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BIOLOGY AND CONTROL OF TSETSE FLIES

by

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1. INTRODUCTION

For centuries human and animal trypanosomiasis have ravaged vast areas of tropical Africa. As recently as 20 years ago sleeping-sickness was considered one of the most terrible of all endemic diseases affecting the African continent. Animal trypanosomiasis render stock-raising difficult, if not impossible, in many areas, and in cattle-grazing areas bordering on the Glossina zones, livestock is weakened and does not supply any draught-animal (Vaucel et al., 1963; Wilson et al., 1963; Ford, 1963).

Research efforts undertaken both in the laboratory and in the field have supplied in recent years better methods of prevention, detection and treatment of trypanosomiasis.

Human sleeping sickness prevalence has been reduced to an extremely low level, but the disease is far from eradicated and many small foci either remain active or appear in previously cleared areas. The situation is slightly better in West Africa, where the parasite Trypanosoma gambiense has apparently no animal reservoir, than in East Africa where occurs also T. rhodesiense with both human and animal hosts (Robertson, 1963; Willett, 1963).

Glossina-borne animal trypanosomiasis are always very widespread and hinder economic development of the majority of African states. Chemotherapy cannot be extended to all domestic animals and has its setbacks, including drug-resistance of the trypanosomes. So tsetse fly control has an important part to play in the development of the African continent.

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## 2. GEOGRAPHIC DISTRIBUTION OF TSETSE FLIES

Glossina sp. infest about 10 000 000 km<sup>2</sup> on the African mainland. Their present distribution has been recently summarized by Ford (1963) but more accurate data for French-speaking states of West Africa can be found in Rickenbach (1961), Maillot (1952), Rageau & Adam (1953) and Finellè et al. (1963).

Tsetse flies are classified into three groups typified respectively by G. palpalis, G. morsitans and G. fusca.

### 2.1 G. palpalis group

The palpalis group includes five species and four sub-species and is restricted to West and Central Africa, with relics in Ethiopia and Arabia.

G. tachinoides occurs in the Sudanese savannah and in the southern part of the Sahelian area of West Africa with residual foci in North-Eastern Africa, and can withstand very dry conditions but congregates in the dry season around water holes, residual pools of temporary rivers, and so on.

G. palpalis and G. fuscipes occur in the forest as well as in the Guinean and Sudanese savannahs, but in these last environments they are restricted to rivers and rivulets in the neighbourhood.

G. pallicera and G. caliginea occur in high forest areas, but the first can be encountered sometimes in the gallery forests of the Guinean savannah.

### 2.2 G. morsitans group

The morsitans group includes seven species and three sub-species, all inhabiting savannahs.

G. morsitans complex occurs mainly in Sudanese savannahs, with G. submorsitans in West and Central Africa and G. morsitans in East Africa.

G. longipalpis is restricted to Guinean savannahs of West Africa.

G. austeni is mainly a coastal species of East Africa.

G. swynnertoni and G. pallidipes are highland species of East Africa, the first being restricted to Kenya and Tanzania and the second species occurring from Ethiopia to Mozambique and being present in some coastal areas.

G. pallidipes has been eradicated from Natal.

G. borgesii has been recently described from Mozambique.

### 2.3 G. fusca group

The fusca group includes 12 species and two sub-species, which inhabit mainly densely forested areas.

G. nashi, G. schwetzi, G. tabaniformis, G. haningtoni, G. severini, G. vanhoofi and G. fuscipleuris occur in the Lower Guinean forest, sometimes in very restricted areas.

G. fusca occurs in all forested areas, from Sierra Leone to Uganda, and G. nigro-fusca is widespread in the Upper Guinean forest and in the northern part of the Lower Guinean forest, from Guinea to Uganda.

G. medicorum is restricted to Upper Guinean savannah and forest.

G. brevipalpis is very widespread in gallery forests and savannahs of East Africa from Natal to Eastern Congo (Léopoldville) and to Southern Ethiopia and Somalia.

G. longipennis is also an eastern savannah species, but restricted to Kenya, Ethiopia, Southern Somalia, South-Eastern Sudan, North-Western Uganda and Northern Tanzania.

## 3. BIOLOGY OF TSETSE FLIES

### 3.1 Reproduction cycle

Tsetse flies mate during the days following emergence, when the females are teneral. One insemination is sufficient for the whole life of the female, but males mate several times during their life and perhaps some females do the same. Non-teneral wild caught females are always inseminated. Homologous matings are the rule but sometimes mating occurs in nature between closely related species; such matings are generally not fertile and can be lethal for the female.

The two ovaries are composed of two ovarioles each, and each ovariole develops in turn (Saunders, 1962; Challier, 1963b). The first ovulation occurs three to 11 days after the emergence of the female; the mature ovocyte is not laid, but passes into the female uterus where fecundation occurs, then the larva grows inside the uterus, the food being supplied by the "milk glands" of the female; the late third instar

larva is laid on the ground and pupates about two to five centimetres below the surface, some hours later. Larval development, in utero, takes about 10 days, during which the female bites at least three times, but the first larva is laid when the female is about 16 days old. When the first larva is laid the second ovocyte passes into the uterus, and so on. The duration of the pupal life varies from 20 to 60 days, according to temperature.

The adult can fly some hours after its emergence from the puparium, and is able to bite the following day.

### 3.2 Feeding habits

Both sexes of tsetse flies suck blood, and they do not use any other food. They do not ingest usually either water or nectar but seem sometimes able to pierce plants for sucking sap.

Each species of tsetse fly exhibits definite feeding preferences, but the majority of Glossina are able to bite a great variety of vertebrates. The known trophic preferences are the following (Weitz, 1963) according to 22 640 blood meals identified: G. swynnertoni, G. austeni, G. fuscipleuris and G. tabaniformis feed mainly on suids, with bovids and other vertebrates (rhinoceros, hippopotamus, porcupine) as secondary hosts.

G. morsitans s.l. feeds equally on suids and bovids, warthog (Phacochoerus sp.) being the preferred host; man is also used as host, mainly by submorsitans of West Africa.

G. pallidipes, G. fusca and G. longipalpis feed extensively on bushbuck (Tragelaphus scriptus), and the first and second species bite also suids to some extent.

G. longipennis feeds mainly on rhinoceros, with giraffe, elephant, buffalo and ostrich as secondary hosts.

G. brevipalpis feeds mainly on hippopotamuses, suids, buffaloes and bushbuck.

G. palpalis, G. fuscipes and G. tachinoides feed extensively on man, crocodiles, lizards and bovids, the last species being particularly infested to man and cattle.

The behaviour of each species is characteristic and is not entirely dependant on the availability of different hosts; this view is supported by the fact that commonly occurring animals are not fed on by Glossina, the best example being zebra (Equus burchelli) in G. morsitans areas of East Africa, and waterbucks (Kobus sp.).

Few data are available about the adaptability of tsetse flies to a varying host fauna. It is likely that flies like G. morsitans s.l., the G. palpalis group and possibly G. swynnertoni and G. pallidipes would quickly adapt to changes in fauna. The anthropophily of G. palpalis and G. tachinoides increases when the wild fauna and the livestock decrease (Page & McDonald, 1959; Jordan et al., 1961 and 1962; Langridge et al., 1963). However some species with very restricted feeding habits, such as G. fuscipleuris, G. austeni and G. tabaniformis (infeodated to suids), G. longipalpis and G. fusca (infeodated to bushbuck and buffalo), and G. longipennis (rhinoceros, elephant, buffalo), may be very rapidly affected by the removal of only a few species.

### 3.3 Ecology

The subject has been recently reviewed by Langridge et al., (1963) and by Marley, (1963).

#### 3.3.1 Adult flies

Each species of tsetse fly has a specific distribution area, characterized by climate, vegetation and soil, this last element being important for larval deposit and pupal survival.

In each distribution area it is often possible to distinguish three zones (Mouchet et al., 1961):

the permanent breeding-sites, where flies occur all year round and where they congregate in unfavourable seasons, and usually where they lay larvae;

the temporary breeding-sites, where flies occur during the most favourable seasons, usually in the rainy season, but where they cannot survive in the dry season;

the feeding-grounds which are generally open areas, not very far from the breeding-sites, where flies can easily detect their hosts, and feed upon them; feeding-grounds can extend a few kilometres around breeding-sites, but are usually restricted to their immediate vicinity.

In each zone resting-places of the flies vary according to environmental conditions and physiological condition of the fly, but they are usually constituted by poles, small trunks and medium sized branches, up to some metres above the ground.

But some species, like G. swynnertoni and G. pallidipes rest extensively on leaves by night and on the underside of branches by day (Harley, 1960-1963). In wooded savannah areas some species of trees afford better resting-places than others and are regularly selected by the majority of flies.

### 3.3.2 Larvae and pupae

The depth to which the larvae enter the soil varies with environmental conditions; in the rainy season the larva can pupate almost on the ground or only one or two centimetres below. In the dry season the larva can enter five to eight centimetres below the ground before pupating.

The pupae cannot move and so are susceptible to wide variations of temperature and humidity. They can withstand high relative humidities but neither submersion by water nor dryness (Bursell, 1963). High temperatures reduce the length of pupal life, but too high temperatures can kill the pupae in some days and even some hours, and pupal sites are usually situated in well-shaded places, under logs, bushes, and so on.

For some species, as G. tachinoides and G. palpalis, breeding-sites can be entirely man-made, such as mango and banana plantations.

### 3.4 Tsetse fly survival and death-causes

Adults of Glossina have a high survival rate, in the laboratory as in nature; survival for 154 days has been observed in G. palpalis, and average lives of two to three months seem to be the rule. Flies can die from aging, but also from starvation, unfavourable environment changes, or be killed by predators (birds, spiders, insects) or, more rarely, by parasite fungus and protozoa.

Causes of mortality of larvae and pupae are more important because predators are numerous; insectivorous birds, insectivorous insects, ants, and so on. Many insects parasite tsetse pupae; Diptera bombylidae, Hymenoptera chalcididae and Mutillidae. Pupae are also much more easily killed by unfavourable environment changes than adult flies which can move away. In nature probably less than half the laid larvae reach the adult stage.

#### 4. TSETSE FLY CONTROL

In many instances tsetse control is a very efficient way to stop human trypanosomiasis transmission in restricted areas as a complement to chemotherapeutic measures, and tsetse control or eradication is often the cheapest method for preventing livestock trypanosomiasis transmission in cattle-grazing areas of Sudanese and Guinean savannah zones (Hocking et al., 1963).

Methods used for tsetse fly control just before and after the second World War are gradually being replaced by other ones based on residual insecticide applications, and chemosterilization is being investigated. But in the past direct destruction, indiscriminate and selective clearings, and hosts elimination have been extensively used, sometimes with fair success (Glover, 1961).

##### 4.1 Direct destruction of tsetse flies

Direct destruction of tsetse flies by net collection and glued baits has not been very promising in the past, except in Principe Island where G. palpalis was almost eradicated. Destruction by trapping (Harris traps) has been successful in controlling G. pallidipes in a restricted breeding area of Zululand, South Africa, but results have not been very satisfactory in other areas. Some authors, like Morris, (1960-1961) stress that traps give the best way for catching representative samples of flies, whereas others, like Abedi, (1963), consider traps as useless.

##### 4.2 Tsetse fly control by game destruction

It has been observed in the past that tsetse flies and game are often associated, and that game elimination, during rinderpest epidemics for example, are followed by strong reduction or even disappearance of Glossina populations. So game destruction has been used as a routine method of tsetse fly control in Eastern and South-Eastern Africa, and has succeeded in clearing many thousands of square kilometres of flies belonging to the morsitans group, the best known experiment being the Shinyanga one, in Tanganyika (Glasgow, 1960). The method was not cheap; for example in Southern Rhodesia, during the year 1955, slightly more than 41 000 head of game were destroyed by 800 paid hunters, with an expenditure of 107 000 rounds of ammunition (Chorley, 1956).

Judiciously applied game destruction can be an economical and practical means of trypanosomiasis control, as not only hosts of Glossina, but also animal reservoirs of trypanosomes are destroyed in only one operation. However, as stressed by Weitz, (1963) and by Glover, (1964), the palpalis group of tsetse flies cannot be starved except if reptiles and humans also are eradicated, and the control by starvation of many tsetse species (such as swynnertoni, austeni, fuscipleuris, tabaniformis, morsitans and submorsitans) supposes total elimination of suids, which constitute a group more difficult to locate and to kill than antelopes and big game. Besides, as underlined by Dasmann, (1962) and Hocking et al., (1963), game farming can be more profitable in some marginal areas than cattle-raising as a source of meat and skins and also for the tourist industry. So tsetse control by game destruction is almost entirely abandoned now.

#### 4.3 Tsetse fly control by bush clearing

Bushes and trees are widely used by tsetse flies as resting-places, but they are vital as shelters for pupae. Pupae can only survive if the soil is sufficiently shaded, protected from direct insolation and preserved from rapid variations of humidity and temperature.

The clearing of all woody vegetation in a fly-infested area has rarely been used for tsetse fly eradication, but has been extensively employed to provide barrier areas or to reduce the contact between flies and humans around villages and water holes, at river-crossings, and along the main routes of communication of humans and cattle (Le Rouzic, 1948). Such clearings, called "agronomical prophylaxis" in French-speaking countries, can be used for cultivation to be kept clear of trees and bushes. They cannot be extended on large areas in sparsely inhabited zones because they require a larger manpower supply than available, and are very costly if carried out by administrative agencies. However, for special purposes, clearings and protective barriers have been done up to 100 kilometres long and three kilometres wide, as in Southern Rhodesia.

Selective clearing has been much more extensively used for tsetse fly control. It is based on the tendency of flies, in unfavourable seasons, to concentrate in permanent breeding or resting sites that comprise identifiable plant communities and a comparatively small proportion of the bush or woodland as a whole. The requirements of the common tsetse fly vectors of trypanosomiasis have been described and the types



of vegetation most favourable as refuges are known. They must be located before tsetse fly control measures are undertaken. Selective clearing can be done directly, or by use of chemicals; it suffers from the same deficiencies as total clearing; it is a costly measure, the regrowth of bush must be kept down and it is much more efficient in dry areas than in humid ones.

In dry countries temporary control of riverine tsetse flies can be got by use of "obstructive clearing", by felling the trees forming the overhead canopy and blocking the stream-bed to obstruct the tsetse flight-line. The flies cannot move freely under shade and either are starved or forced into the open where the climate in the dry season is intolerable (Nash & Steiner, 1957).

With the discovery of modern insecticides it appears that it is very often more efficient to spray a residual toxicant on the tsetse permanent resting-sites than to destroy them, because tsetse can change resting-sites when the preferred ones are destroyed, but they do not abandon them after spraying (Hocking, 1964).

#### 4.4 Tsetse fly control by insecticides

Insecticides can be used as aerosols of temporary efficacy on huge areas, or as residual sprays on resting places, in traps and on baits.

##### 4.4.1 Insecticide aerosols

Insecticide aerosols have a very short residual effect and kill tsetse flies during some hours only after their application. They can control or eradicate the flies only if they are applied on large areas at convenient intervals to kill, before their reproduction, all flies emerged from pupae since the previous application. A convenient rhythm seems to be about eight applications at intervals of two to four weeks (Burnett, 1962b).

Aircraft application has the obvious advantage of covering large areas quickly, and can be efficient against savannah-inhabiting species like morsitans, swynnertoni and pallidipes; it is less adequate than ground application against riverine tsetse flies like palpalis (Burnett, 1962b), and is almost impossible to carry out against species living in high forest.

Ground application can be done either with lorry-carried generators, or with light generators, like Swingfog (Challier et al., 1964).

Insecticide aerosols can only be applied some hours a day, just after dawn and before dusk, and sometimes by night, when air currents are downwards; during other day-time periods the insecticide cloud disperses very rapidly and, if applied by aircraft, does not reach ground level. Only a very small amount of insecticide reaches each individual fly, and gravid females, less susceptible to insecticides than males and females of other physiological conditions (Burnett, 1962a), are not easily killed by chlorinated insecticides; some OP compounds like fenthion might perhaps be more efficient (Hocking et al., 1963).

For eradication programmes dieldrin and BHC aerosols have been used, mainly in East Africa, with variable results including fair success (Cockbill et al., 1963). The cost of such programmes was very heavy in the first experiments, but has decreased with technical improvements and better knowledge of tsetse ecology, and is now around 800 to 2000 French francs per km<sup>2</sup> (Burnett, 1962; Hocking et al., 1963; Burnett et al., 1964). The cost of operations can be reduced if aerosols are used only for short-term control of tsetse flies in sleeping-sickness foci.

#### 4.4.2 Residual treatment of vegetation

Residual treatment of tsetse fly resting-places must be lethal for the fly on short contact for a longer period than the maximum duration of the pupal life. In such conditions only one spraying may be sufficient to control the species, and perhaps eradicate it, in an isolated area.

The first residual applications have been done against riverine species, like palpalis and fuscipes, with habitats restricted to water edge. In larger gallery forests it is sometimes possible to open paths in the forest, which will be extensively used by moving flies, and to treat them for controlling flies. DDT suspensions and emulsions, which have been used in the first experiments, have usually been replaced by dieldrin emulsions, which are assumed to be efficient almost one year, and sometimes more than one year if applied at 4% (Kernaghan, 1962). However, according to Baldry (1963 and 1964), DDT emulsions have a longer residual effect than dieldrin and telodrin (= isobenzan) when applied at the concentration of 5% and even, in some

conditions, at lower concentrations. Such control procedures are five to 10 times cheaper than bush clearing and of a more permanent effect (Hocking, 1963; Challier, 1965a; MacLennan & Aitchison, 1963).

Improvement on the knowledge of tsetse fly resting-places has permitted the use of residual insecticides against savannah species like G. morsitans and G. swynnertoni, by selective spraying of the lower side of the branches of Acacia trees in fly-concentration areas (Hocking, 1961; Chadwick, 1964; Chadwick et al., 1964). The cost of the control is similar to or lower than by aircraft fogging but the work is more difficult to supervise.

Residual insecticides have been used also against G. tachinoides in Northern Nigeria, and along Tchad-Cameroon border, but that fly is not as concentrated as palpalis along water-places, and trees and bushes must be treated on a large width on both sides of the rivers and water holes (Mouchet et al., 1961). They have also been used with fair success against G. fusca and G. fuscipes in large gallery forests of the Centrafrican Republic (Finelle et al., 1962 and 1963; Yvone et al., 1962).

Tsetse fly control by residual insecticides has not been carried out against high forest species and is only promising when the fly habitats are restricted.

#### 4.4.3 Insecticide treated traps and baits

Residual insecticides have been sprayed inside tsetse fly traps to increase their efficacy with limited results. Insecticides have also been used in combination with attractants, on traps, and the method is always under investigation. Cattle constitute natural attractants and both systematic and residual conventional insecticides applied to cattle are under experimentation for killing tsetse flies in restricted areas where wild game is scarce or absent.

#### 4.5 Biological control

Various attempts have been made in the past to multiply and release natural tsetse fly parasites (Jenkins, 1964) to control these flies, but the results have not been promising.

Trials on hybridization by cross-mating closely related species to produce a high degree of sterility in a fly population have not been successful (Glasgow, 1960) and assume the possibility of raising large numbers of tsetse flies.

Sterilization of flies is possible, either by radiation or with chemosterilants. (Knipling, 1963; Smith & Dame, 1963) and field and laboratory investigations have been carried out. Tsetse fly males sterilized by gamma irradiation are not competitive with normal males, the sterilizing doses being nearly the same as the lethal ones (Potts, 1964). Chemosterilants are not much more promising; the treatment of males alone reduces only by 40% the average number of produced pupae; the treatment of females is more efficient but it seems difficult to treat the female component of wild tsetse fly populations; the survival rate of treated individuals is considerably reduced (Chadwick, 1964). If an efficient control method by chemosterilants is discovered the problem of laboratory mass-rearing of tsetse flies would have to be solved, and will not be an easy task (Maillot, 1958; Nash, 1963; Evens, 1964).

## 5. DISCUSSION AND CONCLUSIONS

Several methods are available for controlling tsetse flies, but all are expensive and assume a good knowledge of the physiology and ecology of the species to assume control under the local conditions. No method is yet available for densely forested areas.

Surveys show that where human population density reaches 40 inhabitants per km<sup>2</sup> their animal hosts disappear, and their resting places are cleared; in such conditions tsetse fly vectors of animal trypanosomiasis are usually no longer a problem (Ford, 1962) (except if "holy woodlands" occur, like in the Mossi country of West Africa, but such woodlands can be easily cleared from tsetse flies by insecticides). Riverine species of Glossina, which transmit mainly human sleeping-sickness caused by T. gambiense, can survive along rivers but are very easily controlled in such restricted habitats. When human density is below 40 inhabitants per km<sup>2</sup> tsetse fly control becomes more and more difficult and costly with the scarcity of inhabitants. Despite our technical ability to combat tsetse flies, it is still not worthwhile to undertake large reclamation schemes except in special instances, where soils and climate are favourable to intensive agriculture as in the Lubu valley of Southern Rhodesia (Cockbill et al., 1963) repopulated by inhabitants from the part of the Zambezi valley flooded by the Kariba Dam, when public health is involved such as in residual foci of sleeping-sickness (Morris, 1962), or to protect cattle during seasonal migrations (Finelle et al., 1962-1963). In other situations insufficient exploitation of the country will permit tsetse flies to repopulate the cleared areas sooner or later and the resources employed for tsetse fly control will have been wasted.

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