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Biology and Control of Tsetse Flies (1)

by

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Biology and Control of Tsetse Flies

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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 & al.,1963 - WILSON & al., - 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. During the same period spreading possibilities of the disease have increased through communication improvements and development of workers migrations between neighbouring countries (ABEDI & MILLER, 1964).

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 even appear in previously cleared areas. The situation is slightly / ...

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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 .

2. GEOGRAPHIC DISTRIBUTION OF TSETSE FLIES .

Glossina sp. infest about 10.000.000 km^2 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 MAILLOT (1952), RAGEAU & ADAM (1953), RICKENBACH (1961) and FINELLE & al.(1963). Tsetse fly distribution is not entirely stable, even in absence of man interference. For example several species retreated from large areas of south-east Africa during the Great Rinderpest of 1896, and since this period G.pallidipes and G. morsitans, followed by G.austeni, move slowly south in Mozambique and Rhodesia, restoring the situation prior to the rinderpest.
In West Africa, during the last 15 years, G.submorsitans has extended northwards its distribution (WILSON, 1958). Such changes in distribution are probably of common occurence, but escape detection by lack of accurate base data and surveys .

Tsetse flies are classified into three groups, typified respectively by G.palpalis, G.morsitans and G.fusca; their distributions are the following ones :

2.1. Glossina 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 in the South-east of the Arabian peninsula. It 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. In the savannahs they are restricted to the immediate vicinity of rivers and rivulets. In forested areas also they congregate along watercourses, but not as strictly as in savannah, using them more for the flight linesthat they effer than for their microclimate.

G.pallicera occurs in rain forest areas, but can be encountered sometimes in the gallery forests of the guinean savannah .

G.caliginosa is restricted to the coastal rain forest and to the mangrove areas .

G.tachinoides, G.palpalis and G.fuscipes are the main vectors of the human sleeping-sickness caused by T.gambiense .

2.2. G.morsitans group .

The morsitans group includes seven species and three subspecies, 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 and to some partly deforested areas of the forest zone of West Africa .

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

G.swynnertoni and G.pallidipes aro highland species of East Africa. The first one is restricted to Kenya and Tanzania. The second species occurs from Ethiopia to Mozambique and is present in some coastal areas; it has occured in the past in Natal but has been eradicated there .

G.borgesi has been recently described from Mozambique (PIRES, 1960).

G.morsitans and G.swynnertoni are the normal vectors of the normal vectors of the second form of human sleeping-sickness, caused by T.rhodesiense; they are also, with G.pallidipes and G.submorsitans very important vectors of several animal trypanosomiasis (caused by T.brucei, T.vivax, T.congolense) . T.rhodesiense has been also recevered from G.pallidipes since 1940 (MacKICHAN, 1944) and more recently from G.fuscipes (SOUTHON & ROBERTSON, 1961 - WILLETT & Al.,1964- WILLETT, 1965) .

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 in some of the larger gallery forests of the guinean savannah .

G.nigrofusca 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 the Upper guinean savannah and forest .

G.brevipalpis is very widespread in gallery forests and savannahs of Mali 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 .

The most common species belonging to the fusca group are important vectors of animal trypanosomiasis caused by T.vivax and T.congolense (JORDAN,1961 & 1965 a).

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 probably some females do the same; recent investigations carried out in Upper Volta by one of us (A.C.) on G.palpalis have shown that non-teneral wild caught females are almost always inseminated; however the percentage of inseminated females with incompletely filled spermathecae reaches about 80% amongst teneral flies, against only 51% in flies belonging to the next two older age groups; so it is very probable that females of G.palpalis mate several times during their first days of life. Females present their maximum attractiveness for males when they are only 3 days old, and are less attractive with increasing age, although being always able to mate (NASH,1955

JORDAN, 1958.).
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, 1963 b). The first ovulation occurs 8 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 usually two to five centimeters below the surface, some hours later. Larval development, in utero, takes about 10 days, during which the females bites at least three times, but the first larva is laid when the female is about 16 days old, or moro. 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. They can feed on insects, as one of us (J.R.) has observed for G.palpalis with caterpillars .

Each species of tsetse fly exhibits definite feeding preferences, which are directly related to their medical and veterinary importance as pathogen vectors (JORDAN, 1965 a), but the majority of Glossina sp. are able to feed on a great variety of vertebrates. The kmown trophic preferences are the following (WEITZ, 1963 a), according to 22.640 blood meals identified :

- G.swynnertoni, G.austeni, G.fuscipleuris and G.tabaniformis feed mainly on suids, with bovids and other vertebrate (rhinoceros, hippotamus, porcupine) as secondary hosts ;
- G.morsitans and G.submorsitans feed equally on suids and bovids, warthog (Phacochoerus sp.) being the preferred host; man is also used

as host, mainly in West Africa by *G.submorsitans* (Jordan, 1965 b);

- *G.pallidipes*, *G.fusca* and *G.longipennis* 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 hippopotamus, suids, buffale and bushbuck ;
- *G.palpalis*, *G.fuscipes* and *G.tachinoides* feed extensively on man, crocodiles, monitor lizards and bovids, but also sometimes on wild game (FOSTER, 1964); *G.tachinoides* is particulary infeodated to man and cattle .

The behaviour of each species is characteristic and is not entirely dependent on the availability of different hosts; this view is supported by the fact that commonly occuring 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.*) (WEITZ, 1963 b).

Few data are available about the adaptability of tsetse flies to a varying host fauna. It is likely that flies like *G.morsitans* and *G.submorsitans*, the *G.palpalis* group and possibly *G.swynnertoni* and *G.pallidipes*, would quickly adapt to changes in fauna; however, following the rinderpest panzootio of 1890-1896 the *G.morsitans* fly-belts have recessed in East Africa, after almost extermination of all favourable hosts (FORD, 1965). The authropophily of *G.palpalis* and cf *G.tachinoides* increases when the wild fauna and the livestock decrease (PAGE & MACDONALD, 1959 - JORDAN & al., 1961 & 1962 - LANGRIDGE & al., 1963). Several 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* (feeding on rhinoceros, elephant and buffalo), may be very rapidly affected by the removal of only a few species.

3.3. Ecology .

Tsetse fly ecology and its physiological basis have been recently reviewed (LANGRIDGE & al., 1963 - HARLEY, 1963 a-BURSELL, 1959, 1960 & 1963) and have been the subject in a recent past of many publications, each of them generally devoted to one or two Glossina species .

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. The recent studies of BURSELL (see above) have clearly shown that one of the major limiting factors for the distribution of many species of tsetse flies is the relative humidity. Adults, which fly and can select their resting-places, can withstand low relative humidities of the general environment, but pupae of many species cannot, and the distribution is under the dependence of the pupal envelop permeability. The pupae of some species, such as those of morsitans, do not lose any water within dry soils, whereas pupae of several other species, such as palpalis, are easily killed by cessication and require for their development an almost saturated atmosphere, but without any free water. Temperature may play a part in limiting the distribution, but mainly in extreme conditions .

At least in the savannah zones, it is often possible to distinguish, in the distribution area of each species, three areas (NASH & PAGE, 1953 - PAGE, 1961 a - MOUCHET & al., 1961 - JACKSON, 1945).

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

- the temporary breeding-sites, where flies occur during the most favourable seasons, usually during 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 kilometers around breeding-sites in rainy season, but are usually restricted to their immediate vicinity during the dry season .

In each area resting-places of the flies vary according to environment and to physiological condition of the fly, but they are usually constituted by logs, small trunks and medium-sized branches, up to some meters above the ground. However 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 a). In wooded savannah areas some species of trees afford better resting-places than others and are regularly selected by the majority of flies.

Tsetse flies are generall active only by day time, but some species of the fusca group are also active by night and G.brevipalpis exhibits a very characteristic crepuscular activity, immediately after sunset and immediately before sunrise (HARLEY, 1965 b). G. palpalis and G.submorsitans bite also sometimes by night when disturbed from their resting places (J.H.,personal observation).

Pupal sites are selected by female tsetse flies and, for a same species and within the same area, their location and relative importance vary from season to season (NASH & PAGE, 1953 - GLASGOW, 1961 - JORDAN, 1965 b). Pupae can withstand high relative humidities but not submersion; high temperatures reduce the length of the pupal period, but too high temperatures can kill the pupae in some days and even some hours; so pupal sites are usually situated in well-shades places, under logs, bushes, in hollow trunks, and so on. For some species, such as G.tachinoides and G.palpalis, pupalsites can be entirely man-made, being provided by mango and banana plantations and even sometimes by granaries, thatch enclosures and other artificial shelters. The depth to which the larvae enter the soil varies with environmental conditions; in the rainy season the larva can pupate on the ground, or only one or two centimetres below; in the dry seasons the larva can enter five to eigth centimtres below the ground before pupating .

3.4. Tsetse fly survival and population dynamics .

Except for their first days of imaginal life, during which the mortality rate is high (NASH & PAGE, 1953 - NASH & KERNAGHAN,1965- A.C. personal observation), adults of Glossina have a high survival rate, in the laboratory as in nature. Average life of two to three months seems to be the rule (HARLEY, 1963 b & 1965 a) and survival for 154 days has been observed in G.palpalis; howerver a very small proportion of the population is likely to achieve such extreme age (NASH & PAGE, 1953) .

Causes of mortality of larvae and pupae are more important because predators are numerous : insectivorous birds, insectivorous insects, and so on; besides many insects parasite tsetse pupae :Diptera Bombylidae, Hymenoptera Chalcididae and Mutillidae. Pupae are also easily killed by unfavourable environment changes. In nature probably less than half the laid larvae reach the adult stage .

Tsetse fly densities do not fluctuate very much from one year to another, as long as the environmental conditions romain constant. G.swynnertoni has been studied during 23 consecutive years in Shinyanga area, Tanzania, during which the highest density value has been 18 times the lowest one. G.palpalis, which has been studied during 16 years in Kaduna area, Nigeria, has even more stable populations in riverine forests, where the highest recorded density was only 3,8 times the lowest one (GLASGOW & WELCH, 1962 - JORDAN,1965 c).

3.5. Sampling methods .

The sampling methods used must be related to the local conditions and to the investigated species.

The most widespread method is based on fly rounds, the fly-catchers moving along standard paths under normalized conditions throu the district under investigations; results are expressed in fly per unit of length of the paths. The bait can be human beings (if so usually the fly-catchers themselves) or a domestic animal, or even a car moving at a very low speed. Catches during fly rounds can also be carried out on resting flies .

Fixed catching stations, used during the whole activity period of the flies (so generally from dawn to dusk) are also widely use baits being humans , or tethered animals, or specially designed traps.

Moving teams collect mainly unfed hungry flies on the baits, with a large excess of males, and engorged and not-hungry flies on their resting places. Standing teams collect a higher proportion of females, mainly when using traps. Moving car baits are sometimes very efficient for attracting non-man-biting species .

Very low densities of tsetse flies are always difficult to assess and may even escape entirely to detection .

4. TSETSE FLY CONTROL .

In many instances tsetse control is a very efficient way to stop human trypanosomiasis transmission in restricted areas, either alone or as a complement to chemotherapic measures. Tsetse fly control or better, eradication, is often the cheapest method for preventing human or livestock trypanosomiasis transmission in areas of Sudanese and Guinean savannah zones (HOCKING & 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 insecticides 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 efficient 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) and FOSTER (1964), consider traps as very inferior to direct catches. Results depends certainly on the species involved and on the environmental conditions .

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 epizootics for example, are followed by strong reduction or even disappearance of Glossina populations (GLASGOW & WELCH, 1962 - WOOFF,1965). So game destruction has been used as a routine method for 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 Tanzania (GLASGOW, 1960). This method, which is always used in some restricted areas, is not cheap; for exemple in Southern

Rhodesia, during the year 1955, slightly more than 41.000 heads of game were destroyed by 800 paid hunters, with au 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 Glossina hosts, 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 are also eradicated, and the control by starvation of many species, such as G.swynnertoni, G.austeni, G.fuscipleuris, G. tabaniformis, G.morsitans and G.submorsitans, supposes total elimination of suids which consitute a group more difficult to locate and to kill than antelopes and big game. Besides, as underlined by DASMANN (1962) and by HOCKING & 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 more and more rarely used now .

4.3. Tsetse fly control by bush clearing .

The tsetse ability to withstand seasonally unfavourable climate depends upon the presence of a favourable vegetation community (NASH,1933). Bushes and trees are widely used by tsetse flies as resting-places; moreover they provide a more or less constant microclimate ensuring the survival of at least a few females even through the most severe dry seasons (NASH & PAGE,1953); they constitute also very often vital shelters for pupae which can only survive if the soil is sufficiently shaded, protected from direct insolation and preserved from rapid variations of humidity and temperature. Man cannot easily alter the climate but he can, at least in savannah areas, alter the vegetation communities that enable the tsetse flies to withstand unfavourable periods of the year .

The clearing of all woody vegetation in a fly-infested area has rarely been used for tsetse fly exadication, 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 congregate 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 the use of chemicals (defoliants, tree-toxicants...); 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 where it does not prevent tsetse flies of travelling and resting (PAGE, 1961 b- FOSTER, 1964).

In dry countries temporary control of riverine tsetse flies has been attempted once 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 could not move freely under shade and either were starved or forced into the open where the climate during the dry season was intelerable (NASH & STEINER, 1957).

With the discovery of modern insecticides it appears that it is generally more efficient to spray a residual toxicant on the tsetse permanent resting-sites than to destroy them, because tsetse can change of resting-sites when the preferred ones are destroyed, as seen in Ankole district of Uganda (HARLEY & PILSON,1961), whereas they do not abandon them after spraving (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, traps and baits.

4.4.1. Insecticide aerosols .

Insecticide aerosols have a very short residual effect, if any at all, 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 having emerged from pupae since the previous applications. A convenient rhythm seem to be about six to eight applications at intervals of two to four weeks (BURNETT, 1962 b), according to the biology of the local population of tsetse flies .

Aircraft application has the obvious advantage of covering quickly large areas, and can be efficient against savannah-inhabiting species like G.morsitans, G.swynnertoni and G.pallidipes; it is less adequate than ground application against riverine tsetse flies like G.palpalis and G.fuscipes (BURNETT, 1962 b), 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 portable mist-blowers (THOMSON & al., 1960 - CHALLIER & 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 even 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, 1962 a), are not easily killed by chlorinated insecticides; some O.P. compounds like fenthion or malathion might perhaps be more efficient (HOCKING & al., 1963) .

For eradication programmes dieldrin, B.H.C. and telodrin aerosols have been used mainly in East Africa, with variable results including fair succes (COCKBILL & al., 1963 - BUICKX, 1965). Technical improvements in the spraying-designs have permitted to use only very small amounts of insecticides, averaging 1,5 kg. of telodrin, or 4,5kg. of dieldrin per square kilometre. These technical improvements and a better knowledge of tsetse ecology have decreased the cost of such programmes, which was very heavy for the first experiments, to around 800 to 2.000 french francs per sq.kilometre now (BURNETT, 1962 - HOCKING & al., 1963 - BURNETT & al., 1964). The cost of operations can be reduced if aerosols are used only for short term control of tsetse fly populations 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 G.palpalis and G.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; the treatment of such paths may be sufficient to get the control of the flies. The same observations have been made in dense bush, where several species, such as G.morsitans and G.palpalis, frequent paths made by man and animals and follow avenues and channels occuring through the bush; concentrations of the flies occur at the intersections of the paths; the corresponding method of tsetse control is based on the opening of parallel paths, some hundreds of metres apart, through dense thickets and wooded areas, and by treating nothing but the paths; this method has been fairly successful in several areas of Kenya, against G.pallidipes, G.fuscipes, and G.brovipalpis (THOMSON & al., 1960) .

DDT suspensions and emulsions, which have been used in the first expériments, 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 & 1964), DDT emulsions have a longer residual effect than dieldrin and telodrin (=isobenzan) ones when applied at the concentration of 5% and even, in some conditions, at concentrations as low as 2,5% (DAVIES, 1964). Such control procedures are five to ten times cheaper than bush clearing and of a more permanent effect (HOCKING, 1963 - MacLENNAN & AITCHISON, 1963 - CHALLIER, 1965 a) .

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 trecs in fly-concentration areas (HOCKING, 1961 - CHADWICK, 1964 - CHADWICK & al., 1964 - WOOFF, 1965). The cost of the control is then similar to, or lower than, by aircraft fogging, but the work is more difficult to plan and supervise. In the dry season G.submorsitans behave sometimes almost like a riverine species and can be controlled by restricted insecticide sprayings (MACLENNAN, 1965 - TEMPLETON, 1965 - JORDAN, 1965).

Residual insecticides have been used also against G.tachinoides in Northern Nigeria and along the Tchad-Cameroons border, but this fly is not as concentrated as G.palpalis along water-places; so trees and bushes must be treated on a larger width on both sides of the rivers and water-holes (MOUCHET & al., 1961 - DAVIES, 1964 - MacLENNAN, 1965 - TEMPLETON,1965). With this species the main difficulty is the exact selection of the vegetal communities to be sprayed, which implies a very close supervision of the spraying-teams, and the accurate timing of the programme, between the end of floods and the beginning of the rains, for the breeding-sites neighbouring the Chad Lake .

Residual insecticides are only promising when tsetse fly habitats are restricted, so they have not been used against high forest species. However they have been sprayed with fair success againts G.fusca and G.fuscipes in large gallery forests of the Centrafrican Republic (FINELLE & al.,1962 & 1963 - YVORE & al., 1962) .

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,an the method is always under investigation. Studies carried out in Aruscha, Tanzania, have shown that aqueous extracts of pig skins and bristles are very attractive for G.pallidipes, but not for G.swynnertoni; the active principle is soluble in lipid solvents; traps treated with this attractant catch two times more Gl.pallidipes that untreated ones and could be used in combination with either insecticides or chemosterilants (ANONYMOUS, 1965) .

4.5. Biological control .

Various attemps 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. The publieshed results are partly contradictory. According to POTTS (1964),males sterilized by gamma irradiation are not competitive with normal males, the sterilizing doses being nearly the same as the lethal ones; however DAME & al. (1965) have found the radiosterilized males very competitive, and having a normal survival rate during their first three weeks of life. CHADWICK (1964) has stressed that chomosterilants are not much more promising than radiations; in his experiments the treatment of males alone reduces only by 40% the average number of produced pupae, and the survival rate of treated males was considerably reduced; the treatment of females was more efficient, but it seems difficult to reach the female component of wild tsetse fly populations. Nevertheless DAME & al. (1965) have published that Tepa - and Metepa-treated males are almost all sterile and that their survival rate is almost normal, the chemicals being applied either on young males or on pupae. If an efficient control method involving chemosterilant use is discovered, the problem of laboratory massrearing of tsetse flies would have to be solved, which will not be an easy task (MAILLOT, 1958 - NASH, 1963 - EVENS, 1964); wide scale experiments are carried out in South Rhodesia to develop more efficient methods of tsetse mass-rearing than these actualy available .

6. REARING PROBLEMS AND RESEARCH NEEDS .

All tsetse fly control methods suppose a very thorough knowledge of the physiology and ecology of the involved species. Moreover, if chemosterilants are promising mass-rearing technics and mating-habits must be studied. Improvement of our knowledge on the biology and ecology of tsetse flies requires mass marking, release and recapture experiments which also imply mass-rearing of standard specimens .

The reproduction rate of Glossina is very low. For example G.morsitans drops a larva every eigth day at 30°C., every eleventh day at 24° and every twentyfifth day at 18° (JACK,1939). The best climatic conditions, for Glossina colonies have been defined by MELLANEY (1937);temperature must be maintained between 25° and 27°C. for almost all species; relative humidity must be high, reaching almost saturation for the riverine species, such as G.palpalis. The maintenance of adults has been done in several types of centainers, including testtubes (FOSTER, 1957), but for massrearing cages are more handable;

Bruce's and Roubaud's small-sized cages have been used as well as bigger Petana's cage. Preliminary trials carried out by one of us (A.C.) have shown that environmental conditions such as lighting, shape and volume of the cages, and fly population density, may be of a primary importance to ensure normal longevity, behaviour and reproduction rate.

High insemination rates may be obtained in colonies, reaching 97% for G.morsitans (FOSTER, 1957) and 88% for G.palpalis (NASH, 1955), but the sterile-male method shall require also a perfect knowledge of the mating behaviour. Some data are already available for G.morsitans and G.palpalis (FOSTER, 1957 - NASH,1955-JORDAN 1958), but several other economically important Glossina species have not been studied yet.

Feeding the adult flies is a very important problem. Too frequent blood meals bring on the production of small larvae and induce abortion;the normal frequency of feeding is two or three times between two successive larvipositions. Guinea pigs have been used as hosts for a long time, but sheep is a better host, ensuring a better longevity and a high reproduction rate of the female flies, and now goats are also used with success (NASH & KERNAGHAN, 1964). Repeated tsetse fly biting brings out a skin reaction of the hosts; however NASH & KERNAGHAN (1965) have developed a method allowing to feed 400 flies every three days on the same goat. Investigations are also carried out involving the replacement of the host by defibrinated blood, tsetse flies feeding through a membrane (SOUTHON & COCKING,1963 a & 1963 b, KIMBER & HARLEY,1965). We may hope that improvements of the feeding procedures will enable the production of larvae and pupae of normal weight, without any high mortality of the newly emerged flies, which is not always the case in tsetse fly laboratory colonies (NASH & KERNAGHAN, 1965).

Emergence rate from the pupae is also an important factor in the establishment of a Glossina colony. A very high rate has been obtained when larviposition occurs in a layer of dry sand just over wet sand (NASH & al., 1950), for G.palpalis, but the problem has to be solved for the other species.

7. DISCUSSION AND CONCLUSIONS .

Several methods are available for controlling tsetse flies, but all are expensive and none of them is yet available for densely forested areas. Besides tsetse flies can reinvade cleared areas if these areas are not isolated from neighbouring tsetse foci, either by natural barriers or by sprayed ones. Tsetse fly control, thereforo, must be planned as a long term programme, on as a wide territorial basis as possible. In many instances eradication is cheaper than control, on a long range, the new treated areas protecting the previously treated ones .

Surveys show that where human population density reaches 40 inhabitants per km^2 the animal hosts of tsetse flies belonging to the *fusca* and *morsitans* groups disappear, and most of the *Glossina* 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 contry of West Africa; but such woodlands can be easily cleared from *Glossina* 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 par km^2 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 (COCKBILL & al.,1963), or when public health is involved such as in residual foci of sleeping-sickness (MORRIS,1962), or for protection of cattle during seasonal migrations (FINELLE & 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 ressources employed for tsetse fly control will have been wasted .

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