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A Review of Recent Knowledge on the Relationship Between the Tsetse Fly and Its Vertebrate Hosts

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P. E. GLOVER

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by

P. E. GLOVER

Tanzania National Parks

ABSTRACT

In this review the relationships between the tsetse fly, its vertebrate hosts and pathogenic trypanosomes are considered.

The senses by which the fly finds and feeds upon its host are discussed. Sight and scent are the major factors involved but sound, touch and taste also play a part. Hunger and movement are important in that the former induces the fly to look for food and the latter acts as an attractant. Tsetse flies are not always attracted to moving objects because they are hungry but often because of a desire to mate or explore large objects which may result in their being passively transported over long distances.

The resting habits of different species of flies are considered and the animals upon which they feed. *G. palpalis* and *G. tachinoides* feed partly on reptiles; most of the other flies favour the *Suidae* and bovids. *G. morsitans* and *G. swynnertoni*, which live in game country, possess habits closely adapted to game animals, especially some of the larger bovids and the *Suidae*.

Trypanosome infection rates in the fly and its hosts are discussed. *T. gambiense* and *T. rhodesiense* are the parasites pathogenic to man. The evidence that wild ungulates can be the reservoirs of *T. rhodesiense* is examined. One of the anomalies of the epidemiology of Gambian sleeping sickness is that it appears to bear little relation to density of fly infestation and the more severe epidemics may occur in regions where fly populations are relatively low. The most important trypanosomes infecting cattle are *T. congolense* and *T. vivax* but *T. brucei* is strongly pathogenic to horses, donkeys and dogs and *T. simiae* and *T. suis* to pigs.

The most effective methods of trypanosomiasis control are drug treatment, bush clearing and the use of insecticides. All of these have limitations but spectacular results have recently been achieved with insecticides in East and West Africa.

The effects of rinderpest epizootics seem to have played a part in convincing field workers that game destruction is a practical means of exterminating tsetse flies. Apparently dramatic results have been obtained with this method in Southern Rhodesia, Uganda and elsewhere but there is no definite evidence that complete extermination of the fly as a result of game destruction has ever been achieved except theoretically in one scientific experiment in Tanganyika, because there is no quick and precise method of determining whether the flies themselves have been eradicated except over a long period of time. In addition, it has been demonstrated that the *Suidae* and some of

the smaller antelope which are favoured hosts of most tsetse flies, are virtually impossible to exterminate. There is therefore no justification for game destruction as a practical method for tsetse control.

Modern trends in tsetse and trypanosomiasis research indicate that scent attractants may prove valuable in assisting to locate tsetse flies when they exist in small numbers and chemo-sterilants and radio-active substances may have some practical application. The use of insecticides, however, seems to be the most effective method available at present. The field of immunology offers some enticing approaches, such as breeding animals tolerant to trypanosomiasis or even producing a method of immunization.

The social and economic aspects of the trypanosomiasis problem cannot be ignored, for so far no practical method of enforcing proper land use after tsetse reclamation has been evolved. This is because of faulty agricultural advice, ineffective administration, or apathy and unwillingness to co-operate on the part of the people.

In spite of the fact that a quarter of the African continent is denied to domestic stock by the presence of trypanosomiasis, the importance of game as a reservoir of pathogenic trypanosomes is negligible compared with over-population and the destruction of the land, which are the greatest problems facing " emergent " Africa today.

In conclusion, the hope is expressed that the interests of politics will not continue to influence the progress of science to the point of no return.

A REVIEW OF THE RECENT KNOWLEDGE ON THE RELATIONSHIPS BETWEEN THE TSETSE FLY AND ITS VERTEBRATE HOSTS

by

P. E. GLOVER
Tanganyika National Parks

INTRODUCTION

The relationships of the vertebrate host and tsetse fly cover a very wide range of inter-related facets, including man and his domestic animals.

The relationship of wild vertebrate animals to tsetse flies is three-dimensional in that wild animals supply the natural food of the fly and at the same time they harbour in their blood pathogenic trypanosomes, which in turn affect the fly and are then transmitted by the fly to man and his domestic animals and/or back to the wild host.

Vertebrate animals and *Glossina* have long been associated. Lamprecht (1964) thought " Exposure to and invasion by parasitic organisms may play an important part among many other intrinsic factors that guide the evolution of animal forms." Miocene fossil remains of tsetse flies were found in Colorado in the U.S.A. (Cockerell 1907), indicating that tsetse flies must once have been much more widely distributed than they are today. The antiquity of this association is further indicated by the fact that some trypanosomes have become almost entirely dependent on tsetse flies for their transmission. They can live indefinitely in the salivary glands and proboscis of the fly and even undergo metacyclic changes in its gut.

Hornby (1953) observed that much work was required to be done to clear up many points in connection with the natural resistance of wild vertebrates to trypanosomiasis but he goes on to say that with the larger game animals there is not much mystery, for to survive as they have done, they must have a high natural resistance. It would seem, however, that the mystery really lies in the fact that most wild animals have never acquired a " solid " immunity but only a premunity; " a term first suggested by Sergent to cover conditions of non-sterile immunity."

Why have these animals, after all these eons of time, not acquired a true immunity ? If the immunologists could solve this problem it might open the way to a new approach (Soltys 1963). Perhaps the solution lies in quite a different direction. "Active immunisation remains virtually an unachieved goal in protozoal disease. Nevertheless, it is a fact that drug treatment of any disease becomes a poor second-best once immunisation is possible" (Willett 1960a).

Hornby (1953) further stated that the examination of a number of blood smears of elephant and hippopotamus suggested that these animals were not important carriers of trypanosomiasis. On the other hand, it is well known that hippopotomus is a source of food to flies of the *G. palpalis* group and elephant are attractive to flies of the *G. morsitans* group. The absence of trypanosomes in the peripheral blood of wild animals does not necessarily imply that they are not infected, as instances have occurred where trypanosomes have been seen in the blood of elephant and rhinoceros in captivity several days after they have been caught. This indicates that stress may cause trypanosomes to appear in the peripheral blood in animals which have at first appeared to be uninfected.

One curious anomaly has been brought to light by recent work. Waterbuck and some of the plains game such as kongoni and wildebeest, have been found, sometimes frequently, to have pathogenic trypanosomes in their blood (Fairbairn 1948; Hornby, 1953, quoting Kinghorn and Yorke, 1912, in Northern Rhodesia; and Ashcroft, 1959a, in Tanganyika).

However, Langridge (1960a), and Weitz (1963), shewed that waterbuck and plains game were seldom fed on by any tsetse flies. For example, though waterbuck was one of the commonest animals in an area in Kenya where *G. longipennis* Corti, *G. brevipalpis* Newstead and *G. pallidipes* Austen were numerous, no feeds on this animal were recorded from *G. longipennis* and *G. brevipalpis* and only one from *G. pallidipes*.

An important economic fact in host-fly relationships is that some tsetse flies, for example *G. palpalis* (R.-D.) and *G. tachinoides* Westwood in West Africa, can exist in the total absence of wild vertebrate animals, living entirely on the blood of man and his domestic stock (Nash 1948; Baldry 1964). Recently in Kenya, *G. fuscipes fuscipes* Newstead = (*G. palpalis fuscipes* Newstead), which is normally a lake-side or riverine fly confined to the western part of the country, has begun to move away from its normal habitat to bush conditions and even to living in the "peri-domestic vegetation of homesteads and animal sheds" in the densely populated country of Central Nyanza. Here there is little or no game and few other wild vertebrates exist.

It can be seen, therefore, that the factors involved in vertebrate host-fly relationships are not only numerous but very complex.

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FACTORS AFFECTING HOST-FLY RELATIONSHIPS
FINDING THE HOST

According to van den Berghe and Lamprecht (1963) " the survival of the tsetse fly depends on its ability to maintain the intersection of the three life lines : climate, food and vegetation. Its behaviour is in direct relation to this struggle. The variables by which the biological equilibrium can be maintained explains differences in behaviour of the same species of flies in different places . . .".

Sight

There is abundant evidence to shew that tsetse flies are attracted by moving objects and that sight is important in guiding them to their hosts. Nash (1930), working in Tanganyika, shewed that *G. morsitans* Westwood released with their eyes painted over were never recovered, whereas a large proportion of flies released with their antennae painted were recaptured.

H. M. Lloyd (1935) and Swynnerton (1936) demonstrated the importance of sight to *G. swynnertoni* Austen, *G. pallidipes G. morsitans* and *G. palpalis* (*G. fuscipes*). They also shewed that more female flies were attracted to a moving screen than males.

Napier Bax (1937) observed that *G. swynnertoni* could see moving oxen up to a distance of 465 feet in bright light but it could not detect them at 600 feet. Moggridge (1936) noted that *G. swynnertoni* would fly out over distances of 100 to 300 yards to visit a group of men and oxen and Swynnerton (1936), observed that although *G. pallidipes* spends most of its time in thickets, it gave him the " impression of being a bold, independent rover."

Harris (1932 and 1938) constructed his famous trap on the principle that *G. pallidipes* reacts in some way to changing light and shade in the bush. Barrass (1960) found that tsetse flies preferred to settle on the sunny sides of screens rather than on the shady sides and that the attractiveness of the striped black and white screen progressively decreased as the width of the white stripes was increased.

Nevertheless, very little intensive work seems to have been carried out on the perception of colour by tsetse flies and none to indicate conclusively that they possess a sense of colour. Although de Costa et al (1915), Simpson (1918), Fuller and Mossop (1929), H. M. Lloyd (1935) and Moggridge (1936) recorded the number of flies settling on cloth and oxen of different colours, they could only shew that they were more attracted to dark colours than light ones.

More recently, Smith and Rennison (1961a), working in south-eastern Uganda, demonstrated that traps covered with natural-coloured hessian took more *G. pallidipes* than those with hessian painted black but this may have been an olfactory rather than a visual response, as *G. pallidipes* is known to be attracted to fresh hessian.

Smith and Rennison also shewed that a white bait ox attracted fewer flies than a darker coloured one and a red ox was most attractive. This experiment, however, does not really seem to have produced any more decisive evidence that flies can perceive colours than any of the previous ones.

Smell

Much study has been made of the olfactory senses of tsetse flies and Swynnerton (1936)) discussed this subject in relation to various food preferences which he and others had observed. He mentions that preferences for individuals of a particular species and a particular sex had been noted in the past.

Nash (1930) found that in the laboratory, blinded *G. morsitans* in tubes with gauze ends, fed as willingly and apparently as often as the controls but flies with painted antennae did not feed, proving that the antennae are olfactory organs. Nash considered that *G. morsitans* hunts its food by sight and suggested that " the normal action of obtaining food consists of a visual and an olfactory tropism " (Swynnerton 1936).

Swynnerton suggested that some species of tsetse flies, such as *G. pallidipes*, *G. austeni* Newstead and *G. brevipalpis*, make more use of scent than do *G. morsitans* and *G. swynnertoni* but the work of Weitz and Glasgow (1956), Langridge (1960b) and Lamprey et al (1962) would appear to indicate that these two latter flies have a keen sense of smell as well as sight.

Chorley (1948) demonstrated that *G. pallidipes* was attracted by the scent of cattle dung and urine and many field workers have observed that tsetse flies appeared to be attracted by the smell of the dung and urine of elephant and buffalo.

Johns (1950), in Zanzibar, found that test catches of *G. austeni* with oxen were considerably greater than with screens, even when attempts were made to impregnate the screens with ox scent.

By means of his " animal " traps, Morris (1960d) shewed that *G. pallidipes* followed herds of elephant passing through fly-infested country in the Busoga district of Uganda.

Hughes (1957) examined the responses of *G. morsitans* to a selection of aliphatic acids, alcohols, esters and amines. Exhaust gases and distillates of sump oil were tested on the activity of *G. palpalis*. The results obtained were consistent with those of other workers, in that it was found that stimulating compounds might be present in very small quantities in sump oil and the caprate series of fats from excretory substances such as sweat are attractive to tsetse flies.

Johns (1959), in the laboratory at Shinyanga, studied the olfaction of *Glossina* and described the olfactory pits in the antennae. Three olfactometers were tried but no satisfactory response was observed when tests were made with *G. morsitans*. Odours from anhydrous lanoline and warthog extract in alcohol or water were tried without success, though these are known to be attractive to flies in the field (Langridge 1960b).

Langridge (1960b) shewed that in Kenya *G. pallidipes* could be attracted to fly-rounds by using bait substances prepared from sheep wool greases and extracts from pig hair-skin scrapings. Further field experiments (Langridge 1961a) revealed that traps treated with attractants were more effective in catching *G. pallidipes* and *G. palpalis* than fly boys. These treated traps quickly revealed the presence of flies where ordinary catching methods failed to do so.

Burtt (1946) induced tsetse flies to probe by placing them in a tube with the open end closed with a piece of mosquito netting, then bringing the mosquito netting close to a guinea-pig.

It is obvious that sight and scent are the major factors in assisting tsetse flies to find their hosts but although sound and touch may not have any direct bearing on fly-host relationships, indirectly they may be important.

It has also been suggested that male flies might be attracted to the females by scent, as happens with many other insects but so far there is no evidence to prove it.

Sound

Buxton (1955) said : " There is nothing to suggest that the sense of hearing is used by *Glossina* in discovering a host." Nevertheless, male flies in search of mates, such as hungry females, which have been attracted to potential hosts by sight or scent, or both, often make a noise.

In tsetse-infested areas, one can normally hear *G. morsitans* and other species of fly making a squeaking note when they have settled on one's back or on the ground nearby. Vanderplank (1948), referring to " mating notes," implied that these are made by " wing beat " and emitted when the virgin female is flying or sitting. He may be right but following, non-feeding males also make this noise. According to Haskell (1961), Landois (1867) " ascribed the sounds emitted by various *Diptera* to the vibration of a series of lamellae situated in the tracheae close to certain spiracles: the lamellae are set in motion by the passage of air produced by respiratory movements." Tape recordings have been made by Langridge (1964) which appear to attract male flies to sounds made by females but from the evidence available it is doubtful whether sound has any practical importance as an attractant, except at very close quarters.

Touch

It is probable that *Glossina* possesses tactile organs on the tarsi which might give important information on the nature of the surface of the skin (Buxton 1955). Similar organs elsewhere on the body of the fly may perhaps perceive convection currents or warmth of the host. Lewis and Langridge (1947) shewed that *G. pallidipes* and *G. austeni*, when placed on warm microscope slides, tried to probe the slides with the proboscis and extruded a drop of saliva. This indicated that the fly is able to perceive body heat in a potential host and that heat stimulates the probing reaction.

Dethier (1952) described the probing response, the stimuli initiating it and the possible sites of the receptors involved, in *G. morsitans*, *G. brevipalpis* and *G. palpalis*. M. Langridge (1962) made similar investigations on *G. pallidipes* and demonstrated that increased temperature resulted in increased probing under both low and high humidities but the optimum range appeared to be 33°C-39°C. Increased humidity resulted in increased probing, at least within the optimum range of temperature. In addition, she described the thermoreceptors in the antennae and curved receptors on the tarsi and legs which appear to be associated with the perception of heat and perhaps humidity.

Taste

Buxton (1955) indicated that after a blood-sucking insect has reached the body of the host, it might be able to taste the surface of the animal. After piercing the skin with the proboscis, the sense of taste and perhaps even of touch might guide the mouth parts of the fly in penetrating the tissue and sucking up blood.

It is known that tarsal organs of taste occur in a number of small muscids and other *Diptera*. Although so far there is no proof of the existence of organs of taste in *Glossina*, there is a rich and varied supply of sensillae on and inside the haustellum, the labellum is particularly well supplied with sensillae of several types and there are numerous internal sensillae in the cavity of the food canal.

The existence of a sense of taste and of touch seems to be borne out by cinematograph films of the proboscis probing the skin of a live animal in which the tip of the proboscis " explores " the tissues in different directions in search of blood vessels or reservoirs of blood. It was shewn by Lester and Lloyd (1928) that tsetse fed through a membrane took more liquids which contained some blood than liquids which contained none.

Hunger

Buxton (1955), in discussing this subject, said: "as to the insects' sensations of hunger, we know little. . . . The fact that the insects swallow blood alone, which is both food and drink to them, makes it difficult to understand the sensations which might correspond to hunger and thirst".

Jackson (1933a), studying the causes and implications of hunger in tsetse flies, devised a method of classifying non-teneral male tsetse flies into 4 stages of hunger from their external appearance when captured. These stages were: 1. *Gorged*, 2. *Replete*, 3. *Intermediate*, 4. *Hungry*.

According to Buxton (1955), "there are large differences between the species of *Glossina* in the choice of host on which the insect will feed in nature. Moreover, such physiological factors as the sex and hunger of the insect, influence its feeding. The effect of hunger becomes clear if one studies the reaction of a species of *Glossina* towards some host which is not very attractive to it". Buxton then quoted the work of Jack (1941) in Southern Rhodesia in which it seemed that male *G. morsitans* are attracted to a moving human being even if they are "not hungry" but they will only come to a stationary human being if they are "very hungry". In a similar way, male and female *G. pallidipes* do not alight on man, even if he is moving, unless they are "very hungry" but they may follow him.

Jackson (1955a) designed a spiral fly-round to study the relationships between *G. morsitans* and game at Daga Iloi in Tanganyika, which revealed that there was a positive correlation between the number of ungulates present and the hunger of the flies but a negative correlation between the number of ungulates and the number of flies (Langridge et al 1963).

Glasgow and Wilson (1953), in studying populations of *G. fuscipes* (*G. palpalis fuscipes*) on Nyalagobe hill on the shores of Lake Victoria, calculated that the population of *G. fuscipes* was 5,000 and *G. pallidipes* 50,000.

By recording the tracks of the different game animals on paths and by stretching strands of cotton 12 inches and 24 inches from the ground on the uphill sides of the paths, they found that the commonest animals were bushpig, of which there were 15; and there were 13 bushbuck. From these results they estimated that on the average every animal supported 1163 *G. pallidipes* and if these flies fed once every 4 days, each animal must support 291 of them a day, or 2 flies every 5 minutes during the hours of daylight. From these figures, Glasgow and Duffy further calculated that one *G. pallidipes* took up 60 mg of blood per feed, so each animal lost 17.5 g of blood per day (Langridge et al 1963).

Smith and Rennison (1961b), conducting experiments with Morris traps in south-eastern Uganda, found that almost no *G. pallidipes* were caught in traps between 18.30 hours in the evening and 6.30 hours in the morning.

Smith and Rennison (1961b) further described catches of *G. pallidipes* made between 08.00 hours and 18.30 hours daily in the early wet season of 1957 and the dry season of 1958, using small East African Zebu oxen, Morris traps and standard fly-round techniques. More flies were attracted to the oxen in the morning and evening than at midday but the evening increase was most marked in the wet season. During the dry season, catches were lowest at the hottest times of the day but rose slightly in the evening. Smith and Rennison also demonstrated that there may be differences in times of feeding between male and female flies. Using traps, most female flies were caught between 12.30 and 14.00 hours at both seasons. Most males were caught between 14.00 and 15.30 hours in the wet season but only in fairly small numbers at any time in the dry season (Langridge et al 1963).

Pilson and Leggate (1960), in Southern Rhodesia, studied the feeding activity of *G. pallidipes* on tethered oxen throughout the day. In the hot dry seasons there was a slight peak in feeding activity in the early afternoon, followed by steady feeding throughout the day. From noon onwards, the feeding activity increased rapidly and ceased abruptly between 18.45 and 19.00 hours. During wet seasons, fewer flies attacked the animals and there was no morning feeding peak but there was a gradual rise in feeding activity until late afternoon, followed by a fall-off and feeding stopped between 18.45 and 19.00 hours (Langridge et al 1963).

Movement

Tsetse flies attracted to moving objects are not always in search of food. According to Buxton (1955), some types of fly movement are caused by a perception of shade, a desire to mate, etc., but there are movements which follow extrinsic stimuli, such as a tendency to explore large objects and to settle on them, which results in the tsetse being passively transported.

Moggridge (1936), in the Lake Province of Tanganyika, observed that *G. swynnertoni* was frequently transported on a team of oxen across an open grassy area about a mile wide and they would remain for 10 to 25 minutes. In the wet season, the flies tended to stay longer than in the dry season, partly because they were less hungry but mainly because more flies were picked up from the bush at that time.

Using men, the flies stayed much longer than with oxen. The explanation was that *G. swynnertoni* is less willing to feed on man than on oxen and therefore it stayed longer and was carried further.

Many other workers have studied the habit of passive transportation in tsetse flies and some have shewn that they can be carried long distances by a man on a bicycle or on vehicles. Lewis (1942, 1947 and 1950) gave a number of instances of tsetse flies being carried on cars, lorries and trains, often far into fly-free country where cattle are kept. In the course of 24 weeks, 5,260 tsetses were caught from the undersides of carriages of goods trains and others on passenger trains travelling between Nairobi and Mombasa in Kenya. Later, Fairclough (1956) described an experiment designed to control the carriage of tsetse flies on trains in Kenya. At Simba, from December 1960 to November 1961, 25,805 flies were caught off trains (MacOwan, 1962).

G. fuscipes is attracted to moving canoes on lakes and rivers. Fiske (1920) observed that it would cross up to 100 yards of water to reach a canoe but would not generally go further. Symes and Southby (1938), however, in studying the movement of marked flies between the islands on Lake Victoria, demonstrated that they could apparently fly unaided across open water up to a distance of 400 yards.

In Northern Nigeria, Nash and Page (1953) recorded that a marked *G. palpalis* moved 3 miles along a stream bed near Kaduna.

Kernaghan (1950-1960), at Kujama about 20 miles from Kaduna, recorded marked *G. palpalis* going at least 2 miles across a watershed away from the river and one fly moved for 2 miles along a river in 2 days.

Simpson (1918), on the Gold Coast, found that the greatest distance covered by a single marked *G. pallidipes* released near a road was 4 miles but along a river bank a single marked fly moved 7 miles.

Nash (1948) recorded that on one occasion in Northern Nigeria, whilst riding a bicycle, he transported a *G. tachinoides* for 7 miles under the rim of his helmet.

Simpson (1918) also demonstrated that marked *G. morsitans* would move up to 4 miles along a road traversed by cattle.

Page (1959), working at Ugbobigha in Southern Nigeria, observed that the maximum distance travelled by marked *G. longipalpis* Wiedemann was 3½ miles. There was also some evidence to shew that this fly might extend its range of movement in wet periods.

Buxton (1955) mentioned 3 known cases of tsetse flies being transported by aeroplanes across the Atlantic.

Buxton (1955) also said there was no question that tsetse flies were frequently carried about by game animals as they grazed, but a very controversial matter of more importance is the possibility that some species of *Glossina* migrate for long distances following game animals.

Swynnerton (1936) indicated that as a result of the habit of tsetse flies to ride on man and animals, a fallacious idea has arisen that a fly community will follow a herd of game animals " sometimes far outside the normal tsetse fly limits." Tsetse flies do not live in continual association with their animal hosts. Quoting Jackson, Swynnerton went on to say that " they feed on the animals when they find them and immediately afterwards fly off to digest their meal." As the need for food only recurs from 2 to 4 days in the dry season and 11 or more days in the wet season, there is plenty of time for the flies to lose contact with a herd. But the regular habits of many wild ungulates in their use of paths, glades and " mbugas " as grazing grounds or passages, have enabled the fly to adopt habits which keep it in contact with resident game animals.

Further, Swynnerton (1936) said that although the fly did not follow game very far, individually a definite concentration of game might indirectly draw in flies from the surrounding bush and so cause a strong local fly concentration. Nash (1933a) determined part of the mechanism by which this came about by showing that the flies tend to follow game paths so that tsetse concentrations could build up in areas of game concentration and persist for some time after the game had dispersed.

Night Activity

It is generally accepted that *G. morsitans* and *G. swynnertoni* are relatively inactive at night and it has long been a habit of cattlemen to move their herds through tsetse country at night. However, *G. brevipalpis* and *G. longipennis* are crepuscular and may be more active at night than is generally realised. In this connection, Swynnerton (1936) remarked that many instances have occurred in the course of tsetse research work in Tanganyika when *G. brevipalpis*, in some numbers, came into the camp at night.

Even as far back as 1912, Neave recorded *G. longipennis* as coming constantly to trains at night. Power (1964), in carrying out an investigation into the activity pattern of *G. longipennis* near Lake Jipe in Kenya, noted that this fly was very active at sunset but much less so at dawn and virtually inactive during the day time, particularly to man. The presence of host animals (rhinoceros) could have an over-riding effect on the fly, inducing limited activity at times other than the normal peak activity periods.

His observations further shewed that the fly activity rose as the saturation deficit increased and as the light intensity decreased until the light was too poor for efficient catching. Results from recaptures of marked flies suggested that this species readily disperses over a distance of at least 600 yards. There is also a possibility that *G. pallidipes* hunts at night as well as in the day time.

Chorley and Hopkins (1942) using a bait ox in the Buruli district of Uganda, demonstrated that *G. pallidipes* was more active on moonlight nights than on dark nights but there was some evidence of activity all through the night even on very dark nights.

Swynnerton (1936), said that " in view (a) of the great size of the night population (of mammals); (b) of the fact that some tsetses are probably partly nocturnal, while others may find an incidental source of food in the night mammals lying up in the day time: and (c) of the possibility therefore, that some of the night vertebrates proper might in some areas play a part were ungulates to be exterminated," the extent to which nocturnal mammals may be used by tsetse is worth mentioning.

Bushpig, of course, is nocturnal and in the following pages it will be shewn that it is an important source of food, especially to the forest-dwelling species of tsetse.

Kernaghan (1950-1960) observed that *G. tachinoides*, marked with fluorescent paint and released at night on the Duddurun Gaya river in Northern Nigeria, tended to perch more often on stems head upwards than on leaves at a height of 3 to 4 feet above the ground. Occasionally they were found on leaves 12 feet above the ground. Darkness did not prevent feeding but once at rest the flies were quiescent and could be picked off the vegetation by hand.

Southon (1958), at Shinyanga in Tanganyika, found that *G. swynnertoni*, marked with reflecting glass beads, and unmarked flies moved at dusk from the normal diurnal resting sites on the undersides of branches to the upper surfaces of leaves and returned to the branch resting sites at dawn. These observations confirmed and extended those made by Jewell (1956 and 1958), and Rennison, Lumsden and Webb (1958). McDonald (1960a), also carried out experiments in Nigeria on the detection of tsetse flies at night with ultraviolet light.

Rest

Jack and Williams (1937), demonstrated that *G. morsitans* entered the darkened portion of an appropriately designed apparatus when the temperature was 32°C (90°F). This " negative reaction to light " might give some idea of the mechanisms which cause flies to avoid high temperatures (Langridge et al 1963). It might also have some bearing on the fact that tsetse flies are attracted to dark from light areas and upon the resting sites chosen by the different species of fly at different seasons. Nash, (1942), in Northern Nigeria, shewed that the movement of female *G. morsitans* away from the forest edge coincided with rising soil temperature in the dry season and rising soil moisture in the rains. It was not the result of any ability on the part of the female fly to detect differences in the dryness of the air but to " a negative reaction to light developed by the whole community under conditions of universally high temperature " so that the period of migration of the tsetse community coincided with the time when shade temperatures approached the point at which Jack and Williams had found the negative reaction to light began.

Langridge et al (1963), quoted the work of a large number of authors on the favoured resting sites of some of the different species of flies.

Langridge (1959), himself studied the resting sites of 5 different species of tsetse flies in Kenya and shewed that the requirements of *G. longipennis*, which lives in rather arid country, are shade during the day time and easy access to open game paths. It rests under dead logs, fallen trees, rock outcrops, on multi-stemmed bushes such as *Cordia* and *Grewia*, and in the folds and fissures of the trunks of larger trees such as baobabs.

In the Central province of Kenya, *G. brevipalpis* disperses after the rains from its normal habitat in tall thicket, when the vegetation is in full leaf, into more open country. Yet, in the coastal forest it rests during the dry weather in places where the evergreen vegetation in the lower canopy is more shady than in the semi-deciduous surroundings. It perches on looped-over or horizontal branches up to 3 feet from the ground near pathways in the undergrowth used by game animals.

On the Kenya coast, *G. austeni* is confined almost entirely to tall thickets and the forests. In the hot, dry weather it uses the dense undergrowth providing the deepest shade, where it can be found on the undersides of horizontal branches up to 3 feet from the ground in places where its range of vision is not obstructed by leaves. It has also been seen resting under curled dead leaves on the forest floor.

In Kenya, *G. pallidipes* occurs within a wide range of conditions. It is an elusive fly, difficult to study and little is known about its resting habits except that at the coast its dry-season resting sites appear to be similar to those of *G. brevipalpis* and in central Kenya it may be found in sites occupied by *G. longipennis*.

Isherwood and Duffy (1959), studied the resting habits of *G. pallidipes* in two transects across the Ruma thicket in the Lambwe Valley of Kenya; (a) in forest dominated by *Euphorbia candelabrum*, (b) in continuous thicket, and (c) in thicket clumps separated by wooded grassland. They observed striking changes in the distribution of resting flies and a large amount of information was obtained concerning the ratios of resting to active flies but unfortunately no information is given about the actual positions in which the resting flies were found.

In the Zambezi Valley in Southern Rhodesia, Pilson and Leggate (1962), found that during most of the year in riverine vegetation *G. pallidipes* rested on branches of trees and shrubs at heights generally over 3 feet from the ground but in hot weather such sites were only used in the early morning and towards sunset. When the temperature rose above 30°C, the flies moved to the boles of trees less than 3 feet from the ground, to fallen logs and to rot holes in large trees.

Fiske (1920), found that *G. palpalis* (*G. fuscipes*) on Lake Victoria in Uganda required two kinds of shelter: " (a) light (shelter) such as serves at breeding grounds and for the active flies, and (b) massive or forest-like (shelter) which is required by the inactive flies."

Nash (1948), discussing the requirements for optimal conditions of " vegetational insulation " in a *G. palpalis* (R.-D.) habitat in Nigeria, said the width of the riverine fringing forest should not be less than 50 yards. In the northern parts of Nigeria, particularly in the Sudan Zone, the fringing forest is usually much narrower, so that here a *G. palpalis* habitat must also include pools of water which help to produce suitable microclimatic conditions within the forest " ecoclimate ".

Little appears to be known, however, about the actual resting sites of *G. palpalis* in Nigeria but they have been observed resting at an average height of 3½ feet above the ground and they have not been seen at heights greater than 7-8 feet above the ground (Mulligan 1952).

Moiser (1912), found *G. tachinoides* plentiful in Northern Nigeria where there was always a pool of water nearby and he found them sheltering in low, straight-stemmed bushes close to the pools. Nash (1948) observed that *G. tachinoides* was confined to riverine vegetation, particularly in the north in the dry season.

Moiser (1912), in studying the resting sites of *G. tachinoides*, found flies at rest on the undersides of small branches, generally within a foot of the ground and most frequently at about 6 inches.

Nash (1935), demonstrated that in the Sudan zone of Northern Nigeria, *G. morsitans submorsitans* Newstead could not withstand temperatures above 106°F (41.1°C) and the " critical zone " lay between 102.5°F (39.2°C) and 106°F (41.1°C), also that 100 per cent mortality occurred in flies subjected to the latter temperature for 60 minutes. Further experiments in the field indicated that in the hot, dry season the temperature on the ground in shade in patches of fringing forest could be as much as 4.4°C lower than sites above the ground, which suggested that on very hot days only the ground in the true forest was safe for tsetse flies. In all other sites, the temperature might enter the critical zone and even reach the upper fatal limit, so that in the late dry season a *G. morsitans* community might be living very near critical temperatures.

Maclennan and Kirkby (1958), observed that in the dry season in fringing forest on the Misau river in the Sudan zone in Northern Nigeria in the day time, many *G. morsitans* rested on tree trunks up to 7 feet above the ground but Davies and Blasdale (1960), working in the same area during the dry season, found that very few of these flies actually rested above 5 feet from the ground during the hottest part of the day.

In the Northern Guinea zone near Kaduna in Northern Nigeria, Nash (1952), discovered that most engorged *G. morsitans* (526) were resting on tree trunks and branches up to 3 feet above the ground in a vertical position with the head upwards. Most of the flies in the " intermediate " and " hungry " stage (152) rested about 6 feet up from the ground, although many were observed to be sitting in a horizontal position with the dorsum downwards to heights up to 14 feet above the ground.

Aitchison (1959), also working in the Northern Guinea zone, discovered numbers of flies resting beneath horizontal branches at heights varying from 7 to 12 feet above the ground at about 10 a.m. in *Isoberlinia* woodland. Invariably those branches which were 3 to 10 feet above the ground were most " popular " and the flies usually rested on their under surface with the head pointing outwards. These high resting places would be particularly advantageous to the fly when the grass was tall.

Buxton (1955), quoted C. H. N. Jackson as saying that in Tanganyika male *G. morsitans* commonly rest under overhanging branches up to 12 feet above the ground.

Swynnerton (1936), found *G. swynnertoni* using *Acacia* woodland both as a feeding and a breeding ground at Banagi on the edge of the Serengeti plains where game is very abundant and he said that it appeared likely that where blood could be obtained at any moment by the fly, the need of the dense shade element in the flies' vegetational requirements was reduced, but this happened only very rarely and locally.

Langridge et al (1964), studied 6 types of vegetation communities inhabited by *G. swynnertoni* in the Mara area of Kenya and found that small patches of thicket with scattered trees and grassland carried the greatest number of flies (30 per cent. of the total number caught). Escarpment woodland and *Acacia drepanolobium* (gall acacia) communities also carried a fair number of flies (22 and 21 per cent.). Large thicket patches carried approximately half the number found in the small thicket communities, i.e. 16.4 per cent., but riverine thicket and open plains with scattered trees carried the least (5 per cent. each).

Within these plant communities, which were in the process of destruction by elephant and fire, Langridge studied the importance of the different species of plants as resting sites for *G. swynnertoni* and found that those which had developed an umbrella shape as a result of being browsed or rubbed upon by animals standing in the shade, or had their lower branches burnt by grass fires, were the most favoured sites of this fly. In the small patches of thicket, the woody, multi-stemmed shrubs, *Grewia trichocarpa* and *Cordia ovalis*, were used most frequently as resting sites by the fly. In the escarpment woodland, *Lannea stuhlmanii* was most frequently used. In the gall acacia community, *Ac. nilotica* was used most frequently when it occurred on the edge of this vegetation type but in this community grass fires caused fly numbers to drop very low, probably as a result of loss of shelter and the movement away of giraffe (a favoured host which browses on the acacias when the leaves are fresh and green). In all these resting sites the flies were usually found on the under sides of branches with the head facing outwards where visibility was good and a host could be easily detected. The umbrella-shaped shrubs and trees also afforded good shady places for game animals such as topi, zebra and impala to lie up, but *G. swynnertoni* does not normally feed on these animals (Langridge 1960a).

Although two or three species of woody plants were found to be most attractive to the fly as resting sites, it was really their shape and growth habits which were responsible for this fact.

Chadwick (1964), observed that in Tanganyika the most important resting sites for *G. swynnertoni* were beneath the branches of trees. Seventy-seven per cent of these sites were on branches between 1 inch and 4 inches in diameter; 87 per cent were on branches below 35 degrees in angle and 32 per cent were between 4 feet and 9 feet from the ground. The flies were invariably found to be directly below the axes of the branches. It was estimated from apparent density calculations that about one-third of the population was seen and Chadwick concluded that from these observations, treating only the undersides of branches with insecticides between the limits where the flies are known to rest, might have a good chance of success.

THE FOOD OF TSETSE FLIES

Swynnerton (1936), in discussing the subject of animals used for food by tsetse flies, said that the difference in the prey of different species of fly are the result of varying habitat-combinations which bring flies into contact with different combinations of food animals. For example: *G. palpalis* living near water comes more into contact with crocodiles and monitor lizards than does *G. morsitans*, but *G. tachinoides* can be equally independent of game. *G. morsitans* and *G. swynnertoni* live in game country and therefore their habits are closely adapted to game animals.

G. brevipalpis, which spends the day time in dense thickets, would be more in contact with forest animals such as bushpig, buffalo, elephant, baboon, etc., than other flies.

G. pallidipes hide, breed and attack in thickets but they are able to search freely by day in open savannah or woodland which forms the normal home of *G. morsitans*. Swynnerton stressed the importance of bushpig (*potamochoerus*) as hosts for the three flies *G. pallidipes, G. brevipalpis* and *G. austeni*.

Further, Swynnerton (1936), in considering the general relation of tsetses to the diurnal vertebrates which include reptiles, carnivores, domestic ungulates, primates, insectivores and bats, rodents (porcupines) and birds, said that there is no mammalian group which can compare with the ungulates as food for the open-woodland (or savannah) tsetse flies *G. morsitans* and *G. swynnertoni* but the riverine and lake-shore fly, *G. palpalis* (*G. fuscipes* in East Africa) could adapt itself to an avian diet and he quoted the findings of Carpenter (1924).

In addition, Swynnerton (1936), in discussing the relation of the density of *G. morsitans* and *G. swynnertoni* to that of the ungulates, quoted Nash (1933a) as saying that the " game factor " is thought to be the least important of the three factors—season, vegetation and game. Nash remarked that it was surprising that when game seemed to be exceedingly scarce, the fly continued to be well fed.

In this connection, Jackson (1933a), said that " broadly speaking, if food is adequate to support permanently a few tsetses, it is adequate for any number. If food is absent or inadequate for a large number of tsetse, then not even a few can exist ". In the light of more modern information on the effects of game destruction on the smaller ungulates, this point is important (see later).

A vast amount of information on this subject has been accumulated since 1900, but it is only in the past 40 years that serious attention has been given to serology as a means of identifying the blood meals of engorged tsetse flies.

One of the earliest methods of investigating the food supply of tsetse flies was by measuring the red blood cells taken from engorged wild flies. In this way, Lloyd and Johnson (1924), in Northern Nigeria, demonstrated that of 215 blood specimens taken from *G. morsitans*, 93 per cent were from mammals and 7 per cent from birds. Of the mammalian portion, 4.2 per cent consisted of man, monkey, dog, jackal and hare, which could not be distinguished because of the similarity in size of their corpuscles.

In 1927, the practicability of the precipitin test as a means of identifying the blood in engorged tsetse flies was first investigated by Lloyd, Johnson and Rawson in Northern Nigeria. They shewed that *G. tachinoides* fed more frequently on primates than *G. morsitans* did, although a large proportion of this fly's feeds was also on primates and it was claimed that the presence of baboons in large numbers could provide an alternative supply of food to ungulate blood.

Symes and McMahon (1937), used the precipitin test to study the food habits of *G. swynnertoni* and *G. palpalis* (*G. fuscipes*) in Kenya but the method had technical disadvantages which discouraged its general use at that time.

Fiske (1920), designed some simple experiments on Lake Victoria to determine the host preferences of *G. palpalis* (*G. fuscipes*) by exposing a crocodile, a *Varanus* lizard and a goat on a small island where the fly density was high. He also exposed cattle, sheep, pigs and man with *Varanus* and found that *Varanus* was always bitten more frequently than the others.

In 1952 Weitz devised a method of testing the antigenicity of sera of man and animals by the preparation of specific precipitating antisera. In 1955 he produced a more specific test involving the " inhibition of agglutination of tanned red blood cells " which made it possible to determine accurately on what animals engorged flies had fed (Weitz and Jackson 1955). This test has since made it possible to study the host preferences of 15 species of tsetse flies in various parts of Africa (Weitz 1963).

Using Weitz's new method, between 1955 and 1960 at the West African Institute for Trypanosomiasis Research in Northern Nigeria, it was shewn that out of 756 wild *G morsitans submorsitans* feeds, 54.9 per cent. were from *Suidae*, 20.4 per cent. were from primates and 11.9 per cent. from *Bovidae*, only 0.5 per cent. were from reptiles and 3.8 per cent. from birds. Out of 122 specifically identified primate feeds, 93.4 per cent. were from man (Willett 1960b).

In the same period, data collected from various localities within 100 miles of Kaduna in Northern Nigeria, shewed that 41.7 per cent. of wild *G. palpalis* (R.-D.) feeds were on reptiles, 28.3 per cent. on primates, 19.6 per cent. on *Bovidae*, 5.4 per cent. on *Suidae* and 2.5 per cent. on birds. Of 62 specifically identified primate feeds, 91.9 per cent. were from man. This fact is important for it shews that man is by no means a casual source of food for *G. palpalis* in Nigeria. The high proportion of feeds on reptiles shews that the monitor lizard population must be great and easily available. The large number of bovid feeds is also significant because 3 out of 11 collected in 1956 and 4 out of 15 in 1957 were from ox, indicating that *G. palpalis* does feed on cattle.

Taylor (1930), in describing an epidemic of sleeping sickness which took place at Ganawuri in Northern Nigeria in 1929, said that at that time the food supply of *G. palpalis* (R.-D.) on the streams was derived entirely from man and his domestic animals which included sheep, goats, dogs and horses. Game was entirely absent.

Jordan et al (1962), shewed that out of 426 blood-meals of *G. tachinoides* collected from widely separated areas in Northern Nigeria in 1961, 30 per cent were from man and 8 per cent from reptiles. A number of the feeds were from oxen but the indigenous species of *Bovidae* appear to have been of limited importance as hosts. Jordan et al also shewed that although Lloyd et al (1927), had found that the proportion of non-mammalian blood in *G. tachinoides* feeds at Gadau was highest at the end of the wet season and lowest at the end of the dry season, even allowing for inaccuracies in the early techniques, there were marked differences in the feeding habits of *G. tachinoides* in the vicinity of the river Jema'ari, near Gadau, between 1923 and 1961. In 1923, wild game had been more common in the areas concerned. There were no cattle and the human population was low. In 1961, the human population was very much greater and there were numerous cattle. This change in the feeding habits of *G. tachinoides*, it was claimed, was related to the change in availability of the various host species. However, although *G. tachinoides* will feed readily on cattle, no feeds were identified from sheep and goats which were common in the fly habitats.

Of 153 blood meals of *G. tachinoides* collected by Baldry (1964), from Nsukka in eastern Nigeria, in the *wet season*:

54.7	per	cent.	were	domestic pig
7.6	,,	,,	,,	bovid (probably cattle)
2.5	,,	,,	,,	roan antelope
2.5	,,	,,	,,	porcupine
1.7	,,	,,	,,	man
29.9	,,	,,	,,	unidentified mammal

The large proportion of unidentified mammal feeds was interesting and Baldry thought they might be from rodent. If this were so, it would throw new light on the reservoirs of *T. gambiense* in sleeping sickness area, as it is well known that *T. gambiense* lives quite well in some laboratory rodents.

In the *dry season*:

94.5 per cent. of the feeds were from domestic pig; and
5.5 ,, ,, bovid.

Collections of the gut contents of some 200 *G. austeni* made by Johns (1950), in Zanzibar revealed that nearly 30 per cent of the feeds were on pig.

The natural feeding habits of 7 species of tsetse flies in Tanganyika were investigated by Weitz and Glasgow (1956). Significant preferences for *Suidae* were observed with *G. morsitans*, *G. swynnertoni* and *G. austeni* which derived at least half of their feeds from pigs. *G. fuscipes* fed mainly on reptiles and birds; bushbuck formed the greater part of *G. pallidipes* feeds and *G. brevipalpis* shewed a preference for hippopotamus in an area where other game had been partly eliminated.

At Kiboko in Kenya, Weitz et al (1958), found that 74 per cent of G. longipennis feeds were on rhinoceros, 16 per cent on buffalo and 10 per cent on birds, elephants, pigs, cats and unidentified bovids. Single feeds were observed on ox, dog and porcupine. *G.longipennis* did not appear to feed on zebra, waterbuck, impala or Grant's gazelle, although these animals were very common. Lesser kudu, buffalo and eland were important sources of food for *G. pallidipes* in that area.

In the Mara area of Kenya Masailand, *G. swynnertoni* fed on a high proportion of *Suidae* (62 per cent) and ruminants (27 per cent)—chiefly giraffe and buffalo.

Glasgow and Isherwood (1958), collected engorged *G. swynnertoni* and *G. pallidipes* at Shinyanga in Tanganyika throughout the year and found that at all times *Suidae* were the most important hosts. Active male *G. swynnertoni* averaged about 76 per cent *Suidae* in their feeds; resting males about 80 per cent, resting females about 90 per cent and both sexes of *G. pallidipes* about 94 per cent.

Lamerton (1960), reported the preliminary results of an experiment carried out in two areas near Kondoa in Tanganyika, giving blood-meal analyses of *G. morsitans* and *G. pallidipes* correlated with game spoor observations. It appeared that *Suidae*, together with the larger bovids, were the most important food animals of *G. morsitans* in these areas. The numbers of *G. pallidipes* caught were too small to yield conclusive results. The spoor of the largest animals (elephant, giraffe and rhinoceros) were recorded most often. This fact demonstrated the inaccuracy of estimating food preference of tsetse flies by spoor observations alone.

Lamprey et al (1962), working at Tarangire in the Northern Province of Tanganyika, shewed that although warthog, rhinoceros and buffalo comprised only 3 per cent, 0.2 per cent and 0.02 per cent of the large mammal population in the area, they provided 77 per cent, 2 per cent and 14 per cent of the food of *G. swynnertoni*. Impala, however, which comprised 70 per cent of the large mammal population, provided only 1 per cent of the *G. swynnertoni* feeds. These workers calculated that each warthog in that area must lose 13-27 gm of blood a day.

Langridge (1961a), studied the host animals of *G. pallidipes*, *G. austeni* and *G. brevipalpis* in the forest of the coastal region, those of *G. pallidipes*, *G. longipennis* and *G. brevipalpis* in the savannah country of central Kenya at Kiboko and those of *G. pallidipes* and *G. swynnertoni* in the thicket areas of Masailand. The extent to which the feeding habits of *G. pallidipes* and *G. longipennis* were transferred to domestic animals, when these were suddenly introduced, was also investigated at Kiboko in dry savannah country.

Detailed records obtained from spoor paths of the numbers of game animals present in the experimental areas, were collected simultaneously with the engorged flies to determine the true host relationship of these 5 different species of tsetse flies. Langridge's findings confirmed those of Weitz et al (1958) and shewed that the principal hosts of *G. longipennis* at Kiboko were rhinoceros, buffalo, elephant and giraffe.

The relative preferences for the four animals mentioned above were in the ratio of 4:2:2:1 respectively, over a period of a year, calculated from spoor records and blood-meals and the discrepancy from the actually observed proportions of 15:7:4:1 was the result of the relative abundance of the four different animals.

Using true preferences in conjunction with spoor records, it was shewn that the fly was not totally dependent on the preferred hosts in any locality because when these animals temporarily disappeared from the experimental areas, the fly did not die out but transferred its feeding habits to other less favoured animals, even cattle, but it still did not feed on waterbuck, Grant's gazelle or impala.

At Talek, in Masailand, 70 per cent of the feeds of *G. pallidipes* were on buffalo, which were common there, and 14 per cent on pig. In the same area, *G. swynnertoni* took 40 per cent of its feeds from warthog, 19 per cent from buffalo and 14 per cent from giraffe but no zebra feeds were found and only a few from hartebeest, impala and gazelle, although they were the most common animals there.

Blood meals of flies from other parts of the country are shewn in the following table:

	Rhino-ceros	Ele-phant	Buff-alo	Gir-affe	Wart-hog	Bush-pig	Dui-ker	Others
G. longipennis	58.4	17.9	13.8	4.2	*	*	*	6.3
G. swinnertoni	*	*	20.1	15.8	52.1	*	*	11.2
G. austeni	*	*	*	*	*	46.8	22.2	29.3
G. brevipalpis (dry savannah)	44.1	40.2	7.4	†	*	*	*	7.4

G. brevipalpis (coastal forest)	*	*	*	*	*	80.6	6.3	*
G. pallidipes (dry savannah)	37.8	18.1	6.4	12.8	*	*	*	25.0
G. pallidipes (coastal forest)	*	*	*	*	*	58.8	8.8	33.8

* Did not occur or was rare

† No record

Langridge et al (1963), quoting Ford (1962), shewed that in the Zambezi area of Southern Rhodesia, the broad picture revealed by the analysis of blood-meals of *G. morsitans* did not differ significantly from that found elsewhere. *Suidae* markedly predominated as hosts of *G. morsitans* during the wet weather but during the hot dry weather *Bovidae* became more important than pigs. This might be associated with the seasonal distribution of the game animals and the fly. During hot weather, both the fly and the animals tended to concentrate on rivers and when this happened, the antelope became more easily available to the tsetse. At the onset of the rains, when the fly and the game disappeared into the general woodland, pigs became the favoured hosts of the fly. In the same area, a small number of engorged *G. pallidipes* collected in 1957 shewed that this fly appeared to feed predominantly on buffalo.

De Andrade Silva and da Silva (1958), demonstrated that the main hosts of *G. austeni* in southern Mozambique were suni (*Nesotragus livingstonianus*) and grey duiker (*Sylvicapra grimmia*). Pires (1951), also in Mozambique, established that *G. brevipalpis* on the Maputo river was largely dependent on hippototamus for its food supply.

Isherwood et al (1959), studying the animal hosts of *G. pallidipes* in various vegetation phases in the Lambwe Valley in Kenya, revealed that bushbuck was by far its most important source of food in this area and confirmed the findings of Weitz and Glasgow (1956).

Isherwood (1958), observed engorged *G. fuscipleuris* Austen alongside fed and unfed *G. pallidipes* in the forest of Mitoma county of Ankole in Uganda, so that it seemed that in this area at least *G. pallidipes* and *G. fuscipleuris* may have similar resting sites. He was able to catch only one engorged *G. fuscipleuris* and it had fed on pig.

Jordan et al (1961), collected 2,234 blood-meals from 8 species of tsetse flies inhabiting the forest belt of Nigeria and the southern Cameroons. They found that *G. palpalis* (R.-D.) fed largely on man and reptiles but when they were not available, it fed on game animals. *G. pallicera* Bigot fed mainly on *Bovidae* and birds. Ninety-five per cent. of the *G. longipalpis* meals were on bovids, bushbuck being the most important single host. *G. tabaniformis* Westwood and *G. fusca* Walker from the rain forest at Ugbobigha and *G. tabaniformis* and *G. haningtoni* Newstead and Evans from the Cameroons forest, fed largely on red river-hog but in forest islands, riverine forest and in the drier rain-forest, *G. fusca* and *G. medicorum* Austen fed mainly on *Bovidae*, particularly bushbuck. *G. nigrofusca* Newstead, occurring in the same habitat as *G. tabaniformis* and *G. fusca*, fed largely on *Bovidae*. Only a few of the blood meals of the flies mentioned above were from duiker, waterbuck and elephant. In the Northern region, however, Jordan et al (1962), did not find any flies which had fed on kob, waterbuck, hartebeest or gazelle.

These findings are interesting because they are consistent with those in East Africa. They also demonstrate that although the different species of tsetse flies feed on a large variety of hosts, the *Suidae* are important sources of food to all of them The significance of this fact is discussed later.

Bursell (1961), in studying the fat content and residual blood-meals of tsetse flies, sampled them in 4 different ways: (1) by standard catching parties; (2) from resting catches; (3) from bait animals; and (4) from vehicles. His results indicated that the fat content of male flies containing blood in late stages of digestion was high for the standard, low for resting and bait animal catches and intermediate for vehicle catches. The fat content in females was low in the standard catch, high in the resting and bait animal catches and intermediate in the vehicle catches.

These findings Bursell interpreted in terms of changes in the behaviour of flies in the course of the hunger cycle and recognised 4 phases in the male hunger cycle:

1. inactivity;
2. activity characterised by sexual behaviour;
3. activity characterised by behaviour relating to feeding reaction but indifference to moving objects;
4. as for 3. except that moving objects were an adequate stimulus for the feeding reaction.

He concluded that the bearing of these results on the problem of "host preferences" and the possibility that quiescence and shade are important components of the stimulus conditions which control the feeding reaction in tsetse flies, might go some way towards explaining the striking discrepancy between apparent availability of different species of potential host animals in a tsetse habitat and the frequency with which they are fed on by tsetse flies.

The present writer cannot quite understand the logic of this argument, as some animals are not fed on at all, even though they may be most numerous and available at all times.

TRYPANOSOME INFECTION IN HOST AND FLY

Morris (1959, 1960a, 1960b, 1960c) has dealt at some length with the epidemiology of sleeping sickness in East Africa.

It is well known that wild animals act as the reservoirs of trypanosomes pathogenic to domestic stock but it was not until 1909 that Kleine discovered that tsetse flies which had been fed on animals infected with *Trypanosoma brucei* Plimmer and Bradford failed to infect fresh animals for 14 to 20 days after taking an infected feed but after that period the flies remained infective. It was in this way that the metacyclic development of certain trypanosomes in the gut of tsetse flies was discovered.

Fairbairn (1948), said there were two schools of thought as to how *Trypanosoma rhodesiense* Stephens and Fantham causes epidemics of human trypanosomiasis. The English School believed that *T. rhodesiense* is the game trypanosome *T. brucei* which has become acclimatised to man and that if *T. rhodesiense* were transmitted from man back to game and maintained solely in game, it would lose its infectivity to man and revert to *T. brucei*.

The German School maintained that *T. brucei* and *T. rhodesiense* are distinct species and not convertible into each other. But it has been proved conclusively that game animals can be infected with *T. rhodesiense* and that this trypanosome can still be infective to man after more than twelve years' residence in nothing but game.

If the English School were correct, epidemics of *T. rhodesiense* were likely to start at any time " from West to East Africa and from the Sudan to Zululand (where the disease has not appeared as yet), wherever game carrying *T. brucei* is in close contact with man in fly bush."

Sir Guy Marshall (1948), challenged Fairbairn's statement that it had been established that game is a source of danger in starting or maintaining sleeping sickness in man, and said: " I venture to state that no such fact has been scientifically established and there is no authentically recorded case of a man having acquired sleeping sickness from wild game away from a laboratory". Unfortunately, Sir Guy was wrong as will be seen below.

Ashcroft (1959c), in a critical review of the epidemiology of human trypanosomiasis in Africa, described briefly the discovery of the morphologically identical polymorphic trypanosomes *T. brucei*, *T. gambiense* Dutton and *T. rhodesiense* and discussed the controversy over the relationship between *T. brucei* and *T. rhodesiense*. It appeared that these two trypanosomes were distinct because of the absence of *T. rhodesiense* sleeping sickness from some areas where *T. brucei* was present in animals and the stability of the pathogenicity of *T. rhodesiense* infections to man when strains were transmitted experimentally through animals. However, he thought it was difficult to estimate the importance of wild animals as reservoirs of *T. rhodesiense*.

Fairbairn's (1948), prediction was confirmed by Heisch et al (1958), who isolated a strain of *T. rhodesiense* from a bushbuck from the Utonga peninsula in Central Nyanza in Kenya, which was strongly pathogenic to man. They considered that the technique employed was very important and claimed that it was " essential to inoculate enough blood (30 ml at least) from the animal killed into enough rats (six at least)", otherwise light infections would easily be missed.

Jackson (1955b), working in Tanganyika, observed that 27 Africans became infected with *T. rhodesiense* in 3 different places closed to settlement. Most of the cases of trypanosomiasis to which he referred came from around Kakoma, eight of them camps some miles away from any permanent route. Jackson thought, therefore, that wild animals must form a reservoir of the disease as they had been shewn to do experimentally.

Jackson's conviction was supported by MacKichan (1944), who obtained a strain of *T. rhodesiense* from a wild *G. pallidipes* at Lugala in Uganda. Since then, other isolations of *T. rhodesiense* have been obtained from *G. pallidipes* (Rennison 1956; Willett 1958) but the first isolation of *T. rhodesiense* from *G. fuscipes* (*G. palpalis fuscipes*) was not made until 1961 (Southon and Robertson 1961) and it was also from the Lugala area. So far, *G. brevipalpis*, the remaining species of tsetse fly in this area, has not yet become implicated in the epidemiology of *T. rhodesiense*.

Because *G. fuscipes* is now known to be able to transmit the Rhodesian as well as Gambian type of sleeping sickness, a very dangerous situation has arisen in Kenya and the contiguous parts of Uganda, for at the present moment most sleeping sickness cases in Kenya are of the *T. rhodesiense* type. Further, *G. fuscipes*, in part of the Nyanza region, appears to have adapted itself to living in bush away from permanent water and even in the hedges around homesteads, so that now man-fly contact has become much closer and widespread epidemic conditions can be expected unless strenuous efforts are made at once to exterminate this fly from the area concerned (Southgate 1964).

Willett (1963), in his paper on some principles of epidemiology of human trypanosomiasis in Africa, said: " The maintenance of a disease complex such as (human) trypanosomiasis in Africa depends on the interrelation of three elements, the vertebrate host, the parasite and the vector responsible for transmission. . . ."

" Between the three elements in the disease complex there exists necessarily three sets of interrelations: (a) between the vertebrate host and the parasite, (b) between the vertebrate host and the vector, and (c) between the vector and the parasite".

Nash (1948), working with *G. palpalis* in Northern Nigeria, described two types of man-fly contact. Along the rivers of the Northern region, the time of concentration of *G. palpalis* varied with different streams, the dry reaches being vacated first in favour of the vicinity of permanent pools. Should a village be near these pools, the man-fly contact then became very close, the same flies biting the same people every time they came down to the pools—this Nash called " close personal contact ". The situation in a mild year in which the members of a fairly large fly population moving up and down a stream bite the villagers in passing, he called " impersonal contact ".

These are very important factors in the epidemiology of sleeping sickness in Northern Nigeria.

In discussing man-fly contact, Willett said: " It has long been recognised as one of the anomalies of the epidemiology of Gambian sleeping sickness that its incidence bears little relation to the density of fly infestation and that, in fact the more severe epidemics may occur in regions where fly populations are relatively low and that this effect is not merely due to differences in predominant species. . . . In large areas of West Africa, *G. palpalis* and *G. tachinoides* are widespread and abundant but sleeping sickness is either rare or absent. On the other hand, in areas where these species are far less abundant, particularly towards the northern limits of their distributions, sleeping sickness is much commoner and has in some regions broken out in devastating epidemics ".

Fairbairn (1948) gave the following list of infection rates in game animals which he and his colleagues had examined: " Eland 25 per cent to 60 per cent; waterbuck 52.7 per cent to 69.2 per cent; kudu 57.1 per cent to 100 per cent; bushbuck 20 per cent to 70 per cent; hartebeest 16.6 per cent to 17.1 per cent; reedbuck 63.1 per cent; oribi 23 per cent; duiker 11.1 per cent to 28 per cent; buffalo 22.2 per cent; hyena 66.6 per cent; warthog 9.4 per cent to 21.1 per cent; situtunga 50 per cent; roan 9 per cent to 15.4 per cent; impala 5.2 per cent to 20 per cent; puku 11.1 per cent to 20 per cent; topi 17.6 per cent; zebra 8.3 per cent to 25 per cent; giraffe 20 per cent to 47.6 per cent; dikdik 9.1 per cent to 14.3 per cent; steinbuck 16.7 per cent". Some of the percentages, however, were based on small numbers

Ashcroft (1959a), in Tanganyika, considered recent work on the identification of animals on which tsetse flies fed in relation to previous investigations on the incidence of trypanosomiasis in these hosts and their susceptibility to experimental infection with trypanosomes. He reached the conclusion that some animals, such as warthog, may be less important as reservoirs of trypanosomiasis than might be expected from their importance as hosts of tsetse flies, whereas other animals such as kudu, giraffe and reedbuck might be more important. He suggested also that the number of tsetse flies carrying trypanosomes and the relative proportion of the different species of trypanosomes occurring in an area might be closely related to the host animals on which the tsetse fed.

Ashcroft et al (1959) further attempted to infect wild pigs, porcupines, several species of antelopes and monkeys with *Trypanosoma rhodesiense*, *T. brucei* and *T. congolense* Broden. They also reviewed the results of attempts of other workers to infect the same and other species of animals with these trypanosomes and recorded new evidence on the close similarity between the course of infections with *T. rhodesiense* and *T. brucei* in wild animals.

A *T. rhodesiense* strain, which was apparently latent for more than three months and subsequently always cryptic, persisted for nearly a year in one of their bushpigs. Only a few of the flies which fed on this animal during its prolonged period of infection with *T. rhodesiense* became themselves infected.

Infections of wild animals with *T. rhodesiense and T. brucei* in the laboratory, fell into groups according to the degree of susceptibility of the animal. These groups were compared with recorded data on the extent to which the animals concerned were fed upon by tsetse flies under natural conditions. Certain factors responsible for the importance of a species as a reservoir of trypanosomiasis were also considered. The existing evidence shewed that animals to which *T. rhodesiense* and *T. brucei* were fatal, were not fed upon very frequently in nature. Tolerant hosts included those animals normally fed upon by the tsetse but high resistance to trypanosome infection did not correspond with the importance of the animal as a source of food for the flies.

These authors suggested that the number of infected flies occurring in nature might bear some relation to the species or groups of species of animals used as hosts by the flies. They also cited evidence that wild pigs were probably more favourable as hosts for some other species of pathogenic trypanosomes than they were for those of the *T. brucei* sub-group.

Robertson and Baker (1958), in studying the epidemiology and virulence of human trypanosomiasis in south east Uganda, noted that during and immediately after the rains in May and June 1957, the incidence of sleeping sickness increased in the villages on the inland fringe of a *G. pallidipes* fly belt as a result of the seasonal extension of the range of this fly but the local distribution of the disease suggested that game was not a major reservoir in this area and that man-fly-man passage was continuous.

Langridge et al (1963), quoting Steele (1962), stated that *T. rhodesiense* was endemic in some areas of Rhodesia but seldom reached significant proportions.

T. gambiense was reported on both lakes Tanganyika and Mweru as early as 1907 but there were no reports of cases of this form of sleeping sickness after 1944. On Lake Mweru, Gambian sleeping sickness seemed to disappear spontaneously and in Tanganyika it was controlled firstly by the evacuation of the population from scattered infected villages and later by the elimination of the vector by direct control measures.

Ford and Leggate (1961) shewed that in Southern Rhodesia trypanosome infection rates in *Glossina* varied in relation to geography and climate and demonstrated a positive correlation between infection rates and the distance from the middle of a *Glossina* belt at a latitude of seven degrees south. They thought it probable that this was the effect of the decrease in mean annual temperature, corresponding to the increase in distance from the equator.

Ashcroft (1959b), in Tanganyika, investigated the sex ratio of infected flies in trypanosome experiments with *G. morsitans* transmitting *T. rhodesiense* and *T. brucei*. One strain of *T. rhodesiense* was used and two of *T. brucei*: the proportion of male flies which became infected was found to be greater than that of females. In all the experiments the females died sooner than the males.

Lawrence and Bryson (1953), in Southern Rhodesia, demonstrated that the pathogenic trypanosomes infecting cattle were *T. congolense* (65 per cent), *T. vivax* Ziemann (20 per cent) and *T. brucei* (2 per cent). Thirteen per cent of infections were mixed but these were only approximate percentages as there appeared to be wide variation in infection rates from year to year. Since the widespread use of Antrycide, *T. vivax* had formed a much higher percentage of infections because Antrycide is more effective against *T. congolense* than *T. vivax*.

Further, Lawrence and Bryson said that in Southern Rhodesia *T. theileri* Laveran occurs from time to time but no significance is attached to it: sheep and goats were susceptible to *T. congolense* and *T. brucei;* horses, donkeys and dogs to *T. congolense* and *T. brucei* and pigs to *T. suis* and *T. simiae*.

The disease is most severe in cattle but severe mortality is often encountered in donkeys in areas in or near fly. Sheep, goats and dogs are usually only infected in areas with a high fly density.

Ford and Leggate (1961) also indicated that high temperature and possibly a wide temperature range might effect *Glossina* in its role as a vector of trypanosomiasis.

Shaw (1958) estimated that in Northern Rhodesia 60 per cent. of the animal trypanosomiasis was transmitted mechanically. The incidence of trypanosomiasis revealed by recent surveys gave the following information:

	1946-56 per cent	1956-57 per cent
T. congolense	90.0	79.0
T. vivax	7.0	16.0
T. simiae	1.2	2.8
T. brucei	1.3	1.5
T. theileri	0.5	0.7

In 1956 and 1957, the figures shewed an increase in incidence of *T. vivax* and *T. simiae* but the cause of this was not quite clear.

In Northern Nigeria at Sherifuri in 1924, Lloyd and Johnson dissected 534 *G. palpalis* and found that 3.2 per cent of them were infected with trypanosomes; of these, 2.6 per cent were of the *T. vivax* group and 0.6 of the *T. congolense* group.

At Katabu near Kaduna in Northern Nigeria, Nash and Page (1953) examined 3,382 *G. palpalis;* 3.3 per cent of these flies were infected with trypanosomes, 3.8 per cent in the hypopharynx with *T. vivax*, 0.3 per cent had *T. congolense* in the hypopharynx and gut and one fly had a mature *T. brucei-gambiense* infection in the salivary glands.

In the forest belt of Sierra Leone, Squire (1951) dissected 3,226 *G. palpalis* and found a proboscis infection rate of 4.3 per cent; 2,313 of the flies were males of which 3.17 per cent were infected with trypanosomes, 913 were females and 5.8 per cent of them were infected. The infection rate in these flies varied from 0.5 per cent in the dry season to 9.1 per cent in the rains.

At Sherifuri in 1924, Lloyd et al (1927) dissected 26,625 *G. morsitans* and found that 27.4 per cent were infected with pathogenic trypanosomes. Of these, 18.8 per cent were *T. vivax* group, 8.2 per cent *T. congolense* group and 0.4 per cent *T. brucei-gambiense* group. These figures shewed the importance of *G. morsitans* as a vector of animal trypanosomiasis.

At Ugbobigha in Southern Nigeria, Page (1959) dissected 4,360 *G. longipalpis;* 17.6 per cent of these flies had *T. vivax* group infections; 3.9 per cent *T. congolense* group and 0.02 per cent *T. brucei* group. Monthly mature infection rates varied from 10.6 per cent to 36 per cent but the variation was not seasonal.

In Northern Nigeria in 1954-55, a total of 1,013 positive blood slides were taken, almost entirely from Fulani breeding stock in the field by the Veterinary, Tsetse and Trypanosomiasis Unit. They are compared in the following table with records kept at Vom by the West African Institute for Trypanosomiasis Research. These results differ to some extent but this may have been because different methods of sampling were used and because of differences in the types of animals from which the samples were taken, but they do indicate that *T. vivax* and *T. congolense* are by far the most important cattle trypanosomes in Northern Nigeria. Further infection rates in Fulani breeding stock taken from various parts of the country shewed that the incidence of these two trypanosomes can vary very greatly from place to place.

Type of Trypanosome in cattle	Vet Tsetse & Tryps. Unit %	W.A.I.T.R. Previous Records %	W.A.I.T.R. 1953 Records %
T. vivax	33	68	82
T. congolense	59	26	4
Mixed *T. vivax* *T. congolense* ...	7	46	14
T. theileri	0.2	—	—
T. brucei	0.1	0.4	Nil
Total number of slides examined	1,013	965	123

In Kenya, continuous records of trypanosome infection rates were kept in different parts of the country for several years. Monthly fluctuations were studied but bore little relation to season. The infection rates in the more humid regions, such as the coast, appeared to be higher than those in the drier areas up country.

The figures listed below were derived from proboscis and gut dissections. They represent both *T. congolense* and *T. vivax* infections (Whiteside and Langridge 1960).

Region	Climatic Type	Place	Flies Examined	Species	Infection Rate
					%
Coast	Wet	Ngomeni	3403	*G. pallidipes*	11.6
			201	*G. austeni*	9.0
	Wet	Mtwapa	265	*G. pallidipes*	6.8
			46	*G. austeni*	13.0
Lake Victoria	Wet	Lambwe	1311	*G. pallidipes*	12.0
Central	Dry	Kiboko	526	*G. longipennis*	7.2
			128	*G. pallidipes*	9.4
			13	*G. brevipalpis*	—
Central	Dry	Athi-Tiva	841	*G. pallidipes*	6.5
			441	*G. longipennis*	7.3
Southern	Dry	Talek	2901	*G. swynnertoni*	4.3
			31	*G. pallidipes*	3.2

Langridge (1960-62) in studying the attack of *G. pallidipes* on bait cattle, found that the proboscis infection rate of these flies was 5.6 per cent, of which 34 per cent were *T. vivax* infections and 16 per cent *T. congolense*.

METHODS OF TRYPANOSOMIASIS CONTROL

Broadly, there are two methods of controlling trypanosomiasis:

1. *BY ATTACK UPON THE PARASITE*
2. *BY ATTACK UPON THE VECTOR*

Attack upon the parasite with drugs is a most effective weapon in combating human and animal trypanosomiasis, as can be seen by referring to the works of Marshall (1958); Davey (1958); Duggan (1962); Willett (1963); van den Berghe and Lamprecht (1963); D. H. H. Robertson (1963); de Andrade Silva (1958); Whiteside (1958 and 1962); Maclennan (1963), etc., but unassisted by other methods of control, it is still only a palliative. Further, it is not thought to be a very important factor influencing fly-wild-host relationships, except perhaps in Southern Rhodesia where the use of Antrycide may have made it possible for the fly to feed on cattle.

Attack upon the vector can be successfully achieved:

(a) *Indirectly—by removing the bush* which constitutes its habitat, either by hand or with machines. This is a very effective method of exterminating tsetse flies but it has the serious disadvantage of recurrent expenditure in suppressing perennial regrowth (Wilson 1953). Further, the ecological implications of clearing large areas of natural vegetation have never been studied but the catastrophic effect it must have upon the small mammal, bird and insect populations is unthinkable. Nor does anyone know what the long term effects of such drastic measures may be, except that if there is not an immediate follow-up with proper methods of land use, overgrazing, trampling and soil erosion, leading to the ultimate destruction of man's own habitat and that of his domestic animals, must be the inevitable result. Nevertheless, bush clearing as a means of tsetse control has been very widely used in many parts of Africa in the past 50 years (Swynnerton 1936; Nash 1948; Morris 1946; McLetchie 1953a; Kernaghan 1950-1960; Glover et al 1959; Glasgow and Duffy 1959) to quote only a few instances.

(b) *Directly—by applying insecticides* to its habitat. This method also is very effective and has the great advantage of leaving the natural vegetation untouched but it has the disadvantage of being practical only in isolated areas where there is no danger of re-infestation. Again, the ecological implications are unknown, except that its effect upon the habitat appears to be much less drastic than bush clearing. Although instances have been reported where bushbuck, reptiles and sometimes domestic stock have been poisoned through carelessness, no evidence has been produced so far to prove that intensive or lasting damage to the ecological complex has been brought about. There has been some cause for anxiety in Europe and America, however, on the long term effects of agricultural pesticides on man and non-harmful living organisms such as birds, small mammals and insects in those countries (Carson 1963).

Nevertheless, with the appearance of residual insecticides like DDT and dieldrin towards the end of the 1940's, a powerful and effective anti-tsetse weapon came into being (Glover and Langridge 1962).

The first really large-scale and successful use of insecticides for tsetse control was made in Zululand in South Africa (du Toit 1954; du Toit et al 1949 and 1950) when they found that they could not exterminate the fly by destroying the game alone (Glover 1950).

Similar work on the application of insecticides from the air and on the ground was carried out in East Africa by the Tropical Pesticides Research Institute and recent trends have been described by Hocking et al (1953, 1954, 1956, etc.); Burnett et al (1961) and Yeo and Simpson (1960), etc.

Wilson (1953) demonstrated that insecticides could be successfully used on a large scale against *G. fuscipes* in Kenya. Subsequent improvements in the methods of application (Burnett et al 1957) led to the adoption of highly efficient insecticidal operations on the rivers and shores of Lake Victoria (Glover and Langridge 1962).

From 1954 onwards, various insecticide spraying schemes were undertaken in Northern Nigeria (Kernaghan 1950-1960; J. B. Davies 1960; Kernaghan 1961; Maclennan and Kirkby 1958; H. Davies and Blasdale 1960, etc.). Today, insecticides are the principal means of controlling tsetse flies in Northern Nigeria.

In the Komadugu Gana area in the Sudan zone of Northern Nigeria, up to April 1961, 480 square miles of country were actually sprayed, making safe 4,200 square miles of grazing at an overall cost of £150 per square mile. A further area of 840 square miles in the Katagum drainage system has actually been sprayed, releasing from the threat of trypanosomiasis a further 4,600 square miles (H. Davies 1964).

Similarly, in Uganda, large-scale bush clearing and insecticide spraying schemes are now in progress to supplement or replace the elimination of game (Bernacca 1964).

(c) *By destroying the important game animals* upon which tsetse flies feed.

Reference to the early literature indicates that game destruction as a means of tsetse control originated in the observations of explorers and early scientific workers on the effects of rinderpest upon the fly as a result of the elimination of its important host animals.

In the 1890's, a vast rinderpest epizootic swept across Africa from the Ethiopian region to the Cape, killing untold numbers of wild ungulates. At the same time, *G. morsitans* disappeared from big expanses of Southern Rhodesia and the Transvaal. This contraction in *G. morsitans* distribution was claimed by many to be the result of the drastic reduction in the numbers of the big game in the areas concerned, caused by the epizootic (Buxton 1955). On its way southwards, the same wave of rinderpest is said to have caused recessions of *G. morsitans* over large tracts of country in Tanganyika, Northern Rhodesia, Nyasaland and Portuguese East Africa.

Since then, recurrent outbreaks of rinderpest have taken place in various parts of Africa. Between 1917 and 1926, rinderpest is claimed to have greatly reduced the numbers of *G. morsitans* in Northern Uganda (Kennedy 1929; Carmichael 1933).

From the records available, there seems to be little doubt that the disappearance of the game resulting from rinderpest did have an effect on the distribution of *G. morsitans*.

Nevertheless, Stevenson-Hamilton (1912), in South Africa, disagreed with this view. He had known the Northern Transvaal before the rinderpest outbreak of 1896 and had lived and hunted in Southern Africa for a long time. He had observed that the epizootic had killed almost all the cattle, buffalo, eland, kudu, warthog and several other species of ungulates, but sable antelope, roan antelope and wildebeest were not much affected and impala appeared to be untouched. Therefore, he claimed that enough game had survived to support the fly, at least in favourable places.

Sir Guy Marshall, who had been in the Northern Transvaal in 1893 before the rinderpest outbreak, supported Stevenson-Hamilton and said that *G. morsitans* had not been widespread in the area when he was there.

It was therefore obvious that the game-rinderpest-fly relationship was not a simple one and experiments were carried out by Carmichael (1933) to discover if the fly itself could be infected with rinderpest virus, which shewed that it was " impossible to obtain any evidence that rinderpest virus, as it exists in the peripheral blood of infected animals, in any way affects *Glossina morsitans* either directly or from the point of view of reproduction."

Swynnerton (1936), after visiting the Kruger National Park with Stevenson-Hamilton in 1933, observed that there might be evidence to support the suggestion that it was a special and essential association with buffalo in the dry season haunts of *G. morsitans* that led to this insect's undoing in the Northern Transvaal, because it had suffered very severely from the effects of the rinderpest outbreak.

According to Duke (1919), in Uganda in the Masinde area in 1917, an early but prolonged drought led to an unusually complete burning of the grass and bush at the same time as an outbreak of rinderpest. This doubly handicapped the fly; firstly, in that its food supply was diminished by the loss of numbers of game animals from rinderpest and, secondly, by depriving it of shelter and destroying its breeding grounds with fire, coupled with other adverse conditions resulting from the prolonged drought.

Therefore it might be assumed that in the Northern Transvaal and in Uganda, recession of the fly could have been caused by the effects of rinderpest reinforced by other adverse conditions such as drought. This explanation, however, might not apply equally to the great Rhodesian fly belts evacuated at the same time (Swynnerton 1936).

Carmichael (1938), in Uganda, quoted Lugard and Sharpe as mentioning that buffalo, eland, warthog and wild pig were the chief victims of rinderpest; he also gives a list produced by Poulton (1927) shewing the susceptibility to rinderpest of a number of game animals, i.e.:

Insusceptible:	Rhinoceros, elephant, hippopotamus
Insusceptible—or only slightly so:	Waterbuck, roan antelope, hartebeest, topi, reedbuck.
Variable susceptibility:	Bushbuck, situtunga, impala, oribi, duiker.
Highly susceptible:	Buffalo, giraffe, eland, bushpig, warthog.

Wildebeest (*Connochaetes taurinus*) had been proved to be susceptible by Cornell (1933). Kudu was known to be highly susceptible and reference is made by Selous (1908) to deaths of this animal in the Eastern Transvaal in about 1896. Fox and Varian (1911) also mention deaths of kudu in East and Central Africa in the same epizootic but say the disease did not reach Angola.

Carmichael's own findings confirm those of Poulton to some extent by shewing that the disease can be fatal to situtunga, bushbuck, reedbuck and oribi but he says that "specific susceptibility of game seems to vary considerably at different times and at different localities. . . ."

It would seem that in many ways the effects of rinderpest epizootics on wild game populations and hence the tsetse fly, do resemble those of game destruction as a means of tsetse control. Therefore the early observers were correct, especially concerning *G. morsitans* and perhaps *G. swynnertoni* which have been shewn to be dependent on the *Suidae* and larger bovids for their food. However, as will be seen later, it is practically impossible to exterminate warthog, bushpig and the smaller antelope upon which most tsetse flies feed, by organised shooting, so that a rinderpest epidemic is probably more effective in eliminating the food supplies of tsetse than shooting. This might explain why the great Rhodesian fly belts referred to by Swynnerton (1936) were evacuated by the fly.

THE FACTS ABOUT GAME DESTRUCTION

It is now necessary to consider whether game destruction is effective in tsetse control and if so, is it justified.

" The destruction of game as a method of controlling tsetse and trypanosomiasis of domestic stock is regarded by everybody as regrettable and is a matter on which the public is much exercised. As considerable misunderstandings have arisen and as ignorance continues to be prevalent, the facts should be considered and discussed at length " (Buxton 1948).

Nevertheless, Buxton was clearly in favour of game destruction under certain circumstances, for he said that the evidence available (at that time) shewed convincingly that *G. morsitans* and probably its relatives could be completely expelled from an area by the destruction of game. Hornby (1949) thought the same. One wonders, however, if Buxton would still have held that opinion had he possessed the information about the feeding habits of tsetse which has since been acquired as well as the findings of Lovemore (1963) and Bernacca (1963b) on the effects of shooting on the smaller ungulate populations?

Even Weitz (1964) seems to be in favour of game destruction as a practical method of tsetse control. In a further article on the feeding habits of tsetse flies he says: " The organisms that cause the disease, trypanosomes, live in wild animals and are collected by the blood sucking flies when they feed. Thus both the fly and the trypanosome reservoir can be destroyed by killing off the appropriate wild animals".

Later, he writes: " The elimination of tsetse fly by insecticide spraying is very efficient but it has the serious disadvantage of leaving the main reservoir of trypanosomiasis untouched ". He indicates that the idea of controlling or eliminating tsetse flies in selected areas by killing the game is attractive and suggests that the species of animals that are never attacked by tsetse flies could reasonably be left without providing new sources of food. But flies such as the *palpalis* and *morsitans* groups probably have too wide a range of possible hosts to suffer greatly by the selective elimination of their preferred hosts, although other tsetse flies such as *G. pallidipes, G. longipalpis, G. longipennis* and *G. fusca* might suffer much more severely by the removal of the few hosts they normally preferentially feed on.

These arguments are not only difficult to follow but are contradictory, because: (1) If all game animals were destroyed except zebra, waterbuck, wildebeest, impala, hartebeest and most small mammals, the fly might be eliminated by starvation but the trypanosome reservoir would still remain; and he recognises this fact because he says "The comparatively high rate of infection with trypanosomes of species such as zebra, impala and hartebeest which are infrequently bitten by *Glossina* suggests that infections are transmitted by other vectors. These might be tabanid flies or *Haematopota* carrying infected blood on the proboscis". (2) His suggestion that in addition to *palpalis*, the *morsitans* group has too wide a range of possible hosts to suffer greatly by the selective elimination of their preferred hosts, is contrary to the findings of Potts and Jackson (1954) and apparently ignores the fact that all the game destruction campaigns in Southern Rhodesia, Northern Rhodesia, Mozambique, Uganda and the Sudan were directed against *G. morsitans*, with the indecisive results so often repeated in this paper. (3) The suggestion that *G. pallidipes* might suffer more severely by the removal of the few hosts it normally feeds on is again contrary to the findings of Potts and Jackson (1954) who demonstrated that in the game destruction experiment at Shinyanga, *G. pallidipes* was the most difficult fly to eliminate. In Zululand, an attempt to exterminate *G. pallidipes* by means of game destruction failed (Corson 1957). Furthermore, *G. pallidipes* is itself a member of the *morsitans* group (Buxton 1955).

According to Hocking et al (1963), Southern Rhodesia, Northern Rhodesia, Uganda, Portuguese East Africa and Bechuanaland have all used game destruction as a means of tsetse control and have cleared many thousand square miles of fly but they also say that "every government in Africa should be aware by now of the potentialities of its game stock and of the necessity for slowing down destruction while the best ways of exploiting its value are worked out". This statement is particularly important in view of certain plans and policies to be noted later.

Game destruction was first introduced into Southern Rhodesia in 1919 as an experiment. From 1922 onwards it was generally adopted as an effective method for dealing with tsetse advances. Ten thousand square miles of country were freed of fly between 1932 and 1948 by killing the game and it was claimed that by so doing 51,000 square miles of country was protected from tsetse invasion (Thomas 1955). But it must be remembered that observation, not scientific tsetse fly food checks, was the main criterion in those days.

Between 1950-51, 28,489 head of wild animals were destroyed in tsetse control measures in Southern Rhodesia (Whellan 1953). Twenty-three species were involved.

Since 1951, many thousands more animals have been shot in Southern Rhodesia in tsetse control operations in different parts of the country. In every area the fly numbers were reduced to nil, or a very low figure, and so was the incidence of trypanosomiasis in the local herds of cattle. Now, however, there are again build-ups of fly and encroachments of trypanosomiasis in many of these " cleared " areas.

As a result of requests from the " East African Standing Committee for Tsetse and Trypanosomiasis Research," a game destruction experiment was begun in Shinyanga in Tanganyika in 1945. (Potts and Jackson 1952). " The experimental area comprised some 600 square miles of uninhabited bush country. . . ."

" The primary object (of the experiment) was to determine whether the common savannah species of tsetse, *Glossina morsitans* Westwood, *G. swynnertoni* Austen and *G. pallidipes* Austen, could be eradicated by the destruction of the hoofed game animals under conditions prevailing in Tanganyika and if so, over what period and at what cost.

" Twenty species of game animals were shot according to orders and the total number of animals recorded as killed was 8,554. In addition to these, 7 species of smaller animals were believed shot against orders; these included the *Suidae*. Lion and leopard were shot or trapped wherever possible.

"At the beginning of the experiment the density of animals in the area was about 10 to the square mile, which is very low compared with records from national parks, and the authors said that the evidence available shewed that the Tanganyika bushland was understocked with game. It is very much more so now.

"*G. morsitans* and *G. swynnertoni* were exterminated and *G. pallidipes* "may or may not have been exterminated but it was certainly very rare. This result was achieved in spite of a considerable invasion of the area by cattle. . . ." The cost was £50 per square mile and the experiment took 4½ years to complete. The authors concluded by saying that " game destruction is not recommended except in isolated areas of manageable size. . . ."

In the light of more recent knowledge, one wonders if the same result would have been achieved if the *Suidae* and 7 species of smaller antelope had not been shot " against orders ".

Lloyd et al (1927), devised a game exclusion experiment at Sherifuri in which they fenced half a square mile of *G. tachinoides* and *G. morsitans* infested country around a pool. The fence was 5½ feet high and cost £700 but warthog and even duiker broke through it and a second run of wire 2½ feet high had to be erected. Before it was fenced, the pool had been used by antelope, buffalo and other animals. Birds and monitor lizards were abundant but they could not be excluded by the fence. *G. tachinoides* seemed to be unaffected by the absence of game animals. The density of *G. morsitans*, however, was markedly reduced but the absence of its natural food necessitated its feeding more frequently on birds and man. Although promising, it was concluded that this experiment was not a success as a practical means of tsetse control, but it did indicate that *G. morsitans* might change its feeding habits if forced to do so.

However, Nash (1948), thought that in Northern Nigeria the indirect evidence that *G. morsitans* occurred only where game had survived and the human population was scanty, strongly suggested that game destruction in small *G. morsitans* belts might be a cheap and successful method of exterminating this fly.

The effects of hunting are considered by Nash (1948) in discussing a serious outbreak of sleeping sickness which had occurred in the Rukuba country on the edge of the Jos plateau in Northern Nigeria in 1944. He said: " Game is completely absent, the pagans going as far as 20 miles to hunt, even then they do not seem to get much, as I saw some 500 painted warriors return with only 1 much-speared serval cat. No trace of monitor lizards was seen and there can be little doubt that the fly (*G. palpalis*) are dependent on man, his goats and his dogs. Man-fly contact was extremely close ".

Fortunately, Nigeria has never resorted to game destruction as a means of tsetse control and now with their successful modern methods of insecticidal spraying, the thought of it is no longer necessary.

On the Gold Coast, Morris found that by shooting four species of game animals only, i.e. roan antelope, hartebeest, waterbuck and warthog, their numbers were reduced and with them the numbers of *G. morsitans*. As the animals filtered back after shooting had ceased, the fly population increased (Fairbairn 1948).

From Weitz's serological tests it seems likely that only two of these species of animals were important to the fly, i.e. roan antelope and warthog. Furthermore, Morris's results are not unlike what has occurred in Southern Rhodesia since shooting was stopped there.

Game destruction as a practical means of tsetse control was started in Uganda in 1945. A. G. Robertson and Bernacca (1958), in their paper on the subject, said " With a strictly limited amount of assistance from subsidiary bush clearing, the application of tsetse control measures of game elimination in the long-grassed *Combretum* savannah areas of Central Uganda during the years 1945-1957 was successful in:—

"(a) halting at least two major advances of *G. pallidipes* and one of *G. morsitans*, which between them constituted extremely serious threats to the cattle industry of the Protectorate and also by threatening to spread Rhodesian sleeping sickness from the area of the 1941-42 outbreak in South Busoga to the people of the greater part of Buganda;

"(b) reclaiming entirely from *G. morsitans* and *G. pallidipes* some 4,800 square miles of country, consisting of—(i) 2,500 square miles infested by *G. pallidipes* and *G. morsitans* in Buruli and Bulemezi, Mengo district; (ii) 500 square miles infested by *G. pallidipes* in Bugerere, Mengo district; (iii) 1,800 square miles infested by *G. morsitans* in Acholi district;

"(c) making good progress in the reclamation of—(i) 700 square miles from *G. morsitans* and *G. pallidipes* in Maruzi-Kwani, Lango district; (ii) 800 square miles from *G. morsitans* and *G. pallidipes* in Buruli, Bunyoro district.

" Totals of animals shot by tsetse control hunters to achieve these results in the fully reclaimed areas were 2,179 buffalo, 59 hippopotami, 10 rhinoceros and 25,163 smaller game animals. Bushbuck, which have been shewn to be a specially favoured food of *G. pallidipes*, gave the most numerous kills of the smaller game animals with a total of 4,901. On the basis of a total hunting area of 4,500 square miles, these figures give a mean kill of 6 animals per square mile ".

The overall cost of these operations was approximately Shs. 2/- per acre. Veterinary statistics also shewed that the cattle population of Uganda increased between the years 1945 and 1956 from 2,294000 to 3,094,000—an increase of 800,000, worth about £10,000,000. It was claimed that a large proportion of this prosperity in the cattle industry could be ascribed to successful game elimination operations but no mention is made of the effects of the tremendous trypanocidal drug campaign carried on simultaneously in Ankole alone by the Uganda Veterinary Department.

Successful as these operations seemed at the time, re-invasion took place in some of the areas concerned.

In the foreword to his 1960-61 Report, A. G. Robertson (1962), wrote:

" During the 1930's and early 1940's, the cattle industry of Uganda was very seriously threatened by a series of widespread and rapid advances of the savannah tsetse *G. morsitans* and *G. pallidipes*. These advances occurred mainly in Central and Northern Uganda, in the Buganda and Northern Provinces. In all, they spread over and hence denied to cattle, more than 8,000 square miles of the best grazing lands in the country.

" By 1956, more than 7,000 square miles of this newly-infested country had been successfully reclaimed. But meanwhile, and despite four years of very strenuous operations of a special C.D. and W. scheme of reclamation by discriminative bush-clearing (undertaken by the East African Trypanosomiasis Research Organisation), a further major advance of *G. morsitans* had occurred in Ankole district in Southern Uganda. With the primary objective of preventing still further extension of this fly-belt, intensified bush-clearing measures were applied during 1956/57; but most unfortunately these proved quite ineffective. It thus became necessary—as the only feasible means of putting an early end to still further advances of fly—for the Uganda Government to embark, in mid-1958, on reduction of the game populations around the northern and easter margins of the vastly expanded fly-belt. By mid-1961, after three years of hunting, this primary objective had been achieved; along much of the former fly-front a recession of from ten to twenty miles had been brought about and the stage had thus been set for work to begin on the extensive task of reclaiming the core of this *G. morsitans* belt by insecticidal means.

" Since about mid-1958, widespread upsurges in populations of the savannah tsetses have occurred in several of the residual reclamation areas in Northern and Central Uganda. In these areas also much still remains to be done therefore to complete the resolution of the major reclamation tasks which faced the Department of Tsetse Control when it came into being in 1947."

The reason the C.D. and W. scheme of discriminative bush-clearing failed was because the ecology of *G. morsitans* under the conditions pertaining in Ankole at the time was not clearly understood.

In the meantime, re-invasion by *G. morsitans* of the eastern part of Uganda, which had been successfully reclaimed between 1951-56, took place. " Intensive survey from November 1960 to March 1961 revealed that, having broken through a ' weak link ' in the north-eastern part of the northern Bunyoro consolidation line (in the region south of Kigumba), *G. morsitans* had pentrated some 15-20 miles southwards and re-established itself in appreciable density in a ' focal area ' of some 16 square miles in the Bunyoro Ranch. By means of combined spraying and hunting measures introduced early in 1961, a considerable improvement in the situation had been effected by the end of the report period ".

In his 1961-62 Annual Report, Bernacca (1963a) wrote . . . " In the Ankole-Masaka *G. morsitans* belt, where hunting operations which started in July 1958 had by mid-1961 reduced the tsetse populations to extremely low levels, further very satisfactory progress was made. Since the end of 1961, in large portions of the former tsetse-infested area of Masaka and in the central part of the Ankole area, the hunting effort was maintained at the minimum required to prevent extensive influx of game. For much of the period it appeared that it remained only to demonstrate that most of the area was at last free of tsetse. This, however, has proved to be less easily accomplished than had been hoped and both in Masaka and Ankole surprises have occurred.

" In Masaka during the latter part of 1961, the hunting effort was progressively reduced, as only two *G. morsitans* had been caught since July 1960; one in the eastern part of the area in January 1961 and one in November 1960 near Ankole border. Unfortunately in December 1961 three *G. morsitans* were caught within a few miles of each other in the far north near Kakoma. This was eighteen months after the last tsetse had been seen anywhere in Northern Masaka "

The eradication of *G. morsitans ugandensis* Vanderplank from the Jur Narrows in the Sudan is described by Abdel el Tahir Abdel-Razig (1964); " Here game destruction combined with the use of insecticided bait animals during the final stages of reclamation worked out successfully in reclaiming four islands of the Jur Narrows of the Sudan from *Glossina morsitans ugandensis* in slightly more than six years ". The author claims that game destruction was justified for the special conditions of the Jur Narrows where other methods were either too expensive or not applicable for several environmental, social and economic reasons and says that some methods, like aerial spraying, besides being too expensive are not reliable as they would not effect a 100 per cent. control. It is unfortunate, however, that he does not appear to have tried ground application of insecticides in the same way as they have been used in Northern Nigeria and in Uganda, where 100 per cent control has been effected after one application only.

The experiment was started in 1954 and covered an approximate area of 15,000 square miles in the Bahr el Gazal region of the Upper Nile Province.

Data obtained from precipitin tests shewed that *G. morsitans* fed mainly on buffalo, tiang (*Damaliscus korrigum*), and warthog and, to a lesser extent, on bushbuck, oribi, kob and baboon in this order.

Reference to the tables indicates that according to Weitz's findings, a number of different animals were killed unnecessarily, for instance waterbuck, and one wonders whether warthog, duiker, bushbuck, etc., were really exterminated. Nevertheless, if the survey methods used were reliable, the fact that in many of the areas concerned no flies have been caught for more than five years makes it reasonable to claim complete eradication but the scientific validity of the experiment is marred by the introduction of other methods, i.e. bait animals and bait screens.

The above information stresses the importance of the fact that a fly and trypanosomiasis-free period of at least five years is necessary to prove extermination.

Lovemore (1963), in discussing the effects of anti-tsetse shooting operations in Southern Rhodesia, said: "It is pleasing, however, to record that this distasteful method has now been almost completely abandoned in favour of discriminative spraying, with residual insecticides applied from the ground".

The Sebungwe shooting operation in Southern Rhodesia was in force from June 1958 to October 1960 and Lovemore gives a list of the animals killed, which were: elephant, buffalo, eland, roan antelope, sable antelope, kudu, waterbuck, tsessebe, zebra, impala, reedbuck, duiker, steenbuck, Sharpe's grysbok, warthog, bushpig, hyaena and wild dog.

Elephant were soon eliminated and presented little difficulty during the last twelve months of the work.

The number of larger antelope, e.g. sable, roan, eland and kudu shot at the end of the operation had been reduced to just over half what it was at the beginning. It was thought that the explanation for this was that these animals represented the "overflow" from the untouched population north of the game fence which had been constructed to protect the reclaimed area, as it was believed that very few resident animals remained within it.

The numbers of warthog decreased markedly and by the end of the first year had been reduced to about 50 per cent but after the wet season of 1959-60 the number killed began to increase and it seemed as if some form of balance had been created between the warthog population and the hunting. It was not thought that their numbers could have been supplemented by immigration since these animals tend to be local in habit. A similar effect was noted with bushpig and these are favoured food hosts of *G. morsitans*.

A total of 10,836 duiker were shot within the area during the 29 months of hunting but it appeared that even using shot-guns, the number killed had not begun to surpass the natural increase from the breeding population of these animals. This, Lovemore said, is a point in favour of retaining duiker for a game cropping regime since they are not favoured food hosts.

Lovemore ends by saying that from these results it might be concluded that where a zone of country adjacent to an extensive source of game is demarcated by fences, intensive cropping of game animals can be carried out without noticeably depleting the general population outside the killing zone. The larger antelope cease to be resident but maintain a steady immigration. The smaller animals, such as duiker and warthog, remain " and perhaps relieved of the competition from other animals as a result of the shooting, appear to flourish ".

Apart from their cropping value, these results do not support a case for further shooting campaigns: (a) because they shew that it is impossible to exterminate the smaller ungulates, and (b) because the larger animals are able to continue to migrate into the shooting areas from outside.

In Uganda after 4½ years of shooting in the Ankole area, Bernacca (1963b), recorded similar results; buffalo, waterbuck, eland, warthog and oribi were entirely eliminated, though a few persisted by immigrating into the shooting area. Duiker appeared to be unaffected by shooting, bushbuck were reduced by 33 per cent and were still declining very slowly but given time the population might stabilise at one-third of the original. Reedbuck were reduced by 50 per cent and appeared to be still going down very slowly. The fly (*G. morsitans*) appeared to have been exterminated but the question now arises as to whether this could not have been done by shooting only buffalo, eland and warthog.

It is curious that the warthog should have been eliminated so easily when duiker, bushbuck and reedbuck were not but the figures shew that the wart-hog population was not very great when shooting began and the area concerned may not have been a suitable habitat for this animal, so that it was easy to exterminate where it may not have been elsewhere under more favourable habitat conditions.

There are other aspects to this problem which require consideration. Bere (1963), said " shooting as a means of eliminating tsetse becomes intelligible only if the land cleared is immediately put to intensive human use; and this does not always happen, nor is the land indeed always capable of supporting such activity ".

There is further the psychological effect of public opinion to be taken into account. A good example of this is given by Bere (1963), in the same article when he says: " Early in the nineteen-fifties a conservation-minded district officer asked his district council to discuss game control and preserva-tion in general. This was in the Acholi district where there is a long tradition of highly organised tribal hunting. In due course the council passed a distressing resolution—that from time immemorial the tribe had practised conservation through their traditional hunting system but that the govern-ment appeared to be against the policy of conserving wild animals as was evidenced by the widespread tsetse control hunting in their country ".

Fairbairn (1948) quotes Sir David Bruce in 1914, who was referring to conditions in sleeping sickness areas in Nyasaland where man and game animals lived in close association, as saying: " It is self-evident that these wild animals should not be allowed to live in 'fly-country' where they constitute a standing danger to the inhabitants and the domestic animals. It would be as reasonable to allow mad dogs to live and be protected by law in our English towns and villages. Not only should all game laws restricting their destruction in 'fly-country' be removed, but active measures should be taken for their early and complete blotting out".

It is difficult to understand such an attitude today but there is little doubt that it was largely responsible for much of the thoughtless and wanton destruction of wild animals that took place for a long time.

Next there is the practical problem of making proper use of the land after it has been reclaimed from tsetse. Lewis (1952), in a report on land use and tsetse control to the East African Advisory Council on Agriculture, Animal Husbandry and Forestry, said: "It is clear that unless the gains achieved against this fly (*G. morsitans*) by game control are consolidated by supplementary bush-clearing and full utilisation of the land reclaimed, or by constant vigilance on a long front for an indefinite period, there will always be danger of re-infestation and of its consequent disasters".

Because of the apparent diversity of views on this subject, it is felt that the evidence both for and against game destruction as a practical method of tsetse control needs to be summarised and more carefully assessed.

A. *Advantages:*

1. Game destruction is a quick method of reducing tsetse populations, particularly *G. morsitans*, but only in the early stages, becoming more and more indecisive later on.
2. Compared with bush-clearing and the application of insecticides, it is easy to carry out. Nevertheless, extensive and highly organised shooting teams are required.
3. It is cheaper than any other known method, especially in the early stages. This would appear to be so according to the findings in Southern Rhodesia and Uganda, but Clarke (1964), in Northern Rhodesia said: "Game elimination, if it is to be successful, is a lengthy process extending over many years and apart from the repugnance which must be felt at the thought of the destruction of the indigenous fauna, the costs are likely to be high, so that all efforts should be made to ensure that the most effective use is made of this method".
4. Applied in conjunction with insecticides and bush-clearing, even quicker and more decisive results may be expected, but because of the very nature of such combined operations there is no means of assessing to what extent game destruction has contributed to their success or otherwise.

5. The results of game destruction may be particularly quick and effective in areas where the fly is near the limit of its range if the controlling factors are climatic, e.g. rainfall, latitude or altitude. These may have contributed to the initial spectacular successes in Southern Rhodesia and Uganda. But even so, no completely decisive results have so far been recorded from these countries or even the Sudan, as there, game destruction was carried out in conjunction with the use of insecticides.

B. *Disadvantages :*

1. Game destruction has only been shewn to be effective against *G. morsitans* and *G. swynnertoni* in one scientifically conducted experiment. Since Potts and Jackson's work was done, no one else has attempted to exterminate *G. swynnertoni* by game destruction and from the results of Weitz's serological tests it would seem unlikely to be successful again, particularly on a large scale. *G. morsitans* can adapt itself to feeding on cattle, other domestic stock and even man. Pilson and Harley (1959), found that 52 out of 98 engorged *G. morsitans* collected from the game eradication area in Ankole had fed on cattle, so that under conditions obtaining there, *G. morsitans* might be able to maintain itself on cattle alone.

2. Lovemore, in Southern Rhodesia, and Bernacca, in Uganda, have both shewn that it is impossible to exterminate many of the smaller ungulates, e.g. the *Suidae* (in S. Rhodesia), bushbuck, reedbuck and duiker, yet some of these animals, notably warthog and bushpig, are the favoured hosts of most tsetse flies, even *G. morsitans.*

3. After the initial spectacular reduction in fly which usually occurs with game destruction, the rate of reclamation decreases in spite of more intensive shooting (Langridge et al 1963, quoting Ford) and some animals may even continue to flourish as Lovemore and Bernacca have shown .

4. Most game destruction operations are carried out over large tracts of country, therefore unless the areas concerned are flanked on all sides by open fly-free country or dense settlement, there is always a danger of re-infestation (Bere 1963; Lewis 1952).

5. If it is the intention to follow up tsetse eradication with proper methods of land use, such as close settlement and intensive cultivation, what is the point in destroying the game by shooting, as both the game and the tsetse will be eradicated automatically by the settlement ?

6. No effective method of assessing very low tsetse populations has yet been devised. It is therefore not safe to claim complete eradication in any particular area until no flies and no cases of trypanosomiasis have occurred for at least five years. The importance of this fact has been shewn clearly in Kenya where small numbers of *G. fuscipes* on the Kuja and Nyando rivers were suddenly found in areas which had been thought to be freed of fly after the use of insecticides and where constant fly patrols had been carried out for nearly five years.

Apart from the six disadvantages listed above, there are other factors not purely materialistic to be taken into account:—

I. " *The scientific case for the preservation of wild life* in Africa for the direct benefit of humanity is very strong; also the provision of meat, the conservation of vegetation and thereby the vital soil. If we add the aesthetic recreational and educational value of wild life and even its economic value as a tourist attraction, is not our case overwhelming? We ask for a reconsideration everywhere of the policy of slaughter so that wild life, for its own sake and for the sake of humanity, may remain alive in the environment to which it is so beautifully adapted " (Oryx 1959).

Surely the living beauty of nature itself is worthy of conservation as well as intelligent utilization.

II. Professor Pearsall (1959), in discussing *game protection as a form of land-use*, indicated that there are two facets to the problem. The first is that we are unlikely to find domestic breeds of animal which are so well attuned to their habitat as wild animals. Therefore, game is a valuable protein reservoir. The second is that herding, overgrazing and the constant use of fire by pastoralists (and primitive mixed farmers) degrade the vegetation from types selected naturally for high protein production to fire-resistant unpalatable species.

Professor Pearsall concludes by making a plea for the detailed study of the natural ecological systems " in their entirety before they have been wholly destroyed in favour of alleged improvements ".

Unfortunately, in Kenya in almost no instance where land has been reclaimed from tsetse, has there been a follow-up of proper land use because so far no agriculturist or administrator has been strong enough to enforce it or instil into the minds of primitive people the discipline of correct land usage after tsetse clearance.

III. As has been shewn, a great deal of information is now available about the use of insecticides, bush control and other methods of tsetse reclamation which have been used successfully at low cost in East, West and Central Africa.

In opposition to this statement, it has been argued that the damage done to the fauna in areas treated with insecticides must be very great but apart from the trivial instances quoted earlier, there is no evidence to support this argument. This fact is corroborated by the results of an experiment carried out in Uganda when the present large-scale insecticidal operations were begun in Ankole: "As fears had been expressed that the spraying operations might result in high mortality among wild birds and mammals, searches after spraying were made in an area where a very carefully planned and supervised experiment had been mounted using sprays at a concentration of 3.1 per cent dieldrin. Three small birds and one rodent were found dead but on one day alone, 15 game animals were observed alive and apparently healthy. At no time during or after this spraying trial was any game animal found dead or suffering from anything that could be attributed to poisoning by insecticide" (Bernacca 1963a).

It is clear, therefore, that the five apparent advantages in favour of game destruction are far outweighed by the six disadvantages and three other considerations.

In spite of this fact, however, there are rumours abroad that large-scale tsetse operations are being planned for certain parts of Southern Rhodesia and that one of a combination of methods to be employed will again be "game destruction".

A serious increase in fly and hence an increase in the incidence of trypanosomiasis, has been claimed in several areas where shooting has been discontinued but the converse argument that fly numbers have increased because complete extermination was not achieved before the killing of game was stopped, would seem the more valid one.

Further, it has even been suggested that attempts to maintain cattle in tsetse infested areas with the use of trypanocidal drugs has led to an increase in the fly because the tsetse are adapting themselves to feeding on cattle. In fact, the findings of Pilson and Harley (1959), in Uganda support this theory. Viewed logically, it means that cattle too should be eliminated if they occur in tsetse areas, particularly if the advice of Sir David Bruce were to be heeded.

To support the rumours about Southern Rhodesia, this paragraph appeared in the July 1964 number of Scientific South Africa (p. 355): "TSETSE THREAT —An insidious and little publicised threat to the Republic is the advance of tsetse fly towards the country's northern border from Southern Rhodesia. The present state of knowledge of preventive measures involves either aerial spraying, which is prohibitively costly, or large-scale destruction of wild game. For the last four years little or no game destruction has been practised in Rhodesia and this may explain the alarming advance of the pest. Whether it does or not, there is promise of maddening argument between agriculturists and preservationists ".

Finally, the following abstract may be of interest, particularly as Zululand is much further south than Southern Rhodesia and therefore even more " marginal " as a tsetse habitat:—

" Game destruction was carried out within and on the perimeters (buffer zones) of the three game reserves in Zululand with the object of protecting farmers' livestock from *Glossina pallidipes* and of observing the effect on the density of this tsetse fly. The game reserves were the Umfolosi (in the angle between the Black and White Umfolosi rivers), the Mkuzi (on the south bank of the Mkuzi river about 50 miles N.W. of the Umfolosi reserve) and the Hluhluwe reserve (between the other two). Two campaigns were conducted; from June 1929 to December 1930 the shooting was done chiefly on the perimeters, 36,704 animals being killed including 1,530 zebra; from 1942 (Umfolosi) and 1944 (Mkuzi) to 1950, animals were shot both in the perimeters and within the reserves and 8,499 were shot on the shores of Lake St. Lucia. Altogether, 138,339 animals were killed. The total area in which the shooting was done was only 400-500 sq. miles. The shooting ceased in May 1950 and in September of that year duiker, steenbuck, warthog, bushbuck and reedbuck were found to be very numerous in the Umfolosi reserve where 70,000 animals had been shot in the preceding seven years.

" The density of the tsetse flies was greatest in 1931; it decreased steadily until 1938, remained steady until 1941, then increased rapidly until 1947 when an attack was made with insecticides sprayed from aircraft.

" The author concludes that the increase of the fly-density was not prevented by the destruction of the wild game " (Corson 1951).

The attack with insecticides in Zululand, though costly, proved completely successful (du Toit 1964). Great advances have been made in the use of insecticides since that time, particularly in methods of applying them from the ground and today they are the most effective weapon in use against the tsetse.

Although Hocking et al (1963) claim that game destruction has been and still in some circumstances may be an economical and practical method of tsetse control, the writer is firmly convinced both from his own experience and assessment of other workers' experimental data (discussed above), that there is no valid justification for using game destruction as a practical or lasting means of tsetse control, particularly on new or future projects.

MODERN TRENDS OF RESEARCH

In order to gain an idea of what the future development in tsetse and trypanosomiasis control may be, some of the modern trends in research are considered below.

At the I.S.C.T.R./C.C.T.A. " Meeting of Experts on Trypanosomiasis " held in Lagos in 1963, the following resolution was passed:

> "The MEETING wishes to emphasise that the magnitude and complexity of the problems of human and animal trypanosomiasis are such that, although very substantial progress has been made in the past, there remains a vast field in which research is still needed to improve understanding and control of the diseases involved. Notable successes have been achieved in the treatment of the diseases of both man and animals and also in control of the vector tsetse-fly, but the presence of tsetse-borne trypanosomiasis in some four million square miles (10 million square kilometers) of Africa constitutes a most formidable obstacle to the development of the continent. Success in surmounting this obstacle depends upon knowledge of many complex factors. . . ."

A great deal has been done on the study of tsetse populations and their assessment to discover: 1. what species of fly occur in any particular area; 2. in what numbers; 3. in what proportions of male, female, young flies, engorged and hungry flies; 4. what are their haunts and habits, etc.

Carpenter (1913 and 1919) and Fiske (1920), in Uganda, devised a method of calculating the density of *G. palpalis* (*G. fuscipes*) by the number of flies taken per catcher per hour from a standing position. This was known as " flies per boy hour ".

Potts (1930) evolved the " fly-round " method of measuring populations of *G. morsitans* in Tanganyika.

Nash (1933b), also in Tanganyika, produced an improved method of estimating tsetse density expressed as " flies per boy per 100 yards ".

At Katabu in Nigeria in 1944, Nash, in studying *G. palpalis* (R.-D.), subdivided the section for each vegetation type into 100-yard long sub-sections and used " F.B.100 Y." for his unit (Nash and Page 1953).

Swynnerton (1936) and his colleagues in East Africa found it more convenient to make the distance unit 10,000 yards.

Nash (1933b) distinguished " apparent density " from " true density " of the total population and eventually Nash's work, his own and that of others, led Jackson (1933b) to the concept of " standard availability ", which was extremely valuable because it made possible the correlation of fly-round data with population studies (Buxton 1955). This method has been in general use in East Africa ever since for studying populations of *G. morsitans* and *G. swynnertoni* but it does not apply well to *G. pallidipes* which does not come readily to man, nor to the crepuscular flies such as *G. longipennis* (Power 1964). Nor does it always apply to *G. morsitans* under different habitat conditions from those in Tanganyika where Jackson worked.

This point is demonstrated by Harley (1958), who obtained estimates of the standard availability of *G. morsitans* in two areas in Ankole in Uganda which gave the maximum and minimum fiducial limits of 2.0 and 0.19 per cent. These were much lower than the estimate of approximately 10 per cent obtained by Jackson in Tanganyika. This difference is of practical importance in that it indicates that a single fly caught in Ankole represents a much larger population than a single fly caught in Tanganyika and may be the explanation for the reason why routine catches around the edges of the fly belt in Ankole reveal very few flies (Langridge et al 1963).

So far, no reliable method of accurately assessing the numbers in tsetse populations has been devised. Therefore, the development of more efficient methods of tsetse survey is essential because there is no means of discovering whether tsetse flies have disappeared from any particular area after control measures have been applied except over a long period of time. Further, many so-called "fly advances" and "recessions" may merely be the result of a build-up or reduction in the numbers of fly which cannot be detected accurately in small numbers.

Arising from this information, the use of efficient scent attractants, radio-active substances and chemo-sterilants may go some way towards solving the problems which are at present so difficult to overcome.

1. *Experiments with attractant substances.* Langridge (1960-62), in a number of field trials, demonstrated that a crude extract of pig hair and skin scrapings applied to traps, screens and even paths could greatly increase the catches of *G. pallidipes, G. swynnertoni* and *G. fuscipes.* But much remains to be done, as it is not yet known what the attractive components of this substance are. When this is known, it may be possible to produce better, more stable attractants which would assist the efficiency of field survey work.
2. *Studies in the use of radio-active and chemo-sterilants* as a means of exterminating residual low fly densities. A successful operation was carried out against screw worm (*Callitroga hominivorax coquerel*) on the island of Curacao by irradiating the pupae of this fly (Baumhover et al 1955).

   Radio-active sterilisation as a means of controlling tsetse flies presents many problems. Potts (1958), found that 3,000 to 30,000 r.s.p. doses of gamma radiation had little effect on pupal mortality but the longevity of male flies was roughly halved, the mating ability was not affected and both sexes retained some fertility (Chadwick 1964).

The use of chemicals in sterilising insects without adversely affecting their sexual vigour and behaviour is receiving much attention in the United States of America (Lindquist 1961). A project for the exploratory study of the practicability of using chemo-sterilisation as a weapon against the tsetse fly is being undertaken in Southern Rhodesia under the supervision of the U.S. Department of Agriculture with funds supplied by U.S.A.I.D. In addition, they are beginning a study of the sterilisation of tsetse by radiation from the cobalt bomb (I.B.A.H. Information Leaflet Vol. XII.—No. 38, June 1964). Apart from their possible effect on low density populations of fly, chemo-sterilants may have interesting possibilities in combination with insecticides, in that insecticides might act more quickly on weaker or less resistant flies and chemo-sterilants on those possessing some resistance to insecticides (Glover and Langridge 1962).

Chadwick (1964b) described some exploratory laboratory work on the effects on *G. morsitans* of two chemo-sterilants " apholate " and " metepa ", tested by the Tropical Pesticide Research Institute in Tanganyika. Wild pupae were collected from the bush near Singida and each treated with 0.1 micrograms of chemo-sterilant on arrival. Adult flies were dosed on the day of emergence from the pupa with 0.5 micrograms of chemo-sterilant dissolved in 0.5 microlitres of methyl-ethyl-ketone " using an Agla micrometer syringe fitted with a ratchet drive ". The results shewed that the two compounds had roughly similar effects on adult flies. Treated males mated with untreated females caused a 40 per cent. reduction in the number of pupae produced. Females treated with apholate did not breed and metepa reduced the number of pupae per female to 18 per cent. of the control group. Treating both sexes with metepa, only a single female produced any pupae. Females treated with apholate had a mean life of 16.6 days compared with 34 days for the control group. With metepa, the mean life of females was 15.6 days. Treated females mated with treated males had a mean life of 8.8 days with apholate and 5.3 days with metepa but untreated females mated with treated males had a mean life of 52 days with apholate and 46 days with metepa, compared with 34 days in the control group. (These results are curious and should be repeated). Males treated with apholate had a mean life of 12.5 days and metepa 13.1 days; those in the control group 17.2 days.

Pupae resulting from matings of treated flies were few but no great reliability can be attached to the figures. However, the emergence was low when only the male parent had been treated with metepa and the effect was less marked with apholate. With untreated parents, the emergence rate in the second generation was 72 per cent. but the life of these flies was very short.

Chadwick concluded that although these experiments were only exploratory, they strongly suggested that the use of these two substances applied "topically" was "not likely to be a rewarding technique in the control of tsetse". He suggested, however, three different possible lines of procedure for the practical application of chemi-sterilants in the field. 1) Dosing wild pupae and placing them in suitable breeding sites, or keeping the treated pupae until the adult flies had hatched and then releasing them. 2) Dosing male flies and releasing them. 3) Applying a residual film of chemo-sterilant to the resting sites of tsetse flies.

Experiments in breeding tsetse flies artificially. Before the two new methods mentioned above can be put to practical use, intensified investigation will have to be undertaken into the artificial production of large numbers of tsetse pupae. This also is being done in Rhodesia.

Other important lines for investigation are:

1. *Ecological studies on the effect of bush clearing on small mammal, reptile, bird and insect populations* should be carried out in addition to physiological studies on tsetse flies affected by different methods of discriminative clearing to ascertain why such control measures are not always effective (Lagos Meeting 1963). These studies are urgently needed and it is surprising that nothing has been done so far.
2. *More intensive scientific studies of the ecology of the fly* particularly its resting sites, its breeding sites, etc. A great deal has been done on the ecology of most tsetse flies of economic importance (Langridge et al 1963) but in Kenya comparatively little is known about *G. pallidipes* and *G. fuscipes*, especially about their resting sites and the assessment of their density. More precise knowledge of the ecology of tsetse flies may have great practical implications in future control measures. This was pointed out by Hocking et al (1963) who said ". . . as knowledge of the habits and behaviour of *Glossina* species grows, the discriminative applications of insecticides can be more precise, economic and effective. This method of using residual insecticides seems to be the most promising for the future".
3. *Closer studies of game-fly relationships are necessary.* Nothing is known about why flies are attracted to some animals and not to others; how they attack the animals; what diurnal and seasonal variations take place in the inter-relationships between different animals and different

tsetse flies; what is the maximum amount of food required to support a fly population of low density indefinitely; trypanosome infection rates in tsetse flies and different game animals, etc. Investigations in Kenya have shewn that the movements of preferred hosts caused by changes in the habitat brought about by fire or climatic variations, may influence the movement of tsetse flies. This in turn may influence the feeding habits of the fly and induce it to attack domestic stock.

4. *More intensive studies of the epidemiology of human trypanosomiasis.* At the meeting in Lagos, it was revealed that, in spite of the efforts made in the past 40 years to control human trypanosomiasis, certain residual foci appear to persist, so that the disease is liable to break out from time to time (Duggan 1962). It would appear that man is not the only reservoir, even to *Trypanosoma gambiense* (Willett 1963). Therefore the study of *T. gambiense* in animals as a link in the epidemiology of the disease is of great importance (Baldry 1964). Integrated intensive studies of the epidemiology of both human and animal trypanosomiasis are especially needed in selected areas using simultaneously the approaches of all pertinent disciplines. The MEETING recommended:

   a) the use of tranquilisers and narcotics to immobilise wild animals to enable samples to be collected for immune-serological and other studies.

   b) methods for testing indirectly the immune state of various species of animals in conjunction with the determination of the hosts of origin of the blood meals of tsetse flies. Game cropping and ranching wild animals should facilitate epidemiological and immunological studies of certain species.

5. *Experimentation in biological control of tsetse flies.* Buxton (1955), recommended that studies should be made of the enemies of tsetse flies as means of control, but since the early work of Lamborn (1925) in Nyasaland, Johnson and Lloyd (1923) and Taylor (1932) in Northern Nigeria, Nash (1933b), and Swynnerton (1936) in Tanganyika and Southon (1959) in Uganda, no further work appears to have been done in this field. Vanderplank (1944), carried out some trials on hybridization by cross-mating closely related species of tsetse flies and succeeded in producing a high degree of sterility in the offspring, but it failed as a practical measure of control.

   Parsons (1954), in studying a breeding place of *G. pallidipes* in riverine evergreen thicket in the Central Province of Kenya, found that the proportion of puparia parasitized by *Thyridanthrax* at different times of the year varied between 5 and 77 per cent.

High pupal parasitization has also been reported from other parts. This information lends weight to the statement made by Buxton (1955), that it was clear that nature was continually destroying some tsetse and that power was running to waste because little thought was being given to how it could be used. Further studies along these lines are obviously very desirable.

6. *Studies on resistance to insecticides.* So far there is no evidence of the appearance of resistance to insecticides in tsetse flies but Burnett (1961), demonstrated that old female *G. morsitans* (and to a smaller extent old female *G. swynnertoni*) had a certain amount of tolerance to some chlorinated hydrocarbon substances which are commonly used. Therefore further, more intensive studies along these lines are necessary.

7. *New researches in chemo-therapy.* Schneider (1963), in his review of the treatment of human trypanosomiasis, points out that remarkable results have been achieved by drug treatment both in the cure and the prevention of the disease, but no new or spectacular advances have recently been made.

Finelle (1962), in his report on recent work on the chemo-therapy of animal trypanosomiasis, said that although great progress had been made over the last ten years, chemo-therapy is still only a palliative. Several problems remain to be solved, such as the development of drug resistance in trypanosomes and the inter-relationship between chemotherapy and immunology. We must also await the development of radical methods such as breeding animals tolerant to trypanosomiasis or even an efficacious method of vaccination might be found.

Hawking (1963). in conducting experiments on the action of drugs upon *T. congolense*, *T. vivax* and *T. rhodesiense* in tsetse flies and in culture, discovered that " once the drugs, quinapyramine, Prothidium isometamidium and Berenil, are absorbed from the gut of the tsetse fly, they diffuse into the proboscis and hypopharynx and there destroy *T. vivax* ". This seems a promising line for further studies.

Perhaps it might not be too optimistic to hope that a similar approach to the recent researches into genetics (van Schaik 1964), which have made it possible to understand the chemical nature of the gene so that D.N.A. prepared from normal bone marrow can be used in the treatment of sickle-cell anaemia, might pave the way to a new biochemical approach in the treatment of trypanosomiasis and other protozoan diseases.

8. *New social and economic approaches* to the trypanosomiasis problem are required. It has been shewn that adequate techniques exist for the eradication and control of the disease but although many schemes have been planned in recent years as part of rural development, often the benefits of reclaimed land have been ignored and the land has remained unused, or been misused so that overgrazing and soil erosion have followed. Planning in tsetse control projects has frequently failed to assess adequately administrative and other socio-economic aspects.

   At the Meeting of Experts on Trypanosomiasis in Lagos in September 1963, the importance of this problem was fully appreciated and it was agreed that a MISSION should be formed consisting of experts in trypanosomiasis, rural development and socio-economics to review with local experts the areas of different economic potentials in Africa within the limits of the *Glossina* zone in relation to known techniques of trypanosomiasis control.

   The Mission would also assess the possibilities of success or failure in trypanosomiasis eradication or control schemes considered as integral parts of development plans, especially in the context of independent African nations.

Time is against us—but let us hope that the interests of politics do not influence the progress of science to the point of no return.

In conclusion, readers are referred to the statement made by Langridge et al (1963), that in spite of the fact that a quarter of the African continent is denied to domestic stock by the presence of trypanosomiasis, man and his animals multiply unchecked. Overpopulation is the greatest problem facing " emergent " Africa today, not trypanosomiasis.

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