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TRYPANOSOMIASIS IN ZULULAND AND THE CONTROL OF TSETSE FLIES BY CHEMICAL MEANS.

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CONTENTS.

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I. INTRODUCTION.

The progress of civilization and its extension into the far corners of the earth has, in all probability, suffered no greater setback than in the tropical parts of the continent of Africa. Of all factors responsible for this retardation of development no single cause has played a more profound role than the disease trypanosomiasis, which renders vast tracts of Africa untenable to man.

It has been estimated that the 20 odd species of tsetse flies belonging to the single genus *Glossina*, which transmit the trypanosomes causing the disease to man and animals, range over approximately 4,500,000 square miles of Africa. With the exception of a small area in south western Arabia, the genus is entirely confined to Africa.

In considering the disease as it occurs in man and animals, the highly lethal human forms have played an extremely important part, but the equally fatal forms occurring in domestic animals may be considered to have even more profoundly affected the development of many very extensive areas. Man, being an intelligent and reasoning being, is to a great extent capable of avoiding contact with the transmitting insects whereas he has been virtually powerless in adequately protecting his stock from attack. In his more primitive state and isolated within the extensive land mass of Africa, man cannot be separated from his domestic animals and their products as his very existence depends upon them. Consequently vast tracts have been shunned due to the devastating effect of nagana.

In excluding the encroachment of man into the domain where it lives in harmony with its hosts, the varied natural fauna of Africa, the tsetse fly has prevented to a large extent exploitation by overstocking and its attendant evils soil erosion and denudation of vegetational cover. The demand for expansion and the production of food to meet the ever increasing world requirements is insistent. The country must be rendered productive, particularly for stock raising to which it is well suited, in order to satisfy this ever increasing demand from without.

Very considerable advances have been made and our knowledge in dealing with the problem of animal and human trypanosomiasis has been added to enormously, especially in recent years. Two main avenues of approach to the problem present themselves. These may be described as—

(*a*) the therapeutic approach; and

(*b*) the entomological approach.

(*a*) The therapeutic approach to the problem has met with its greatest measure of success in the human field and in this respect in particular with that form of the disease caused by *Trypanosoma gambiense*. Although it is beyond the scope of this article to discuss the therapy of human trypanosomiasis, the marked success achieved in reducing the incidence of human sleeping sickness by therapeutic means alone in regions such as French Equatorial Africa, Belgian Congo, the Cameroons and Nigeria, etc., must be attributed to the fact that the human being himself acts as the reservoir of infection of *T. gambiense* from whom the vectors acquire infection. In this way the reduction in incidence of the disease by treatment of man has a profound effect in reducing the incidence of the infection amongst the tsetse flies. In the course of time an uninfected population of vector insects results, which appears to have no other source of acquiring infection than from man. However, strains of *T. gambiense* have been isolated from antelopes of which Speke's antelope (*Limnotragus spekei*) plays a major role.

In the case of the zoophilic form of the disease an unlimited source for infecting the tsetse flies exists in the varied fauna of Africa, which serve as hosts for the vectors. No matter how effective a drug may be in eliminating infection amongst domestic stock, reinfection is inevitable within a short time in the presence of a population of tsetse flies which constantly acquires infection from game. This fact alone accounts for the meagre success achieved by what has been termed the therapeutic approach to the problem.

(*b*) The entomological approach, or the elimination or control of the vector insects, appears to offer the only hope of successfully combating animal trypanosomiasis. Various indirect means of achieving this end suggest themselves, such as depriving them of their food supply, (e.g. by game eradication), or rendering their environment unsuitable (e.g. by bush and forest clearing). These methods are frequently impractical when extensive areas have to be dealt with. The labour and expense involved, furthermore, generally offer no permanent solution to the problem, unless an entire isolated community of tsetse flies can be destroyed, as reinvasion so frequently occurs. The direct attack upon the fly itself appears to offer the greatest hope of success. The methods employed in Zululand and the principles upon which they have been based may serve to throw some light upon what, it is hoped, may prove to be a practical solution to the problem of the elimination of tsetse flies from large areas of Africa.

II. The Distribution of Tsetse Flies in Africa in Relation to that within the Union of South Africa.

The accompanying Map 1. indicates, somewhat diagrammatically, the distribution of tsetse flies within the continent of Africa and in an isolated area in Asia.

From this map it will be noted that Zululand, on the eastern seaboard, is the only area infested with tsetse flies within the Union of South Africa. This region (latitude 29° to 27° south) is the habitat of *Glossina pallidipes Aust.*, the dominant species, as well as that of *G. brevipalpis* Newst., and *G. austeni* Newst. The former species is confined to Union territory while the latter two species extend for a variable distance into Portuguese East Africa. It will be shown later that *G. pallidipes* has advanced upon occasion into a limited area in the south eastern portion of Swaziland, but has never made its appearance in the southern portion of Portuguese territory.

Scrutiny of Map 2., studied in conjunction with the previous map, indicates that a distance of approximately 450 miles separates the Zululand fly belt from the more or less continuous fly belts commencing in Portuguese East Africa (latitude 21° south) and extending northwards. This latter zone comprises *G. morsitans* Westw., surrounding an area infested by *G. pallidipes* in addition to it.

III. The Historical Background of Nagana in the Union and the Tsetse Flies transmitting it.

1. *Review of the literature.*

No very comprehensive literature prior to 1920 exists on the incidence of Nagana and on the various species of tsetse flies associated with its transmission in the Union of South Africa. This is perhaps surprising in view of the profound influence a species such as *G. morsitans* has had upon the early development of the Transvaal (Dicke 1932). However, this species had disappeared from the region by the time the association between the tsetse flies of Africa and the trypanosomes connected with Nagana had been impressed upon the scientific world by the discoveries of Bruce (1895).

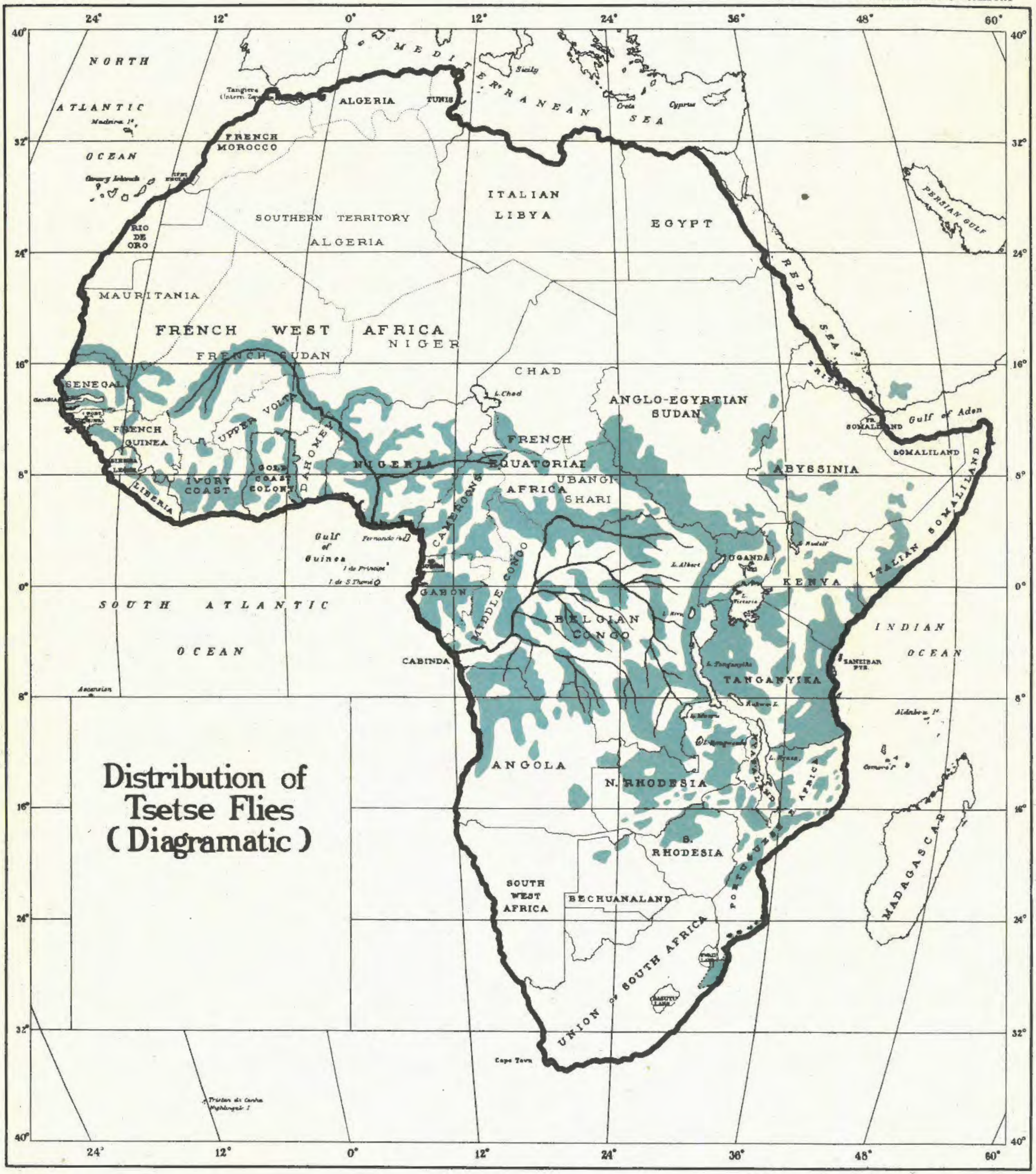
A considerable amount of investigation has centred around the Zululand fly belt, however, the more recent work being recorded in the articles of du Toit, de Kock, Kluge and Fiedler between 1946 and 1951.

Fuller (1923) in discussing the incidence of the tsetse fly, *G. morsitans,* in the Transvaal, comes to the conclusion that its southernmost dispersion did not

AFRICA

MAP 1.

DEPARTMENT OF AGRICULTURE & FORESTRY



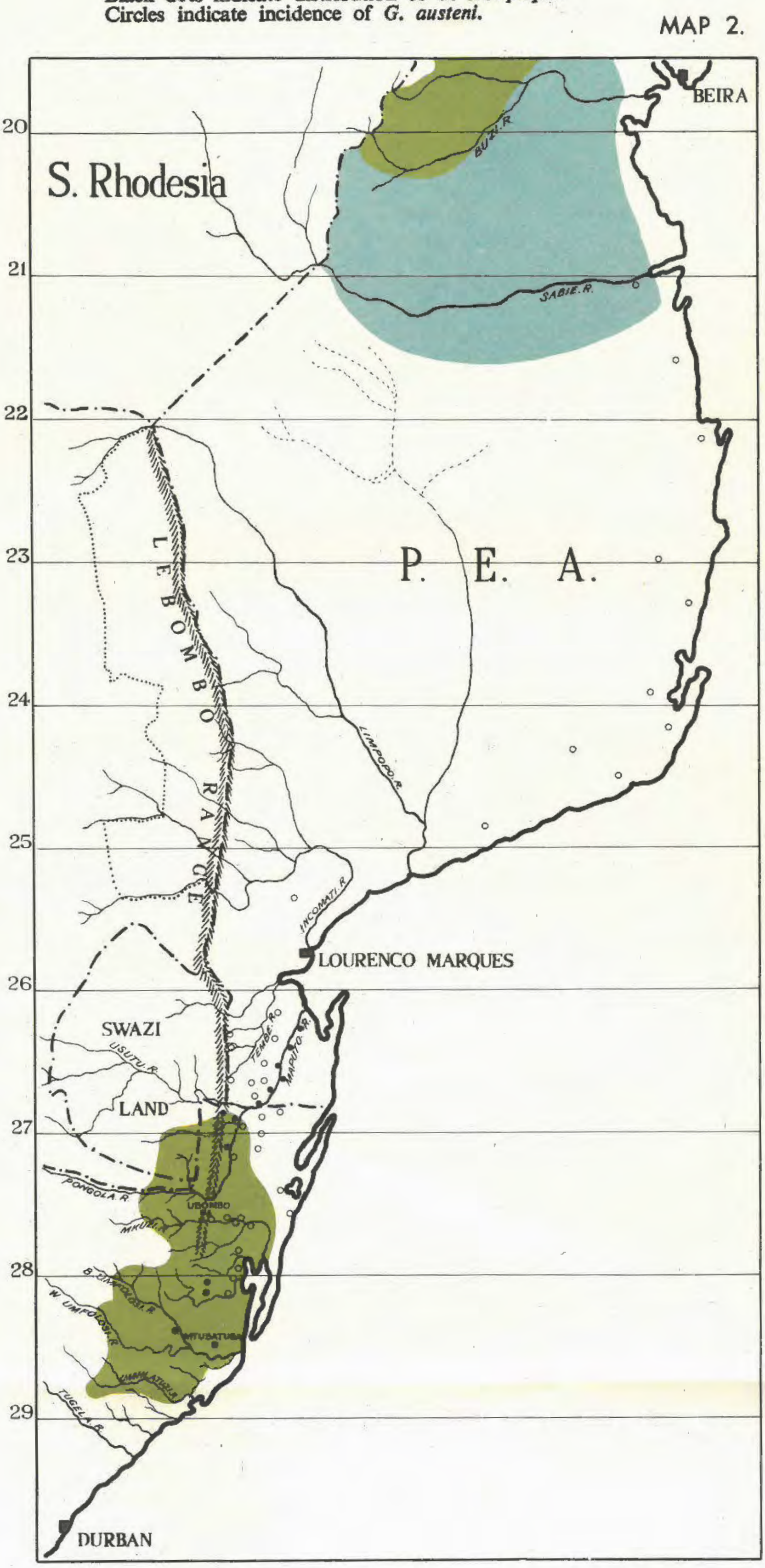
Distribution of
Tsetse Flies
(Diagramatic)

Miles

Map 2.

Map 2 showing the distribution of *Glossina pallidipes* in Zululand in relation to the occurrence of this species in Portuguese East Africa (Olive green).

Area shaded blue represents zone infested by *G. morsitans*.
Black dots indicate distribution of *G. brevipalpis.*
Circles indicate incidence of *G. austeni.*



extend beyond the Umbeluzi river (latitude 26° south) in northern Swaziland (see Map 2). East of the Lebombo mountain range, within Portuguese territory, it may have occupied country slightly south of this point, but the Tembe river appears to have marked its southernmost limit here. To the south a break of some 60 miles occurred in which no tsetse flies could be demonstrated.

G. pallidipes, which takes the place of *G. morsitans* in Zululand, extended from slightly north of the point where the Pongolo river emerges eastwards through the Lebombo (or Ubombo) range (latitude 27° 20′ south) southwards to the Umhlatuzi river (latitude 28° 50′ south). At the junction of the Pongolo with the Usutu river on the border of Portuguese East Africa, evidence of the presence of *G. brevipalpis* exists but not of *G. pallidipes.*

From the information Fuller gleaned from individuals who knew the tsetse fly in its habitat in Zululand and from identifications of specimens submitted. he concludes that *G. morsitans,* in all probability, never occurred in Zululand. The species concerned were *G. pallidipes, G. brevipalpis* and *G. austeni.* The former species extended over practically the whole of the lowveld of Zululand, whereas *G. brevipalpis* was confined to certain more or less isolated localities, such as the Hluhluwe reserve and the Pongola river close to its junction with the Maputo river on the border of Portuguese territory. He makes one reference (page 34) to *G. brevipalpis* having been taken near Ubombo (magistracy), which is situated on the Ubombo range above and to the west of the Mkuzi reserve. (Since the inception of the present campaign in 1945, when intensive surveys over the whole of this area were undertaken, no record of *G. brevipalpis* has appeared anywhere in this vicinity).

Glossina austeni was known to Fuller by one specimen only, alleged to have been captured in the courthouse at Ubombo. This specimen was recorded by Chubb (1916) as constituting a new species and named *Glossina brandoni.* Newstead's description (1912), however, was obviously overlooked.

Curson (1928) made a careful scrutiny of all available literature which may have had any bearing upon the Nagana problem in Zululand prior to his investigations in 1924. From the perusal of the files of various government departments, including the various game ordinances issued by the Natal Provincial Administration and by enquiry from old residents of Zululand, both European and native he has been able to reconstruct a rather incomplete and somewhat unconnected account of scattered outbreaks of the disease in stock from time to time. From his account it would appear that during the reign of the Zulu chief Panda (1840–1872), the disease was well known to natives, but game was actively hunted by the Zulus and their numbers were consequently considerably reduced. The result was that the disturbance of the feeding habits of the fly and its probable reduction in numbers permitted the maintenance of many cattle. The Zulu war in 1879 and the annexation of the country by the British, marked the commencement of a period of game protection during which game increased rapidly and the disease again spread alarmingly.

The advent of the white man and his gradual exploitation of portions of the country, the opening up of roads, and the introduction of animal drawn transport, focussed attention upon the disease to a very much greater extent. Game shooting restrictions were relaxed from time to time in various areas, particularly along the recognised trade routes, and the history of Nagana in Zululand, up until the first World War, appears to have been one of periodic severe epizootics in various localities. In the minds of the inhabitants, both European and native, such epizootics were always associated with the occurrence of game, especially big game, in large numbers.

2. *The earlier attempts to control Nagana in Zululand.*

(a) *Game eradication measures.*

Collins (1924) records the wholesale destruction of game which took place in 1917 in the area known as the Makatini Flats north of the Mkuzi reserve. The natives were emphatic, according to Curson who traversed the area in 1923, that this wholesale destruction very beneficially influenced the incidence of the disease in this region. (So thorough was the elimination of game in this area at the time that its effects could still be observed at the commencement of the present campaign in 1945, in the almost entire absence of both game and fly north of the Mkuzi river).

The investigation of Curson and his co-workers in 1921, followed as a result of very severe epizootics of Nagana in the newly established Ntambanana and Kwambonambi settlement areas in sou hern Zululand in 1919. Losses of cattle from Nagana amounted to approximately one third of the total cattle population and apparently coincided with similar severe epizootics in the regions north of the Umfolozi and Hluhluwe game reserves.

From 1922 to 1927, there are comparatively few references to the disease on any widespread scale. During this period many farming areas, including the Hluhluwe and Mkuzi settlements, were opened up for European settlement. This was followed by a period of rapid increase in the morbidity and mortality rate from Nagana in se tled areas . In the absence of any fly surveys it is not possible to correlate the increase in Nagana with a corresponding increase in tsetse flies. It appears reasonable to assume this, however, in the light of the surveys by means of the Harris tsetse fly trap which followed, and from the observations of workers such as Harris (1930).

Fuller and Mossop (1929) studied the bionomics of *G. pallidipes* in some detail, devoting special attention to its reactions towards its hosts. They demonstrated that sight played only a minor role in attracting the flies to warm blooded animals. This observation appears to have been entirely overlooked by Harris (1930), who based the attraction of the flies to the trap which he evolved, entirely upon the sight factor.

The studies of Whitnall (1934) upon the incidence of trypanosomes in tsetse flies revealed an infection rate, under the undisturbed natural conditions prevailing in the Umfolozi game reserve, of not greater than 4·25% in wild caught flies. Kluge (1944), and from his later observations, was able to demonstrate by means of blood examinations and biological tests in laboratory animals, an incidence of trypanosomes in certain types of antelopes, e.g. kudu, as high as 60%.

(b) *First organized game eradication campaign.*

Prior to 1929, game eradication had been left largely to residents of the area or to casual hunters from elsewhere, and consisted largely in a relaxation of existing game preservation ordinances. In 1929, an organized campaign was inaugurated.

In order to prevent dispersion of tsetse flies into the settled areas surrounding the Umfolozi game reserve by concentrating them within the confines of the reserve, the shooting campaign of 1929 was undertaken. The object was the drastic reduction or eradication of the large numbers of game animals dispersed into the so-called buffer zones (crown lands surrounding the reserve). This eradication campaign accounted for 37,861 head of game both large and small in the two years, 1929–1930. It brought about a very material decrease of game within the Umfolozi reserve itself, due to large numbers of game straying out during the period and being destroyed.

(c) *The introduction of the Harris Tsetse Fly Trap as a means of controlling G. pallidipes.*

Early in 1931, the Harris tsetse fly trap was introduced into the Umfolozi game reserve. At that time *Glossina pallidipes,* the only species of tsetse recorded in this reserve, was extremely abundant. In May of that year, 90 traps accounted for 244,930 flies, indicating a daily average catch of 87·7 flies per trap. In September, 1931, over 2,000,000 *G. pallidipes* were recorded from 983 traps. [Harris (1936), unpublished report.]

At the time of the commencement of trapping, it appears that a very large population of *G. pallidipes* was subsisting on a drastically reduced food supply following the shooting campaign of 1929—1930. In view of this reduction in host animals, activity induced by hunger was extremely evident amongst the flies, resulting in their swarming on and into motor vehicles and feeding freely upon man. Now followed several years of drought with rainfall well below the average in 1932–1934, and coupled with a reduced food supply, the density of fly dropped rapidly. However, the concentration of Harris traps distributed throughout the Umfolozi reserve, reaching a figure of over 12,000, which accounted for many millions of flies, undoubtedly played an important part in reducing the density to a very low figure by 1938.

There was strong evidence at the time in support of the contention that in the Harris trap a weapon had been found which might effectively deal with the tsetse fly. This was borne out further by the spectacular reductions which followed the introduction of the traps into the Hluhluwe and Mkuzi game reserves in addition to Umfolozi. Following upon a period of increased rainfall during 1937 to 1939, a distinct deterioration in the position became evident in 1940. Hereafter tsetse flies increased rapidly with evidence of an increase in the incidence of Nagana amongst cattle in the European settlement areas and native reserves surrounding the game reserves.

The increased incidence of Nagana was general in distribution. Fly surveys by means of Harris traps were instituted in the outlying areas. High densities of *G. pallidipes* were shown to be present in the Ntambanana settlement, to the south of the Umfolozi game reserve, as well as in the areas surrounding the other reserves. Nagana became prevalent with heavy mortality amongst cattle in the Nkwaleni settlement, in the valley of the Umhlatuzi river, to the south west of the Ntambanana settlement.

The heavy mortality in cattle as the result of Nagana which occurred after 1940 in spite of just over 26,000 Harris traps in use, afforded very strong evidence against the trap as a means of effectively controlling the tsetse fly. The Harris trap was used hereafter only for survey purposes, to indicate the presence of flies and to give some indication of their relative abundance in certain areas.

(d) *The creation of barrier clearings.*

Energetic action to control the spread of Nagana was imperative. In an endeavour to arrest the dispersion of tsetse flies, suspected of taking place across the comparatively low watershed separating the crown lands to the south of the Umfolozi reserve from the Ntambanana settlement, a barrier clearing was commenced in 1942. This clearing, undertaken by means of hand labour under the charge of the Veterinary Division on crown lands and by the Department of Native Affairs in native reserves, varied in width from about 500 yards to half a mile. It traversed the high-lying country to the south of Umfolozi from east to west and then turned northwards through the north eastern end of native reserve No. 11, to again run along the western border of the game reserve between the White and Black Umfolozi rivers. A similar clearing was commenced on the eastern border of the Hluhluwe game reserve. It had as its object the protection of the European settlement to the east of this reserve. Some clearing was also undertaken to the south of the Mkuzi reserve to prevent dispersion of fly in a southerly direction. (See Map 6, appended).

In planning these barrier clearings consideration was given to the fact that to be effective, the bush-free barriers should be constructed so far as possible along the normal limits of dispersion of the flies from their concentration areas. Where possible open watersheds were made use of to minimize the amount of bush removal necessary. Furthermore, as far as terrain permitted, bush should not be visible from one edge of the clearing to the other. Finally, the width would be determined by this visibility factor necessitating its variation according to local conditions, the object being to achieve a bush free skyline in the clearing when viewed from the inner edge.

Game patrols were appointed to keep the clearings as free from game as possible. In addition, cattle were not permitted to approach the outer edge of the clearing to within a minimum distance of half a mile.

In spite of these measures, designed to isolate tsetse flies within the game reserves, Nagana continued to exact an extremely heavy toll from the cattle population of Zululand and even continued to spread.

(e) *Second game eradication campaign.*

In December 1942, the decision was taken to extend game elimination to cover the whole of the fly infested area of Zululand, with the exception of the Hluhluwe game reserve which, it was hoped, the completion of the barrier clearing would isolate. At the same time the white rhinoceros, *Ceratotherium simum simum* (Burchell), in the Umfolozi reserve, according to figures then available, were very limited in number. It was thought that they could be confined to a restricted area, thus obviating the necessity of their elimination.

European game rangers, with gangs of from 8 to 10 armed native game guards under their control, were appointed to operate in the various European settlements, native reserves and game reserves. Farmers were provided with rifles and ammunition and encouraged to co-operate in organized game drives on their own and adjacent farms.

In the Mkuzi game reserve, shooting by native game guards under Europeans was confined to the periphery to start with. The object was the gradual decrease of the shooting zone so as to cause as little disturbance of game as possible and, in this way, not run the risk of dispersing game and fly.

The total number of game eliminated during the course of this shooting campaign, finally abandoned early in 1950 and considerably modified even in 1946, is reflected in the following table:—

TABLE NO. 1.

Area.	Big Game.	Small Game.	Total.
Umfolozi Area	5,314	65,298	70,612
Hluhluwe Area	30	1,479	1,609
Mkuzi Area	4,732	33,295	38,027
Farming Areas	1,326	7,173	8,499
Native Reserves	853	19,029	19,882
TOTALS	12,255	126,274	138,529

Big game include:—

Buffalo	*Syncerus caffer* (Sparrm.)
Kudu	*Strepsiceros strepsiceros* (Pallas.)
Waterbuck	*Kobus ellipsiprymnus ellipsiprymnus* (Ogilby.)
Wildebeest	*Gorgon taurinus* (Burch.)
Zebra	*Hippotigris quagga wahlbergi* (Pocock).
Inyala	*Nyala angasi* (Ang.)

Small game include:—

Bushbuck	*Tragelaphus sylvaticus* (Sparrm.)
Duiker	*Sylviacapra grimmi* (Linné.)
Bush pig	*Koiropotamus choeropotamus choeropotamus* (Desm.)
Reed-buck	*Redunca arundinum* (Bodd.)
Rhebuck	*Pelea capreolus* (Bchst.)
Steenbuck	*Raphiceros campestris* (Thunb.)
Warthog	*Phachochoerus sundevalli* (Lönnb.)
Impala	*Aepyceros melampus* (Lcht.)

Theoretically, the removal of the food supply of the tsetse fly must be regarded as a logical means of control. The success achieved by the application of this method in Southern Rhodesia in the case of *Glossina morsitans*, (Tryp. Com. S.R. 1945), would appear to have justified its trial at least for the control of *Glossina pallidipes*.

Fuller, (1923), in reviewing the conditions under which *Glossina morsitans* disappeared from the Transvaal around about 1896, concludes that the disturbance amongst the game, following the advent of firearms in the hands of both Europeans and natives, was such as to upset the balance under which fly had been previously assured of a regular blood meal at suitable intervals. The rinderpest epizootic in 1896 further reduced the already depleted game and constituted the factor finally responsible for the total disappearance of *G. morsitans*.

The success or otherwise of game eradication as a means of controlling any particular species of tsetse fly would depend, therefore, largely upon the food preference and feeding habits of the particular species. *G. morsitans* appears to show a preference for the larger grazing and browsing species of antelopes it comes into contact with regularly in the habitat favoured by it. *G. pallidipes*, on the other hand, by virtue of its dependence upon a rather denser shade cover and its habit of hunting along game paths, encounters and makes use of the small species for food, such as bush pig, bush buck and the thicket inhabiting species, as well as the larger antelopes.

In the Umfolozi game reserve, the total eradication of all species of animals likely to serve as hosts for *G. pallidipes*, excluding the white rhinoceros, was aimed at. The reduction of the thicket inhabiting species to a level where they could no longer support a population of this species of tsetse fly was ultimately found to be so formidable a task as to be almost impossible of achievement. In fairness to the game rangers and their assistants, who exerted themselves to the utmost in endeavouring to achieve the total elimination of the food sources aimed at, it must be stated that accurate counts of the numbers of white rhinoceros made subsequently, revealed a far greater number of these animals to be present than was originally anticipated. The actual figure obtained was 550. So large a number of these bulky animals, whose wandering habits account for their presence in all parts of the reserve, may have played a very considerable part in maintaining the high densities of *G. pallidipes* that persisted. However, game observers reported large numbers of the smaller species of antelopes and evidence of the presence of considerable numbers of the nocturnal bush pig, when to the casual observer, all game appeared to have been eliminated. In fact, a balance appeared to have been struck whereby natural increase in the thicket-inhabiting species balanced the rate at which they were being destroyed.

IV. The Cyclical Incidence of Nagana in Zululand.

The evidence available relating to major epizootics of Nagana in Zululand, points to the disease having occurred in the past in the form of waves. These reached their peaks in cycles of between 10 and 12 years. Thus, according to Toppin (cited by Fuller, 1923), Collins (1924) and Curson (1928), a peak in the incidence of the disease occurred between the years 1917 and 1922. This was followed by a period of comparative freedom from the disease during which cattle farming flourished and stock increased very considerably in numbers. A second peak manifested itself in 1927. The disease spread rapidly and a campaign for the elimination of game, to prevent dispersion of fly from the suspected concentration centres was inaugurated. This epizootic reached its peak, so far as stock mortality was concerned, in 1931 to 1933. Simultaneously, Harris, by means of trap surveys, demonstrated a peak in the incidence of fly in 1931.

Again a period of reduced activity of fly followed and a consequent lowered mortality in stock attributable to Nagana was evidenced. In 1938, flies again showed an upward tendency and surveys, conducted principally in the three game reserves, revealed a peak in fly incidence in 1942–1943, closely simulating that experienced in 1931. Simultaneously, Nagana spread extensively beyond the limits to which it had been confined in 1938, and mortality in stock in European settlement areas and native reserves throughout Zululand assumed alarming proportions.

This last peak appears to have been sustained for a period considerably in excess of those experienced with the previous peaks. It culminated in one of the most severe epizootics of Nagana ever experienced in Zululand, during the summer months of 1945–1946. At a conservative estimate over 60,000 head of cattle succumbed to the disease in the Hluhluwe and Mkuzi settlement areas and in the low-lying eastern portions of the Ngotshe district, between the Pongola and Mkuzi reserves (Schulz and Smit 1947).

Surveys conducted at the time revealed considerable concentrations of and extensions in fly incidence into areas formerly looked upon as fly free. Extensions into the south eastern portion of Swaziland occurred, where *G. pallidipes* had been entirely unknown previously within the memory of the local inhabitants. In this respect it must be stated that Fuller (1923) cites the evidence of a farmer, Mr. L. C. von Wissel of Hluti, Southern Swaziland, who points out in a letter da ed 17th May, 1923: "from the oldest resident in this district, Mr. M. van Staaden, Vlakhoek, Dwaleni, I have heard that in the old days there used to be Nagana below Hluti, on the little Isitilo river"; (lat. 27° 15′ south, long. 31° 42′ east).

What appeared to be an unprecedented outbreak of Nagana in 1945–1946, in so far as severity and range of dispersion were concerned must, therefore, be viewed in the light of the above evidence as having been experienced previously. Many years had elapsed, however, between outbreaks comparable in severity with that which occurred during the third peak period described.

No satisfactory explanation for the occurrence of these peaks in fly incidence showing a more or less rhythmical cycle of ten or more years, has been forthcoming. Vanderplank (1941) has demonstrated a cyclical rhythm associated with the lunar phases, but this can have no bearing upon this long term rhythm. The observations of Fiedler, du Toit and Kluge (in press) may serve to throw some light upon the problem. Studies conducted over a period of two years (March 1947 to March 1949) during the course of the present campaign, revealed an extremely high degree of parasitism amongst the pupae of *G. pallidipes* and *G. brevipalpis* at certain times. In the Umfolozi game reserve 51·9% of all pupae of *G. pallidipes* collected in October 1947, and 54·8% of those of *G. brevipalpis* from the Hluhluwe game reserve were parasitized. The parasite which played by far the major role was the newly discovered bombyliid, *Thyridanthrax brevifacies* Hesse (1953). This parasite appears to show a high degree of specificity for tsetse flies, all three Zululand species being subject to its attacks. Chorley (1929) encountered similar high rates of parasitism in *G. morsitans* in Southern Rhodesia in the summer months.

It is perhaps significant that such large percentages of parasitized pupae were encountered in 1947. This may have represented the culmination of the peak in fly abundance experienced during the preceding years. Had it not been for the inauguration of the eradication campaign in April of that year, (to be described later), resulting in a very rapid reduction in fly incidence, a natural decline in numbers of fly may have been experienced over the ensuing years.

From this evidence the theory may be advanced that a parasite, dependent upon tsetse flies for its survival, may build up with its hosts. A point is reached when the effect of the increasing numbers of parasites manifests itself by bringing about a decrease in the number of hosts. The developmental periods of the parasites are considerably in excess of those of the hosts, as shown in the above cited publication, and sufficient parasites continue to emerge from parasitized puparia to profoundly affect the hosts. A stage is reached eventually where the depletion of hosts exerts a limiting effect upon the breeding potential of the parasites. These are now reduced to a very low figure consistent with the limitation of the host species. Survivors amongst the hosts are in a position at this stage to increase in numbers again, unimpeded by parasitism to any extent, and the cycle recommences.

It seems conceivable that such a process, in terms of the entire population of tsetse flies present, is inevitably slow and may require a period of some ten years to complete its cycle.

V. The Bionomics of the Glossina spp. of Zululand.

1. *Glossina pallidipes.*

(a) *Life History.*

Harris (1930) has given a very detailed description of the life history and bionomics of *G. pallidipes*. This represents the results of six years of work in the habitat of this species in the Umfolozi game reserve. From the results of his work and that of numerous other investigators in many parts of Africa, it becomes readily apparent that the reproductive capacity of tsetse flies in general is strictly limited. In fact, it is only under certain fixed sets of conditions that the various species are capable of maintaining themselves at all.

It may be as well to recapitulate briefly the knowledge accumulated on certain aspects of the life history of *G. pallidipes,* which conforms to the general pattern applying to the various species.

The female produces a single egg at a time which is not extruded, but hatches within the uterus. The vermiform larva is nourished by special milk glands within the uterus until mature and ready for extrusion. Within her life span of possibly up to six months, the female produces a maximum of 12 larvae. These are deposited on the ground under the overhanging canopy of shrubs and bushes. As Harris (1930) has pointed out, the mortality, particularly during the histolytic stage of the puparium, may be extremely high so that considerably less than the maximum number of offspring ever reach maturity. Chorley (1929) states that, in the case of *G. morsitans,* 42% op pupae formed may fail to produce flies during the early summer months, June to November, whereas as many as 60% may produce no flies during the late summer months. In other words, an average of about 50% of the puparia formed may produce adult flies, the remainder dying as the result of unfavourable conditions, e.g. exposure to sunlight or heat, desiccation and parasitism.

During the course of the period under review a large number of pupae collected from the various breeding areas in the Umfolozi and Hluhluwe reserves were opened in order to determine whether they were viable or not. Table No. 2 gives the totals of pupae collected and opened in the Hluhluwe game reserve during 1948, and the percentage which had failed to produce viable larvae due to failure to develop or parasitism.

In analysing the above figures, it will be observed that the average mortality in pupae is higher than that recorded by Chorley (1929) for *G. morsitans.* Account must be taken of the fact that the pupae collected were exposed to some degree of rough handling before being received at the field laboratory for weekly examination. Many of those pupae which were in the early stages of development, particularly in the histolytic stage, during which the larva is very susceptible to environmental changes, (Harris, 1930; Jack, 1939, 1941), may have died after collection. This would tend to increase the percentage mortality and may account for the disparity between the findings of Chorley and those presented here.

The general conclusion may be drawn, however, that pupal mortality rises rapidly with the onset of the hot weather from September to March and is considerably reduced during the winter months of April to August.

TABLE NO. 2.

Pupae of G. pallidipes *collected in the Hluhluwe Game Reserve from January to December* 1948, *which failed to develop.*

1948.	No. of Pupae opened.	Percentage Mortality.
January	462	73
February	369	63
March	155	61
April	155	51
May	180	48
June	350	40
July	360	61
August	388	42
September	213	78
October	137	76
November	182	81
December	168	76
TOTAL	3,119	—
AVERAGE PERCENTAGE MORTALITY	—	62·5

(b) *Gestation period.*

The period of development within the uterus of the female fly varies at the different seasons of the year. It averages approximately 10 to 12 days during summer, but increases to between 18 and 20 days during the winter months. A period averaging about 28 to 29 days, however, elapses between the emergence of the female *G. pallidipes* from the puparium and the deposition of her first larva. During this period she requires at least five blood meals to ensure the maturation of her developing offspring. (Harris 1930).

Upon extrusion, the larva burrows actively into the soil to the depth of an inch or less. Within a matter of an hour the characteristic barrel-shaped pupa, bearing the two knoblike spiracles at the posterior extremity, is formed by the shrinking, hardening and darkening of the external covering.

(c) *Pupation.*

The period necessary for the development of the fly within the pupal case varies considerably with the season of the year. According to Harris, who conducted his experiments under inadequate laboratory conditions, where no provision was made for moisture, the minimum pupation period was 22 days during the month of December. The maximum, during the colder months of May and June, was 66 days.

In order to confirm the findings of Harris, an experiment was conducted wherein pupae of known age were exposed to conditions very similar to those occurring in nature. Pupae derived from larvae deposited by captured flies in the laboratory, were placed in sifted, pupae-free soil in shallow metal trays perforated for drainage. The trays were sunk into the earth to the level of their upper margins in a typical breeding site in which numerous pupae and casings had been found. To prevent accidental larval deposition in the trays and in order to retain all flies which emerged, wire gauze covers were placed over them.

Batches of newly formed pupae as they became available were placed in the trays in the manner described and daily observations were made to note the emergence of the adult flies.

The result of this series of observations, which extended from 1st May 1946 to 31st October 1947, are reflected in Figure 1.

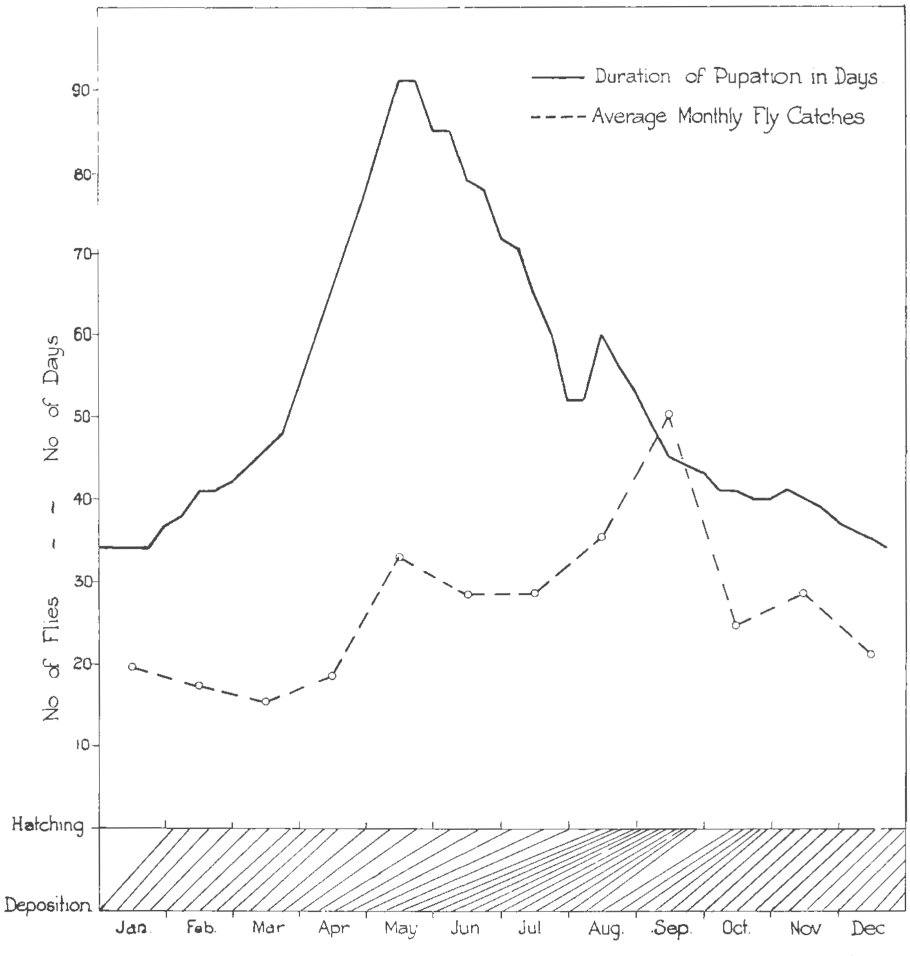


FIG. 1.—Graph of pupal periods of *G. pallidipes* and average monthly fly catches in Harris traps. The extended duration of pupation is indicated below.

The average monthly fly catches from Harris tsetse fly traps in terms of number of flies per trap per month are included. This will be referred to later.

From these figures it will be noted that the average duration of the pupal period follows the same trend as that experienced by Harris during his observations in 1922–1923, namely, the lengthening of the period during the colder winter months and shortening during the summer. The lower limit of 34 days is, however, longer than the 22 days given by Harris whereas the upper limit of 92 days is considerably longer and humidity higher than was the case in Harris' experiments, but unfortunately, no records were kept of actual ground temperatures at the level of the pupae. The absolute limits for the pupation period recorded for this species in the case of individual pupae, varied from as short as 31 days in summer to a maximum of 149 days, or almost 5 months, during the colder months.

The maximum duration of pupation is a matter of the greatest significance when considering the elimination of adult tsetse flies in a locality. It is essential that ample time be allowed for all pupae to hatch so as to ensure their destruction as adults.

The abovementioned observations involved the examination of large numbers of pupae collected during the course of the pupal-casing survey, to be described later. (Chapter VI). The pupae were carefully opened to enable the contents to be studied. This revealed not only the extent of mortality due to parasitism or other causes, but allowed observations to be made on the stage of development of the larvae during the period January to December 1948. During the colder months of the year, from May to August, it was found consistently that a preponderance of pupae contained fully formed flies. These flies, upon being released, immediately extruded the ptilinum, commenced crawling and soon expanded the wings to form fully mature flies. So constant was this finding during the last portion of winter and so large a proportion of pupae opened at this stage showed completion of development, that the only conclusion to be arrived at was that maturation had taken place at some earlier date. Actual emergence was delayed pending the onset of warm weather in spring, when mass hatching of pupae takes place.

These findings are reflected in Table 3.

TABLE 3.

Percentage of Fully Mature Flies in Pupae from the Hluhluwe Game Reserve, examined during 1948.

	No. of Pupae opened.	Percentage Mature Flies.
January	462	4·7
February	369	12·1
March	155	7·6
April	155	8·3
May	180	13·4
June	350	14·9
July	360	9·4*
August	388	13·3
September	213	5·3
October	137	0·4
November	182	3·3
December	168	2·8

* The low figure for July should be compared with the high percentage mortality of pupae for this month shown in Table 2, with which it might be correlated.

In Figure 1, it will be noted that the monthly incidence of adult flies, as shown by the average monthly fly catches in Harris traps, shows two peak periods, one in May and one during the latter portion of August and early September. It would appear that the May peak represents the culmination of the summer breeding activity. The August-September peak, which is consistently higher than that experienced in May, represents the mass hatching of accumulated pupae containing fully matured flies. These emerge simultaneously with the onset of the warm weather.

(d) *Habits.*

(i) *Relation between* G. pallidipes *and hosts of fixed habits.*—According to the work of Jack (1938), Vanderplank (1947) and others, continuous reproduction of tsetse flies is possible only in the presence of an abundance and ready availability of regular blood meals. These are necessary at intervals of 2 to 4 days. Within a well-established community of flies, a balance exists whereby the habits of the host animals make them readily available to satisfy the food requirements of the flies.

G. pallidipes is entirely indiscriminate in its choice of a host and feeds readily upon most animals. To illustrate this point, the Umfolozi game reserve affords a good example. A very material depletion of game took place in this reserve during the shooting campaign of 1929–1930. This reduction in game had the immediate effect of bringing about an apparent increase in the number of flies. This must be attributed to an increase in the hunger urge of the flies, resulting in increased activity thereby rendering them more easily observed and more easily captured in the Harris traps introduced in 1931. Hereafter the incidence of *G. pallidipes* decreased very rapidly due possibly—

(*a*) to the large number caught in the Harris traps;

(*b*) to an adjustment in numbers to conform with a decreased food supply; and

(*c*) to the unknown factors operating between the 10 years cycles mentioned previously.

Thereafter the flies persisted in small numbers until 1939, when as has been shown, an upward tendency in numbers manifested itself. In 1942, a peak in fly abundance became apparent. This led to a concerted game eradication campaign with the object of total extermination of all game in the Umfolozi reserve. The white rhinoceros was not included and were greater in number than was known at the time. After several years of well organized and conscientiously conducted shooting, it was found that a stage had been reached where the natural increase in certain species, notably bush pig, bush buck, steenbuck and duiker, appeared to balance the numbers destroyed. These species had retired to the dense thickets in valleys where their close association with *G. pallidipes* made it possible for them to support this large population. The unexpectedly large number of white rhinoceros which wander over the 100 or more square miles constituting the reserve and its immediate surroundings, served to supplement the food requirements of the fly. This may have influenced the increased incidence of fly.

(ii) *The effect of "population density" upon dispersion of flies.*—A further phenomenon, clearly manifested in Zululand, is the tendency displayed by *G. pallidipes* to disperse well beyond the limits it normally occupies during periods of peak abundance.

This tendency has been observed on several occasions during the severe epizootics of Nagana previously cited. It appears to be less associated with climatic conditions than to peaks in actual fly density. Such extensions of existing fly belts may be due to random movements of flies which, under conditions of high density, would tend to permit of more individuals reaching localities beyond the normal limits of dispersion. On the other hand, when flies become abundant, a " population density " is reached giving the impression that conditions within the normal habitat become crowded. This results in an ever-increasing number of individuals leaving the area and dispersing into neighbouring territory.

A considerable amount of evidence in support of this viewpoint was obtained from various areas during the course of the actual eradication campaign, to be discussed later. (Chapter X). The Mkuzi reserve affords an excellent example of the conditions under which dispersion occurs. The reserve contains a more or less uniformly, heavily bushed area of some 30 square miles in extent. It is surrounded by a number of localities of varying size, equally heavily bushed, separated from the main portion by open treeless country of varying extent. Trap surveys had revealed a high density of fly in the central portion. This area was subjected to a series of applications of insecticide which had the effect of drastically reducing the population of flies within a very short period. From the sixth week after the commencement of spraying, trap surveys conducted within the isolated localities mentioned, which had not been treated, revealed an unexpectedly high incidence of flies. As these surveys were commenced when spraying within what might be termed the high density portion of the reserve had been completed, it was decided to leave them untreated.

The trap surveys were continued within the treated and untreated areas during the ensuing eight months. It was noted that whereas a marked reduction of flies took place initially within the treated area, it was not sustained. In fact, from about the 24th week, a tendency became manifest for the fly population to show signs of recovery. In contradistinction to this trend a steady, although somewhat less rapid but sustained, reduction in fly populatoin was evident in the untreated areas.

Figure 2 indicates the trends in fly reduction in the two areas cited.

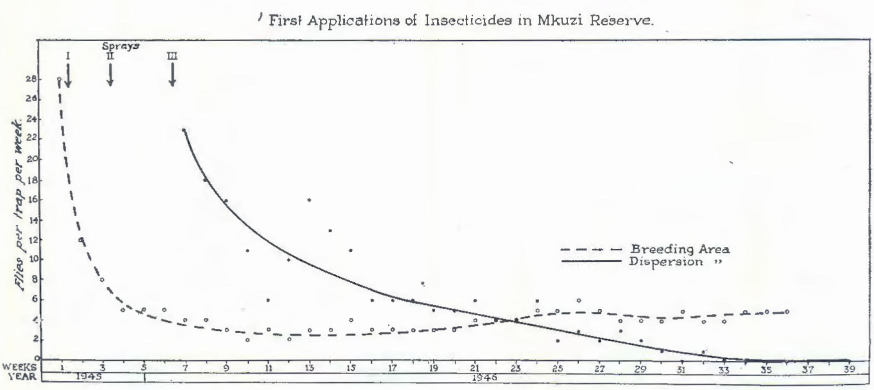


FIG. 2.—Trends in the reduction of *G. pallidipes* in the breeding and dispersion areas of the Mkuzi game reserve.

From the evidence obtained in the localities under review, it was concluded that the treated area represented a breeding area in which the fly population was constantly being added to by actual breeding. This conclusion was corroborated later, as will be shown. (Chapter X). The untreated areas represented dispersion areas in which the fly population present was constantly being supplemented by flies moving into them from the breeding area. Subsequent surveys showed that little or no breeding was occurring within them.

Under the conditions prevailing in the breeding area immediately prior to the applications of insecticide, the numerical total of flies present represented a population of such density that wholesale movement of flies into the surrounding dispersion areas was occurring. The reduction of flies in the breeding area almost immediately relieved this "population pressure" and dispersion ceased. The result, as reflected upon the fly population in the dispersion areas, was a steady and sustained reduction in population, until finally complete elimination resulted. In other words, the curve portraying the reduction in fly population occurring in the untreated dispersion areas represents the dying out, as the result of age, of a population of tsetse flies not being added to by dispersion or breeding.

It must be mentioned here that the breeding area contains an abundance of game animals which ensure an adequate food supply. The dispersion areas, on the other hand, contain little game although they move into them for short periods from time to time. This lack in regular availability of food for the flies, is probably responsible for the fact that little breeding took place within the dispersion areas.

2. *Glossina brevipalpis.*

The bionomics of this large species conforms very closely with that of *G. pallidipes.* The remarks made on this latter species, so far as life history, gestation period and pupation are concerned, apply equally well to *G. brevipalpis.*

The climatic and photobiotic requirements of *G. brevipalpis* vary considerably from those of *G. pallidipes,* however, and exert a marked influence upon its habits, as well as determining the limits of its distribution.

So far as the habits of *G. brevipalpis* are concerned, these might be said to vary only in degree from those of *G. pallidipes. G. pallidipes* is for the most part active during the early morning hours and late afternoons on sunny days, while *G. brevipalpis* shows an even greater degree of restriction of activity during the daylight hours, shunning bright sunlight at all times. The result is that the insect is encountered only within the dense shade of forest or heavy bush, particularly where a high dense overhead canopy exists. Ideal conditions exist for this species in the heavily forested valleys of the Hluhluwe game reserve and in the forest galleries of the Hluhluwe river. Somewhat similar bush types exist in the steep valleys bordering the Black Umfolozi river in the Umfolozi reserve, and here *G. brevipalpis* has been encountered in limited numbers. The riverine galleries of wild fig and other species of trees along the Pongola river in Northern Zululand, close to its junction with the Usutu river on the border of Portuguese East Africa, extend along the Maputo river into the latter territory and afford excellent conditions for *G. brevipalpis.* They occur within these forest galleries in large numbers. It would appear that the numerous hippopotami inhabiting these rivers serve as the chief source of blood meals for this species in these parts.

This restriction to the shade conditions afforded by certain vegetational types, limits the dispersion of *G. brevipalpis* to a very marked extent. It also has a very definite bearing upon the association of this species with the causation of trypanosomiasis amongst domestic stock. Although capable of harbouring and transmitting the pathogenic trypanosomes of Nagana, *G. brevipalpis* can never play a major part in the causation of extensive epizootics by virtue of its restriction to a confined habitat and the very limited contact between it and domestic animals. If and when domestic stock are forced to water in rivers and, in approaching the water, are forced to traverse the forest galleries on the banks which harbour the flies, then only do they become infected. In general, however, isolated cases of Nagana only are encountered, which in no way compare with the extensive epizootics of the disease transmitted by the savannah species, *G. pallidipes*.

3. *Glossina austeni.*

Although conforming so far as its biology is concerned with the two aforementioned species, this small tsetse fly displays certain definite characteristics in habit which serve to differentiate it. The larvae of *G. pallidipes* and *G. brevipalpis* are deposited mainly on soil under the low overhanging canopy of shrubs and bushes, although *G. brevipalpis* frequently shows a preference for the soil between the buttressed roots of certain large trees. *G. austeni*, on the other hand, deposits its larvae on soil under fallen logs, low horizontal branches of trees which practically touch the ground, the soil at the foot of palms, or even under the edges of rocks. Invariably a solid bulky object is chosen, casting a dense shade immediately beneath it, and this knowledge greatly facilitates search for the pupae.

Glossina austeni might be referred to as the coastal thicket species of tsetse fly. In Zululand, it has been encountered only within the comparatively low dense thickets of the coastal plain. Its distribution is patchy and although it covers an area of considerable extent, it is encountered only within more or less clearly defined bush types where a dense overhead canopy exists accompanied by a tangled thicket growth of shrubs and bushes beneath. These are frequently almost impenetrable. Within its habitat the shade conditions are such as to inhibit extensive growth of grass, with the result that cattle are apt to graze around such thickets rather than penetrate into them; *G. austeni* appears to be extremely loth to leave the protection afforded by the shade of such thickets to feed upon them. For this reason there appears to be little contact between it and cattle and, consequently, the species has been responsible for only rare sporadic cases of Nagana and never for widespread epizootics.

The impression has been gained, for which some evidence exists as will be shown later, that *G. austeni* feeds largely upon bush pig, (*Koiropotamus*), and possibly the smaller species of antelopes, e.g. red duiker (*Cephalophus natalensis natalensis* A. Smith) and Livingstone antelope (*Nesotragus livingstonianus zuluensis* Thomas), which are plentiful within its habitat.

The appended Map 5 shows the approximate distribution of the three species of tsetse flies within Zululand.

G. pallidipes is confined entirely to Zululand except for a comparatively small extension into the south eastern portion of Swaziland (Map 5). The other two species extend into Portuguese East Africa where *G. brevipalpis* is confined to the riverine forest galleries of the Maputo river. *G. austeni* is widely distributed, although confined to fairly well-defined areas of a low thicket type of vegetation on the coastal plain, with circumscribed extensions up certain heavily bushed valleys on the eastern slopes of the Lebombo range in Portuguese territory. (See Map 2).

VI. Methods of Survey employed in Zululand for determining the Distribution, relative Abundance and Breeding of Tsetse Flies.

1. *Mortality in cattle as indirect evidence of the presence of tsetse flies.*

Mortality amongst cattle as the result of Nagana has always been regarded as a valuable guide in determining the presence of tsetse flies.

In cases where *G. pallidipes* occurs in low density as, for instance, when it disperses into territory surrounding its breeding grounds, the presence of flies may be extremely difficult to demonstrate. On the other hand, cattle may acquire infection by traversing areas infested with such species as *G. brevipalpis*, e.g. in forest galleries fringing rivers, streams or lakes, where the presence of the fly is not suspected. The incubation period of the disease may vary from two weeks to several months, so that the finding of tsetse flies responsible for the infection may be virtually impossible. *G. austeni* is probably the most difficult of the three Zululand species to demonstrate, due to its habit of remaining confined to thickets and, in general, not being very abundant.

In view of the difficulties experienced in determining the presence of tsetse flies in many cases it is often held that biting flies such as *Tabanidae, haematophagus Muscidae,* e.g. *Stomoxys, Siphona,* etc., play a prominent part in the mechanical transmission of Nagana. There is no doubt that in certain instances mechanical transmission does play a part especially in extending localised outbreaks of the disease, but where Nagana occurs enzootically, its specific transmission is dependent solely upon *Glossina* spp. and is indicative of their presence in the area. [Bedford (1926)].

2. *The Harris tsetse-fly trap.*

Harris (1930) evolved and described a type of trap which has undergone very extensive tests in Zululand. The attractiveness of this trap to the savannah species of tsetse fly, *G. pallidipes,* for which it was designed principally, was based on the premise that the fly seeks its prey by sight alone. It is drawn to the trap by virtue of its bulk. Within the limited range of vision of the fly, the trap is indistinguishable at a distance from the bulk of an antelope and is, therefore, investigated as a possible source of food.

Fuller and Mossop (1929) produced a considerable amount of evidence in support of the view that the sight factor had little to do with the attraction of *G. pallidipes* to cattle. Kluge (unpublished report) repeated the experiments of Fuller and Mossop with similar findings. He demonstrated further, that the effectiveness of the Harris trap in capturing *G. pallidipes* could be very considerably enhanced by bringing cattle into close proximity with it. He holds the view that this enhancement of efficacy is due to the stimulating or activating effect exerted upon tsetse flies by thermal emanations and odours from cattle upon which they attempt to feed. The animals resent the attentions of the flies and endeavour to ward them off, but once stimulated, the flies persist in their attacks. As their range of vision appears to be limited, their attention is caught by the adjacent stationary trap, which they proceed to investigate, and are captured.

An observation in connection with the use of the Harris trap, made on numerous occasions, shows clearly that traps covered with new hessian (or burlap) are considerably more efficient than are those of which the coverings have weathered. The reason for this is not clear, but may be due to thigmotropism on the part of the fly as a result of the hairy surface of the new material. Some olfactory response may also play a part. This seems to be connected with the characteristic odour of new hessian. To maintain efficiency in any tsetse fly survey conducted with Harris traps, it is necessary to recover them with new hessian every three to four months when the coverings have bleached to a silvery-grey colour and have lost the rough hairy appearance of the new material.

Whatever the mode of operation of the trap may be it has played an extremely important role in Zululand. It has demonstrated the presence of tsetse flies and afforded a more or less automatic means of determining their relative abundance. Under conditions where a high density of tsetse flies exists, the Harris trap functions very efficiently. As the density of the flies drops, however, the trap is less successful due to its coming into competitive conflict with the game, which possess a greater degree of attractiveness for the flies. A point is reached ultimately when, due to extremely low densities of flies, its value as an instrument of fly survey falls away entirely.

In the case of *G. brevipalpis,* the Harris trap is much less efficient than for *G. pallidipes.* It does afford some guide as to the relative density of *G. brevipalpis,* however, and due to its convenience and automatic means of operation, has been used extensively in the habitat of this species. When the density fell, however, it had to be replaced by a more efficient means of survey.

The Harris trap must be regarded as practically valueless in the case of *G. austeni* and only occasionally are specimens of this species taken in it. It would seem that either the design of the trap for *G. austeni* is incorrect or that this thicket species does not react to traps, as no trap appears to have been constructed which may be regarded as efficient.

3. *Bait Animal Surveys.*

As stated previously, fly surveys by means of Harris traps have yielded results which could be regarded as satisfactory under conditions of relatively high densities. As these densities dropped, due to the control measures applied, the traps lost efficiency. A point was finally reached at which the evidence obtained from them no longer served as a reliable index of the relative abundance of the flies.

The well known attractiveness of bait cattle to tsetse flies had been confirmed in Zululand and surveys embodying these animals were instituted in 1947. Gradually, by the introduction of larger numbers of cattle, these surveys were extended until the whole of the potential fly infested areas could be covered.

The method adopted consists of using the bait cattle in groups of 2 head each with two natives to each group. The animals are trained so that they can be handled all over by their attendants without flinching or resenting the touch of human hands. Each group is assigned a definite area which it traverses at stipulated intervals from a temporary base. Surveys commence shortly after sunrise and the cattle are moved from site to site at each of which they are tethered to trees for periods of fifteen to thirty minutes. The period from noon to two p.m. constitutes a daily break from surveys, as the flies are not active as a rule during the hottest part of the day. The animals are observed carefully for the presence of flies alighting upon them, generally on the legs below the knee or hock. Such flies are captured by placing a glass or transparent plastic specimen tube over them and are then transferred to gauze cages for subsequent recording.

It was found, to start with, that the tsetse flies visiting the cattle were too numerous to permit of their all being captured before completing their engorgement and leaving the animals. Use was made, therefore, of the observation cited previously, (Kluge, unpublished report), that the close proximity of cattle to Harris fly traps greatly enhanced the efficiency of such traps. The bait cattle were brought to within a few feet of the traps sited in the bush. The majority of flies visiting the animals could, in this way, be captured either directly from them or in the traps.

In order to maintain a high standard of efficiency on the part of the native attendants, a number of bait cattle groups are placed under the supervision of a European. He visits the groups at odd times and the natives are required to collect all biting flies, such as *Tabanidae, Stomoxys,* etc., which feed upon the animals. Experience and a comparison of the numbers of such biting flies captured from the different groups, soon shows whether interest is being maintained and the survey conducted in a proper manner.

The experience gained by the use of bait cattle surveys has shown that the method constitutes a very sensitive index of the presence and relative abundance of *G. pallidipes* and *G. brevipalpis,* particularly under conditions of low density. To arrive at an estimate of relative abundance, the number of flies captured is correlated with the hours worked by the number of groups employed and comparisons are drawn from week to week or month to month. In this way it has been possible to study the progress made with the reduction of tsetse flies in the areas treated. Emphasis must be laid upon the fact that the attraction of bait cattle for tsetse flies remains constant, which is not the case with Harris traps, which lose efficiency upon ageing. The bait cattle survey method forms a more reliable guide of relative abundance for this reason.

In the case of *G. austeni* the bait cattle survey method is only partially effective. The reason appears to lie in the comparatively low degree of attraction possessed by cattle for this species, even when the animals are brought into very close contact with it. This has led to the opinion that *G. austeni* feeds by preference upon the smaller species of wild animals in its habitat. A certain amount of evidence in support of this view has been obtained by using pigs as bait animals in *G. austeni* areas. These animals have proved themselves infinitely more attractive to the flies than are bait cattle.

The following Table, No. 4, is based upon captures of *G. austeni* taken in the False Bay bush area close to Lake St. Lucia. The captures from a single black pig are compared with those from a pair of bait cattle, all operating in the same area close to each other.

TABLE 4.

Comparison between Numbers of G. Austeni *captured from* 1 *pig and from a Group of* 2 *Bait Cattle on Farm* 112, *False Bay Area.* 1950.

Month.	Pig (Captures).	2 Bait Cattle (Captures).	Total Captures.
February	66	29	95
March	98	65	163
April	88	34	122
May	98	77	175
June	82	66	148
July	90	69	159
August	62	57	119
September	79	78	157
October	69	70	137
November	92	74	166

It will be noted from the above figures that if the three animals are looked upon as individual trapping units, the pig used as a bait animal has proved to be more than twice as effective as either of the bait cattle individually.

4. *Determination of breeding areas by means of pupal casing surveys.*

The more or less unco-ordinated search for the immature stages conducted in the past has provided a fairly clear picture of the particular habitats in which the various species breed, and these have been studied in detail. It has failed entirely, however, to provide an overall picture of the *actual* breeding areas of the savannah species, *G. pallidipes,* for instance. Furthermore, studies of the distribution of this species by means of trap and bait animal surveys have been extremely misleading in serving as an index of the breeding areas. The localities in which severe epizootics of Nagana occur, even with the added evidence of a high density of *G. pallidipes,* need not necessarily have any connection with the actual breeding grounds of this species, as has been clearly demonstrated on numerous occasions.

To illustrate the misleading nature of evidence obtained by surveys of tsetse fly density in determining breeding sites, the south-western portion of the Umfolozi game reserve may be compared with the Ntambanana settlement area approximately ten miles to the south. This European settlement area is separated from the above game reserve by a low range of hills only sparsely covered with bush. It was subjected to an extremely severe epizootic of Nagana in 1945. Surveys by means of Harris traps conducted at the time revealed the following:—

TABLE 5.

Incidence of G. pallidipes *in the Umfolozi Game Reserve and the Ntambanana Settlement Area in* 1945.

Section A 1—Umfolozi Game Reserve.

	April.	May.	June.
No. of Harris Traps	2,643	2,643	2,653
No. of Flies caught	46,902	67,115	64,199
Flies per Trap per Month	17·7	25·4	24·2
Average No. of Flies per trap per Month, April–June		22·4	

Ntambanana Settlement Area.

	April.	May.	June.
No. of Harris Traps	55	53	44
No. of Flies caught	2,457	1,897	996
Flies per trap per month	44·7	35·8	22·6
Average No. of Flies per Trap per Month, April–June		34·4	

The above comparison in tsetse fly incidence, as revealed by traps, is open to criticism in that a very much greater number of traps operated in the reserve than in the settlement and their numerical total per unit area was greater in the former than in the latter. On the basis of flies caught per trap per month over the period of three months, however, the density of flies would appear to have