vegetation zones it is also associated especially with rivers and streams, but in the much more humid vegetation of the rain forest, or in secondary vegetation produced by man's activities in the rain forest zone, it can be found well away from surface water.

Glossina palpalis palpalis often occurs with G. tachinoides but does not extend so far into the dry north.

3.2.2 Behaviour In savanna areas, pupae of G.p. palpalis are found especially in denser, forest-type vegetation in low shade provided by shrubs, creepers, low branches, fallen logs, overhanging river banks, etc.

In rain forest, breeding is widely dispersed but still mainly in heavy shade. The pupae are most easily found in sandy soil but also occur in soil containing much decaying vegetation (humus).

In very wet areas, pupae have been found up to 2 m above ground in forks of trees or in tree rot-holes. Pupae are difficult to find in the wet season, which may be due to the use of less specialized breeding sites and/or to the difficulty of handling wet soil.

Daytime resting sites in gallery forest are mainly on the underside of thin branches and stems with diameters up to about 2.5 cm. Flies rest mainly at heights of 0.3 to 2mabove the ground; they rest lower on the vegetation at higher temperatures. Tree trunks are rarely used as resting sites.

At night flies rest higher, especially on the upper surfaces of leaves. Actual resting heights depend on the vegetation; resting flies have been found up to 18 m above the ground.

Dispersal occurs especially along water courses and G.p. palpalis can fly at least 1.6 km (1 mile) in 24 hours.

3.3 ECOLOGY OF GLOSSINA FUSCIPES

3.3.1 Environment Glossina fuscipes has a very wide distribution throughout much of Zaire and nearby countries, extending to the east as far as the eastern shore of Lake Victoria. The present range includes the rain forest area as well as secondary forest and thickets in Zaire, northern Angola, southern Congo, western Tanzania, western Kenya, Uganda, western Rwanda, western Burundi, and southern Sudan. It does not extend into river systems draining into the Indian Ocean.

In Ethiopia and southeastern Sudan there are some isolated belts.

The species is divided into three subspecies: G. fuscipes fuscipes, G.f. quanzensis and G.f. martinii. In this section all the subspecies are dealt with together unless the subspecies is named.

The fly usually lives close to water, in linear forest vegetation along rivers and lakes. In addition, flies may live in less humid habitats some kilometers away from water.

3.3.2 Resting sites By day: in S.W. Central African Republic flies rest on tree trunks, foliage and low branches, with 94% resting between 1 and 1.5 m above the ground.

In S.E. Uganda in the dry season in thickets not near water, 92% rested between 1.5 and 3 m above ground, and 87% were resting on the underside of twigs and branches.

By night: in S.E. Uganda, flies rest up to 6 m, but with 88% resting below 4 m; 68% were on or under twigs less than 2.5 m diameter.

3.3.3 Host animals In the case of G.f. fuscipes in East Africa, feeds were as follows: 38% from bovids, mainly bushbuck; 34% from reptiles; 18% from man; 3% from bushpig; 7% from other manuals.

In one study made on G.f. fuscipes on islands in Lake Victoria, the flies fed on crocodiles and monitor lizards, but after these host animals had been chased away, the flies fed on the party of men.

Around Brazzaville, some G.f. fuscipes populations nearly always feed on man, and have become 'village flies'.

3.3.4 Parasites and predators At Lake Victoria, 1.5% of G.f. fuscipes pupae were found to be parasitized by Syntomosphyrum (Hymenoptera). This parasite was bred and released in large numbers in an effort to control G. fuscipes on an island in Lake Victoria, but only 5% of the wild population of pupae became parasitized.

Predation of pupae by ants has been observed.

3.3.5 Behaviour At Lugala, Uganda, G.f. fuscipes activity started about dawn, with greatest activity occurring near the middle of the day. Activity level fell rapidly in the evening, and there was no activity at night. The pattern is more or less the same whatever the season, or whether the flies are males or females.

At Kinshasa, Zaire, G.f. quanzensis daily activity began when the temperature reached 20° or 21°, and increased rapidly above 23°-24O. Male activity began before female.

When resting flies are disturbed, they fly up but often return to exactly the same spot.

3.3.6 Breeding sites In East Africa, breeding sites are dry sandy beaches under the shade of dense vegetation. Pupae may also be found in dry leaf fragments under overhanging rocks, and in coarse dry sand sheltered by ferns and by the forest canopy.

3.3.7 Adult populations In some areas G.f. fuscipes adults decrease in numbers during the dry season. In other areas the numbers remain roughly constant throughout the year.

In Kinshasa, Zaire, G.f. quanzensis density was found to be highest at the start of the rains, and lowest at the start of the dry season. The percentage of females caught was highest when the total density was highest.

Males may move up to 300-400 m per day in riverine habitats (Uganda).

Males have a four-day hunger cycle. Results of hunger staging studies depend largely on the number of stage 4 (very hungry) flies caught.

3.3.8 Epidemiology and control Glossina fuscipes was the vector responsible for up to 200,000 deaths from Gambian sleeping sickness between 1895 and 1910, in Uganda. This epidemic followed an outbreak of rinderpest which reduced game animals and caused flies to feed from man in greater numbers.

Glossina fuscipes is also a vector of Rhodesian sleeping sickness, on a much smaller scale.

Infection rates with trypanosomes is generally lower in G. fuscipes than in other tsetse flies living in the same areas. This is probably because of the large number of blood meals taken by G. fuscipes from reptiles, which are not reservoirs for Trypanosoma vivax, T. congolense or T. brucei. Infection rates in flies living in sane remote places may even be nil. In other places, vivax type is the commonest infection, and the infection rate is highest in or immediately after the wettest months.

Mechanical transmission of T. gambiense by G. fuscipes has been studied experimentally, and probably occurs naturally. This would help to explain how G. fuscipes can have very low rates of T. gambiense infection even in sleeping sickness areas.

3.4 ECOLOGY OF GLOSSINA TACHINOIDES 3.4.1 Environment

3.4.1.1 Climate Glossina tachinoides is usually found within gallery forests, and its distribution pattern corresponds to the system of drainage lines and streams along which these gallery forests grow.

This thick vegetation lessens the severe effect of the general climate and makes microclimatic conditions (of temperature, humidity and light) that are better suited to the life of tsetse.

A wide variety of host animals live in or near the same habitat, providing permanently available food supplies.

Unusually harsh climatic conditions may greatly alter the environment. Thus the occurrence of a long drought, involving the reduction of riverine vegetation and the drying up of streams, destroys some of the habitat and some of the animals that are essential for the survival of G. tachinoides.

3.4.1.2 Typical habitats According to the season, G. tachinoides may come to occupy different parts of the general habitat.

The habitats that are permanently occupied or visited frequently, consist of vegetation types in which generally one species of tree or shrub is dominant (Morelia, Mitragyna, Mimosa).

The density of the vegetation and the canopy or cover formed by the leafy branches are important in the ecology of G. tachinoides. They provide a refuge for the flies, allowing them to find the conditions required for their survival and their breeding.

3.4.1.3 Other habitats Special circumstances such as forest clearing, or drought, may greatly alter the microclimate and scatter the host animals. Glossina

tachinoides nay then take refuge in other (atypical) habitats, next to villages and in cultivated areas. Eventually they may become established and breed there.

These atypical habitats may be several kilometers from the nearest water; they can be of semi-artificial or artificial type:

(a) Semi-artificial habitats. These consist of various kinds of plantation (such as oil palm, mangoes, bananas, cola nuts, cacao, coffee); cattle control posts may also be used.

(b) Artificial or peri-domestic habitats (peri-domestic = around the hone). These are found in the high rainfall, southerly regions of G. tachinoides distribution. They include villages where the domestic pig and other livestock are kept (see 3.4.1.4).

3.4.1.4 Effect of animal life on G. tachinoides

(a) Animal hosts. Glossina tachinoides feeds on man and a variety of mammals and reptiles (see Volume I, 6.1). The origin of the blood meals depends on the chance or opportunity of the tsetse feeding on one animal host species rather than another: in the natural habitat there is probably not much selection of one host species rather than another, on the part of the tsetse. This is called opportunistic feeding.

In the typical habitat, the host animals most often used are:

- bovids (especially bushbuck)
- suids (especially warthog)
- reptiles (especially monitor lizard and snakes).

These are fed upon in various proportions according to area, season and habitat.

The reptiles are more fed upon in the humid savanna areas, making up more than one-third of the blood meals.

In the dry savanna areas antelopes provide the greater number of blood meals (more than 75%).

Man is only an incidental (occasional) host, and the amount he is fed upon depends on how often he visits the habitat.

In the semi-artificial habitats (see 3.4.1.3) wild hosts are less abundant, and here man, domestic livestock, as well as wild hosts, are fed upon.

Tsetse populations living in artificial peri-domestic situations, have become very specialized in their feeding habits. They feed mainly on domestic pigs, a little on cattle, and only rarely on man. This host dependence is so strong that the removal of the pigs brings about a large reduction of the fly population. This is no longer opportunistic feeding.

(b) Natural enemies. The natural enemies of G. tachinoides have most often been studied in the gallery forest. They are mainly predators and parasites belonging to the Arthropoda (see Volume 3, Appendix I).

Predators active against adult tsetse:

- Rabber flies (Asilidae, Diptera). They perch on look-out places on isolated twigs,within the habitat or at its edge, and oath in flight the tsttses that come within reach.

- Spiders (Araneae). These have their home on the tree trunks which tsetse use as their resting sites. The flies are caught by the spiders and immediately wrapped up in a web cocoon.

Predators active against tsetse pupae:

- Seed-eating birds, while scratching in soil for their main food, may discover and eat tsetse pupae.

- Small mammals may eat tsetse pupae along with a lot of other insects in the soil.

- Other soil arthropods (especially beetles and ants).

It is usually impossible to actually see these predators eating tsetse pupae in the field, so the exact importance of the various predators is not known.

Parasites of pupae (see 1.1.4):

- Thyridanthrax (Bombyliidae, Diptera)
- Syntomosphyrum (Hymenoptera)
- Mutilla (Hymenoptera)

Usually, parasitism is observed only in the hot season, when the pupae are fairly concentrated.

In general, predators or parasites are not restricted to tsetses. The action is seasonal. Rather high rates of parasitism do not necessarily lead to low tsetse numbers.

3.4.1.5 Action of man on the environment Man has an effect on the population of tsetse by

(a) altering the habitat
(b) reducing the numbers of host animals

This effect may come about simply by people cutting down the riverine vegetation where tsetses and wild animals are living. It may not be part of a deliberate control programme, but it can have the same effect.

3.4.2 Behaviour

3.4.2.1 Choice of breeding site Pupae of G. tachinoides are to be found in the habitat of the adult, especially in places protected by a vegetation cover, giving permanent shade and humidity, and cooler conditions Pupae are often found in or near the disturbed soil of animal tracks and animal resting places.

The breeding site can vary according to the seasons, in relation to the change of temperature and humidity. This variation is greatest in regions where the differences between seasons are greatest, and where flooding occurs (gallery forest of dry savanna). In such places the breeding sites are concentrated in the dry season and dispersed during the rains and floods.

The breeding sites also vary according to the general area. In the regions where G. tachinoides occupy atypical habitats (in the southern part of their distribution) the pupae can be found:

- in plantations
- in soil beneath parts of the foliage hanging away from the trunk (bananas, mangoes, etc.)
- in places even within villages, such as underneath water storage vessels, at the base of fences, under heaps of firewood or yams* stored against the walls of village huts.

At the breeding site itself, temperatures vary from 19° to 33°: this causes the duration of the pupal period to be from 38 to 23 days. It is therefore

about 1.6 times longer in the cool season than in the hot season. The humidity there is always between 50% and 80% R.H.; the pupa may die if the humidity goes higher or lower than these limits.

3.4.2.2 testing sites As with other tsetses, G. tachinoides spends its life between long resting periods and brief moments of activity.

The flies settled at true resting sites can be regarded as being asleep, and digesting their last meal.

Under extreme climatic conditions (of heat or cold) they sit quietly and are not disturbed by things going on around them.

The true resting sites are of two kinds, day resting sites and night resting sites.

(a) Day resting sites.

These are on the woody living parts of the vegetation, sheltered from the sun and wind, such as tree trunks, branches and exposed parts of roots.

Glossina tachinoides usually occupies the zone bordering the vegetation, above all when it is of a bushy type (Mimosa habitat); it practically never strays deeper into the vegetation.

The resting sites are widely dispersed in the cold wet season; but they are concentrated in the hot dry season. The tsetses come closer to the water and to the ground when the temperature and dryness are both severe.

The horizontal concentration is best seen when the gallery forest is wide; as in the humid savanna regions when near to 90% of flies are at less than 16 m from the waterside, and 75% are less than 8 m, in a gallery forest of 100 m width.

The vertical concentration is caused by the tsetses searching for more shaded places, during which they always find a; microhabitat having a lower temperature (by as much as 10°) and a higher humidity than the general environment. At temperatures less than 30° the tsetses use all the woody structures to be found under foliage. When the temperature rises, the resting sites come closer to ground level. In the hot period, 99% of flies observed at rest are less than 0.80 m above ground and 80% of them are less than 0.30 m. In northern regions, at hours when the general temperature can be as high as 400-41°, virtually all of the tsetses are then settled at heights less than 0.30 m from the ground.

(b) Night resting sites.

These differ from day resting sites both as regards the plant parts that are used, and their exact location.

The great majority of tsetse rest on the green parts of the vegetation. They also ate found in higher, more scattered sites than during the day.

3.4.2.3 Activity Glossina tachinoides is active only during the day, when temperatures are between 18° and 41?. Activity is greatest at 31°. It rises rapidly as this temperature is approached, then drops very rapidly above this temperature.

The pattern of daily activity therefore varies according to the season.

- There is a single maximum of activity at midday in the cool season.
- There are two maxima (in the morning and evening) in the hot season.

- There is fairly steady level of activity in intermediate seasons (notably the rainy season).
- On very hot days, midday activity is totally absent.

Variations of humidity do not seem to have much influence on the amount of activity; but when humidity is high flies may be active a little longer than usual.

Variations of light intensity: when the temperature conditions are right, flies may be active in poor light, but a strong light intensity reduces activity.

Tsetses are drawn towards the light when the temperature is lower than 31°, but above that temperature they look for shady places.

3.4.2.4 Dispersal Individuals of Glossina tachinoides can move around (disperse) within their, habitat or even beyond.

This may be done by flight in the normal way, or it may be done by the flies being carried along by a vehicle, an animal or a man, on which the flies may settle temporarily.

Dispersal within the normal habitat is done throughout the days of the cool or intermediate seasons, but only in the mornings and evenings of the hot season. By ordinary flight, G. tachinoides can spread 1 km per day, following tracks cleared in the undergrowth.

In the hot hours, when activity is low, flies move towards shadier places in which to find resting sites,or to deposit larvae.

Dispersal away from the main habitat occurs when the temperature and light are favourable. That is the case early in the morning or late in the afternoon of the hot season. It also happens during the rainy season throughout the day, when the rains have reduced the temperature, and when mists or cloud reduce the brightness of the sun.

It allows a wider scattering of the resting sites at night at this season. As a result of such dispersal, a certain number of tsetse may be carried well away from their usual homes and come to occupy other habitats, lying sometimes several kilometers distant.

3.4.3 Populations The breeding sites of pupae are described under 3.4.2.1.

3.4.3.1 Sex ratio This is often written as the percentage of females in a sample.

- At emergence: the females make up 50% of the emerging flies.
- Among active flies captured by hand net: females make up on average about 30% of the sample. This value remains steady for most of the year, with some increase at the end of the rainy season and some decrease in the middle of the hot season. The figure only occasionally reaches 50%. In daytime captures, the figure increases as the light fades.
- Among flies captured by Challier-Laveissiere traps: a higher percentage of females is taken by these traps than by hand net collection.

3.4.3.2 Age The length of life of females is generally between a minimum of one month (in the hot dry season) and a maximum of 3 months (in the cool season).

3.4.3.3 Physiological state Sampling may allow the physiological state (hunger state, pregnancy state) to be studied, as well sex ratio and age.

The results differ enormously according to whether captures are made by hand net or by trap:

- traps and men with handnets both catch hungry males, but older flies are caught by traps

- traps capture a smaller proportion of teneral males, and a higher proportion of older females
- among the parous females (females that have already deposited at least one larva) hand nets take a higher proportion of females with empty uteri, than traps which take a greater proportion of gravid ones (females carrying an egg or larva in the uterus).

3.4.3.4 Density

(a) Apparent densities vary in the course of the year and especially when the seasons are very marked, causing alteration of habitats.

In the northern regions of dry savanna, the apparent density passes through two maxima, one in May, the other in October, periods of the year during which the flies are concentrated in the only habitable places.

In intermediate seasons, the apparent densities are much less because the flies disperse.

(b) Real densities, estimated from capture-recapture studies, also show changes in the year. In a habitat where tsetses are apparently abundant, one can estimate the densities of populations of about 1500 tsetses/hectare. Where populations are very thinly scattered, estimates are difficult or impossible to carry out.

(c) Natural enemies of tsetse are thought to keep numbers down (but exactly how important predators and parasites are we do not know).

Host animals put a limit on the number of flies that can live in a given area.

Usually, any alteration to the environment leads to some thinning out of the tsetse population.

3.4.4 Epidemiology and control Glossina tachinoides is the most northerly of the tsetses in west and central Africa. In the northern part of its distribution area, where other species are not found, it is of course the sole tsetse vector of animal and human trypanosomiasis.

Its epidemiological importance is increased by

- its feeding on a variety of animals
- its need to take frequent meals
- its close association with man and domestic animals in the peri-domestic habitats of the south: risks of human sleeping sickness are obviously increased when domestic pigs are healthy carriers of Trypanosoma gambiense.

Knowing (a) the seasonal distribution and (b) the daily activity rhythms of G. tachinoides tells us how to avoid fly/nan contact, or fly/livestock contact. Infested zones should not be entered in the middle of the day in the cool season, or in the mornings and evenings of the hot season, as these are the periods of greatest fly activity.

The control of G. tachinoides by discriminative and selective spraying of a residual insecticide takes account of variations in the resting places according to season and hour of day. These methods keep to a minimum the amount of surface that has to be treated, so saving cost and avoiding unnecessary pollution.

3.5 ECOLOGY OF GLOSSINA CALIGINEA. AND G. PALLICERA

3.5.1 General information Not very much is known about either of these species.

In the case of G. caliginea the centre of distribution is southern Nigeria and southern Cameroon. The species spreads as far as Ghana in the west, to the Central African Republic in the east, and to Gabon in the south.

In the case of G. pallicera there are two subspecies. Glossina pallicera pallicera is distributed from Sierra Leone to Cameroon (except at the savanna gap that comes to the coastline in Togo and Benin). Glossina pallicera newsteadi is distributed in the Zaire river system.

Both species live in high rainfall, generally thickly forested areas.

Neither species is important economically as far as is known.

3.5.2 Glossina caliginea The most favoured habitat is near the coast in the freshwater swamps and the mangrove forest vegetation zones.

The fly can occur locally in large numbers in these zones.

It may penetrate inland for some distance along rivers and streams into the rain forest vegetation zone.

The natural hosts are not known. Man is probably not a favoured host as the proportion of females among flies attracted to man is very low. Male flies are known to feed on man.

It can be heavily infected with trypanosomes: 38% of flies dissected in Cameroon were infected.

3.5.3 Glossina pallicera This species is limited to the rain forest zone but can be found far from surface water. It is usually found along forest paths, or in open spaces in the forest.

It often perches on look-out sites such as fallen logs, and other low places, such as leaves, trunks and buttress roots.

It flies rapidly away from and back to the same spot.

A few blood meals have been identified from Nigeria and Cameroon. A wide range of hosts are fed upon, including bovids, suids, reptiles and birds. Man is not attacked.

Flies dissected and examined for trypanosomes had only a 2.5% infection rate.

CHAPTER 4

ECOLOGY OF FUSCA GROUP SPECIES

4.1 ECOLOGY OF GLOSSINA LONGIPENNIS

4.1.1 Environment This species is distributed mainly in Kenya and northern Tanzania, but belts also occur in southern Sudan, southern Ethiopia, and in Somalia.

It inhabits generally very dry country, even semi-desert. The typical habitat is dry thorn bush. It may also be found in riverine thicket, and in such places it can live side by side with G. pallidipes and G. brevipalpis.

4.1.2 Resting sites The resting sites of G. longipennis are logs, the shady side of tree trunks, and the underside of branches.

4.1.3 Host animals The usual host is rhinoceros (60% of feeds), but buffalo (14%), elephant (12%) and ostrich (8%) are also important. Rhinoceros is selected probably because of its regular territorial habits.

4.1.4 Parasites Several species of Thyridanthrax have been bred from the pupae.

4.1.5 Activity Adults may be active by day and to some extent by night. Large numbers of adults may be spread by cars, lorries and trains.

4.1.6 Breeding sites Breeding is not limited to the densest part of the bush, but pupae may be found in the shade of single isolated trees. The pupae are very resistant to dry conditions.

4.1.7 Epidemiology This species is not involved in spreading human sleeping sickness, nor is it very important as a vector of cattle trypanosomiasis. Where

it occurs, it is less important as a vector than G. pallidipes.

4.2 ECOLOGY OF G. BREVIPALPIS

4.2.1 Environment This species is widely distributed in eastern Zaire and in countries to the east and south. The habitat is waterside evergreen thicket, and forest islands in savanna. The species is not found above 1500 m.

4.2.2 Resting sites In Burundi, flies were found resting at 2-4 m above the ground on tree trunks in dense shady thickets. Males often rest on the ground, but these may be temporary resting places.

In Kenya flies rest on thin looped-over and horizontal branches about 1 m above the ground, near game paths in evergreen vegetation.

4.2.3 Host animals Approximately 40% of feeds are taken from hippopotamus, 30% from bushpig, rather *wore* than 10% from buffalo, less than 10% from bushbuck,with about 10% from other animals.

4.2.4 Predators and parasites Thyridanthrax (Bombyliidae), mutillids and various other parasitic wasps have been bred from pupae.

4.2.5 Behaviour Flies bite man around the head and fly with a loud droning noise.

Greatest activity is in the early morning and at or after dusk; both times coincide with the wandering of hippopotamus to and from their night grazing areas.

4.2.6 Breeding and breeding sites Pupae have been found in humus beneath dense low shrubs, in the shade of large trees close to a game path. In forest islands in savanna pupae have been found beneath fallen logs alongside pupae of savanna tsetse species.

The pupal period varies from 73.5 days (males) and 69 days (females) at 19.5°, to 27 days (males) and 25.5 days (females at 28.3°).

4.2.7 adult populations About half of the teneral females collected are inseminated.

The interlarval period lasts 10-11 days.

In samples of captured flies, males are usually in the great majority.

Much greater numbers of flies are caught when a bait ox is used, compared with a patrol of men only.

Flies may be carried for several kilometers by pedestrians, by game animals, and by trains (in Kenya) •

In a collection made at Lugala, Uganda, many individual flies were thought to be more than 80 days old.

Flies caught at night are younger on average than those caught during the day.

4.2.8 Epidemiology and control Infection rates of G. brevipalpis with trypanosomes is fairly low. The main reason may be that this species takes rather few meals from bovids, whereas other species (G. pallidipes, G. fuscipes) living in the same area take more meals from bovids.

Glossina brevipalpis does not appear to become infected with T. rhodesiense.

Although the species has no importance in spreading sleeping sickness, it may be locally important in passing trypanosomiasis to cattle and pigs.

4.3 ECOLOGY OF OTHER FUSCA GROUP FLIES

4.3.1 Introduction With one exception (Glossina longipennis), the twelve species of the fusca group are forest flies inhabiting either rain forest or isolated patches of forest and riverine forest in the savanna zones.

There are two blocks of rain forest in Africa:

(a) along the West African coast from Guinea to Ghana,

(b) along the West African coast from southern Nigeria eastwards and in the basin of the R. Ogooue and R. Congo/ Zaire, especially in Cameroon, Gabon, Zaire and Angola.

The two blocks of rain forest are separated by savanna extending to the coast in Togo and Benin.

The following species of the fusca group have generally western or central African distribution:

G. fusca, G. haningtoni, G.nashi, G. tabaniformis, G. schwetzi, G. vanhoofi, G. fuscipleuris, G. nigrofusca, G. medicorum and G. severini.

Glossina brevipalpis and G. longipennis are exceptional and occur in eastern Africa. They are dealt with under 4.1 and 4.2.

In many areas, suitable habitats for the fusca group are rapidly disappearing as man destroys forest vegetation and kills the wild animals on which the flies feed. In many countries these flies are confined to forest reserves and to well-wooded areas far from human settlement.

The distribution of many, and probably all, species is discontinuous as man has broken up once uniform habitats.

The species of the fusca *group* are not attracted to man. Cattle are very effective bait animals.

4.3.2 Ecology of Glossina fusca There are two subspecies of G. fusca;

(a) Glossina fusca fusca occurs in and around the rain forest in Guinea to Ghana

(b) Glossina fusca congolensis occurs in and around the block of rain forest in Nigeria, Gabon, Zaire, etc. It occurs particularly around the edges of the rain forest. A few specimens have also been recorded from Ghana, in the G. fusca fusca zone.

The following is a general account and does not refer to either subspecies in particular.

Although G. fusca can be found well within the rain forest, it is usually found on the edge of the rain forest and also in riverine forest and isolated forest `islands' in the savanna.

In the rain forest in Nigeria, G. fusca feeds especially on red river-hog. In riverine forest in savanna the main hosts are bovids, particularly the bushbuck.

Glossina fusca rests on the trunks of small trees, on vertically hanging creepers and on thin saplings about one inch in diameter. Most rest head downwards. A few flies rest on horizontal creepers or branches or on the trunks of large trees.

Flies are not attracted to man but cattle are effective baits. They will enter moving vehicles but not Morris traps.

In rain forest in Nigeria, numbers of G. fusca caught on a bait ox are higher in the rains than in the dry season but the difference is much greater in riverine forest.

In the wet season flies can be caught throughout the day but most are caught just before dark. In the dry season hardly any flies are caught during the hot midday period. Flies also live longer in the wet season.

Little is known about the breeding sites of G. fusca, and larvae may perhaps be deposited more or less at random in the forest. Pupae have been found under logs in rain forest.

A trypanoscme infection rate of 15.8% was found in 1,301 G. fusca dissected in Nigeria.

The species has some economic importance where it occurs in riverine forest or forest outliers in savanna.

4.3.3 Ecology of Glossina haningtoni Very little is known about this species.

Glossina haningtoni occurs in dense rain forest on the western side of Africa from Nigeria to southern Gabon. It extends well inland through Cameroon and Gabon into Congo and Zaire.

It is not attracted to man. Cattle are probably effective bait animals.

Resting flies can be found on vertical creepers and on thin saplings.

Flies may be caught in a certain area on one day but none may be found on a second visit. This may be related to movement of host animals.

In a small sample of blood meals identified from flies caught in Cameroon, 95% were found to be from the red river-hog.

Five of 59 G. haningtoni dissected in Cameroon ware infected with trypanosomes.

It has no economic importance.

4.3.4 Ecology of Glossina nashi Glossina nashi has a similar range to G. haningtoni (although it has not been found in Nigeria) but is much rarer.

Very little is known about this species but it seems to occur especially in dense rain forest in hilly country.

It has no economic importance.

4.3.5 Ecology of Glossina tabaniformis Glossina tabaniformis overlaps the range of G. haningtoni but extends much further both to the west (to Liberia) and to the east (to the western border of Uganda).

It is a rain forest species, but extends into drier'forest than G. haningtoni and G. nashi.

Flies are not attracted to man but are attracted to cattle. Domestic pigs do not attract the flies and Morris traps do not catch G. tabaniformis.

In rain forest in Nigeria seasonal dispersal and concentration is not marked but there is variability in the number of flies caught on a bait ox. Most flies are caught in the middle of the rains and fewest in the dry season. High temperatures and low humidities are probably unfavourable to the fly.

In rain forest in Nigeria and Cameroon, G. tabaniformis feeds especially on red river-hog.

The flies rest in similar sites to G. fusca. The head is usually downwards.

There are early-morning and late-afternoon peaks of activity. There is almost no activity at night.

Little is known about the breeding sites of G. tabaniformis. Pupae have been found in the decaying vegetable matter on the forest floor, and, like other rain forest species, it may be that larvae are not deposited in any special site.

A little more than half of flies caught on a stationary bait ox early and late in the (Say are males whereas during the middle of the day females greatly outnumber males. Catches from stationary or moving oxen usually contain 60-70% females.

Most flies are caught in areas where game animals are undisturbed by human activity.

A trypanosome infection rate of only 3.2% was found in more than 3,300 G. tabaniformis dissected in Nigeria.

It has no economic importance.

4.3.6 Ecology of Glossina schwetzi Glossina schwetzi has a central African distribution, occurring in Gabon, Congo, Zaire and Angola, extending well to the east in the last two countries.

Very little is known about this species. It seems to be associated with relic forest and forest islands and is probably not a true rain forest species.

It probably has no economic importance.

4.3.7 Ecology of Glossina vanhoofi Glossina vanhoofi has been found only in dense forest in north and east Zaire.

It is not attracted to man.

Resting sites are especially on small saplings and most flies rest head downwards.

Most resting flies are found early in the morning and there is a sex ratio of 1:1 in catches made throughout the day.

Pupae can be found in the forest under logs, overhanging earth banks and between buttresses of trees.

It has no economic importance.

4.3.8 Ecology Of Glossina fuscipleuris Glossina fuscipleuris extends to the north and east of the main rain forest belt from Cameroon in the west to Western Kenya in the east.

Little is known about this species but it probably mainly inhabits patches of surviving forest and forest islands in savanna outside the main rain forest zone.

It is most active in the early morning.

Pigs (giant forest hogs) provide most meals but in some areas hippopotamus is extensively fed upon.

It probably has no economic importance.

4.3.9 Ecology of Glossina nigrofusca Glossina nigrofusca extends across Africa in a relatively narrow band from Sierra Leone to Uganda. There are two sub species, G. nigrofusca nigrofusca to the west and G. nigrofusca hopkinsi to the east. The following account does not distinguish between the subspecies.

In some areas the species occurs in rain forest but it also occurs around the edges of the rainforest and in forest outliers at or beyond the limits of the rain forest.

Glossina nigrofusca is not attracted to man. Cattle are attractive baits; more males than females are caught off moving oxen.

As with some other species of the fusca group, there is a suggestion that the local distribution of G. nigrofusca may be related to movements of host animals. Flies may be caught in an area on one day but none may be found on a second visit.

In Nigeria, G. nigrofusca feeds mainly on bovids, especially bushbuck.

It is believed to be of little car no economic importance.

4.3.10 Ecology of Glossina medicorum Glossina medicorum occurs in West Africa from Liberia to Nigeria. It has also been found in west Gabon, separated by extensive rain forest from the main area in which it occurs.

It occurs in drier forest, in forest-savanna mosaic vegetation, in forest islands, in riverine forest and in low forest thicket. In Upper Volta it has been recorded in riverine forest as far north as the northern Guinea savanna vegetation zone.

Flies are not attracted to man or screens, but are attracted to cattle used as bait and to slow-moving vehicles. Morris traps are not effective but flies will readily enter both white and blue Challier-Laveissiere (biconical) traps.

More flies are caught in the rains than in the dry season. Activity is greatest in the early morning.

Flies usually rest head downwards on thin saplings and on vertically hanging creepers.

In Nigeria, 70% of feeds are from Bovidae, the bushbuck being particularly important.

Pupae of G. medicorum have been found under logs in forest islands.

It is probably of little economic importance.

4.3.11 Ecology of Glossina severini Glossina severini is restricted to eastern Zaire.

Little is known about this species but it probably occurs in forest-edge type vegetation rather than in true rain forest.

It probably has no economic importance.

INDEX

A

B

C

D

E

F

G

H

J

Julbesrnardia 23

M

N

P

R

S

T

V

Z

NOTES