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THE INFLUENCE OF THE TSETSE FLY ERADICATION CAMPAIGN ON THE BREEDING ACTIVITY OF GLOSSINAE AND THEIR PARASITES IN ZULULAND.

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During the course of the tsetse fly eradication campaign in northern Zululand, where the new contact insecticides D.D.T. and benzene hexachloride (B.H.C.) have been used on an extensive scale for the first time in the history of nagana control, a study was conducted concurrently over a period of two years (March 1947 to March 1949) of the effect of these insecticides upon the parasites of tsetse flies.

METHOD.

Commencing from the end of the year 1946, a pupal survey was instituted. The object was to determine the actual tsetse fly breeding areas by means of the pupae and pupal casings found. The pupal casings represented the accumulation of several years. Observations upon the state of preservation of such casings, exposed over a period of 4 years under natural conditions, indicated that no obvious deterioration takes place in that period of time.

A number of groups of specially trained natives under the charge of European supervisors were employed to search carefully the upper soil layers to a depth of 1½ inches in localities where experience had taught, larval deposition was likely to have occurred. All dipterous pupal casings were collected in addition to those of tsetse flies and subsequently sorted in the laboratory. The daily finds for the various localities searched were presented in terms of the number of pupae or casings per searcher per day. The resultant figures served to indicate whether an area could be regarded as a breeding locality or as a dispersion area in which little or no breeding had taken place. The findings of this survey formed the basis of the campaign from the point of view of efficiency and economy, as it was upon these predetermined breeding centres that insecticidal control was concentrated.

Apart from the determination of breeding areas, the pupal survey offered the further advantage of showing the extent to which breeding was occurring. This was indicated by the number of viable unhatched pupae found, thus affording a further check on the other methods of survey employed, namely bait animal and trap surveys of adult flies. In addition, the accumulated tsetse fly pupae collected from the two main breeding areas, Umfolozi and Hluhluwe, were stored until hatching had occurred, in order to determine the degree of parasitism.

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Parasites.

The tsetse fly species *Glossina pallidipes* Aust., occurs in both reserves and it is to this species only that nagana in epizootic form in Zululand is attributable. In addition to this species the forest dwelling *Glossina brevipalpis* Newst., occurs in the Hluhluwe Reserve. The main parasite of both species is the bombyliid, *Thyridanthrax brevifacies* Hesse. The following parasites have also been recorded: they are placed in the order of their importance; *Mutilla auxiliaris*, Turn., (Mutillidae), *Syntomosphyrum glossinae* Waterst., (Eulophidae), *Thyridanthrax abruptus* Lw. (Bombyliidae) and *Trichopria capensis robustior* Silv., (Diapriidae).

It was possible to confirm the observations of Chorley (1929) in Southern Rhodesia regarding the distinct seasonal activity of these parasites. He found that they reached a peak towards the end of the dry season (September–November) and were at their lowest ebb during March to April. Furthermore, the observation made by Chorley, that a large percentage of the tsetse fly pupae collected failed to hatch after exposure to sunlight could be confirmed. The maximum pupal mortality (over 70%) was not quite as restricted to certain periods as had been observed in Rhodesia, but remained restricted nevertheless to the hot season (November to March).

In analysing the percentage mortality amongst the pupae collected in the Umfolozi Reserve, an area fairly readily accessible to aircraft for the dispersion of insecticides, it is significant that the mortality amongst the pupae in this reserve was greater than in the Hluhluwe reserve (Table 1). This may be correlated possibly with the heavier applications of DDT and BHC in the former reserve than in the latter where the area as a whole was less accessible to aircraft. The effect of the insecticides upon the adult flies may have been responsible for this in the production of less virile larvae from them following sub-lethal exposures.

The Campaign.

From the commencement of the campaign, in which the insecticides were applied in the smoke (or aerosol) form, a marked reduction in the monthly fly catches was apparent (see Figs. 1A and 2A). The actual fly catches in the Umfolozi Reserve were reduced approximately 500 times during the period under discussion. This is reflected by a steadily dropping curve (Fig. 1A). In the Hluhluwe Reserve the results were not as favourable and the combined curve for the two species (A Fig. 2) declines more slowly. This can be accounted for by the fact that the fixed-wing aircraft were unable to operate successfully in the northern mountainous section of the reserve and that the other means of insecticide dispersion resorted to, namely D.D.T. smoke generators and D.D.T. dusting, did not bring about the same rapid rate of reduction. Initially the fly catches did decrease rapidly but thereafter the rate of decrease slowed down very considerably. Only after the advent of the helicopters in December 1948, which were able to negotiate all the steep, formerly inaccessible valleys, did the rapidity of decrease in fly catches accelerate towards zero (Figs. 2 and 3A).

The Effects of the Campaign.

From the results of the pupal survey it was possible to draw a comparison between the decrease in fly catches and the breeding activity of the flies. At the same time it was possible to show the effects of the campaign upon the tsetse fly parasites. As the results obtained from the campaign vary in the two areas, owing to geophysical differences, it is advisable to analyse them separately.

TABLE 1.

	UMFOLOSI.		HLUHLUWE.			
	G. pallidipes.		*G. pallidipes.*		*G. brevipalpis.*	
	Tsetse hatched.	Pupae dead.	Tsetse hatched.	Pupae dead.	Tsetse hatched.	Pupae dead.
	Percentage.	*Percentage.*	*Percentage.*	*Percentage.*	*Percentage.*	*Percentage.*
1947—						
March	34·5	64·6	7·9	76·3	2·4	86·5
April	43·8	46·6	33·7	36·1	50·5	43·5
May	19·7	69·0	10·5	53·6	37·0	55·0
June	17·5	69·9	16·5	69·7	37·2	55·2
July	12·2	85·2	23·7	70·1	30·2	42·2
August	11·1	68·8	6·3	66·8	2·1	47·9
September	10·1	59·6	28·9	50·4	2·4	42·8
October	5·6	42·5	31·6	45·2	3·4	47·9
November	1·0	63·2	13·5	62·9	11·2	60·7
December	1·5	71·7	7·1	71·5	8·0	68·0
1948—						
January	3·7	92·4	27·2	59·8	12·7	69·3
February	2·0	96·9	36·9	51·5	29·4	56·1
March	3·6	92·6	39·3	56·8	25·9	65·3
April	6·8	93·2	49·0	39·4	36·1	50·3
May	1·9	97·8	51·6	41·7	51·0	37·2
June	0	100	59·7	30·9	52·4	24·2
July	2·5	96·7	57·9	35·9	36·9	42·5
August	0	100	39·2	50·5	19·0	52·3
September	0	100	15·0	71·0	8·1	64·4
October	15·4	84·6	16·3	73·7	0·44	82·0
November	100*	0	24·8	72·2	11·8	77·0
December	0	0	30·8	57·5	10·6	70·0
1949—						
January	0	0	80·8	17·1	26·1	56·5
February	—	—	40·8	59·2	51·9	48·1
March	—	—	60·0	40·0	47·9	31·6

* One pupa only.

UMFOLOZI RESERVE.

In the Umfolozi area (Fig. 1) the steadily declining curve (A), representing the monthly fly catches in Harris traps, is closely followed by the curve (B), representing the percentage of unhatched *G. pallidipes* pupae. From the figure 3·1%, at the commencement in September 1947, the curve declines steadily to reach elimination point in December 1948. This indicates that the number of pupae being deposited was so small, on account of the markedly reduced fly density, that they could no longer be determined.

The curve of the parasitized percentage of the pupae collected (C) closely follows those of the decreasing fly catches (A) and the unhatched pupae (B) during the initial months (September to December 1947), despite the fact that this period represents the yearly peak of parasitism. In January 1948 a rapid decline in parasitism occurred, and from February onward, parasitism appeared to play no further role. In August 1948, when normally a peak could be expected, parasitism ceased entirely. The parasites, as the result of the D.D.T. and B.H.C. applications, disappeared even before their hosts. It may be deduced from these observations, that in an area well suited to the aerial method of insecticide application, the parasites are eliminated before their hosts, the tsetse flies.

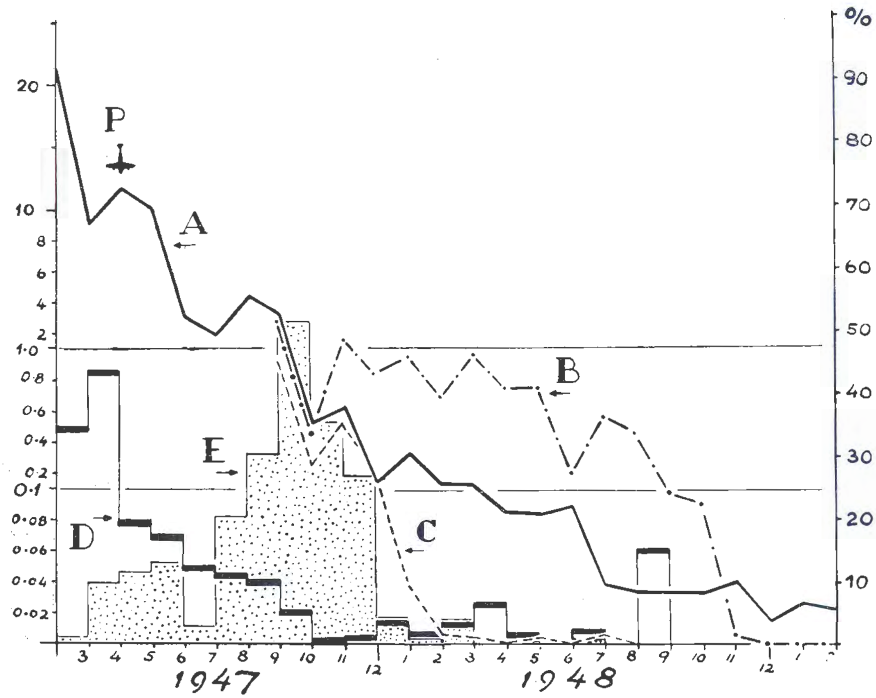

Fig. 1 : Umfolozi (*G. pallidipes*)

EXPLANATION OF FIGURES 1, 2 and 3.

A.—Number of tsetse flies per trap per month.

B.—Percentage of unhatched tsetse pupae (in relation to gross total—pupae and casings).

C.—Percentage of parasitised tsetse pupae (in relation to gross total—pupae and casings).

D.—Percentage of tsetse flies hatched from pupae collected.

E.—Percentage of parasites hatched from pupae collected.

P.—Commencement of insecticide applications by fixed wing aircraft.

H.—Commencement of insecticide applications by helicopters.

Scale on the left governs graphs A, B and C.

Scale on the right governs graphs E and D.

If the number of flies hatched from the pupae collected are compared with the number of parasites which emerge, in order to arrive at the relative rate of parasitism, the following picture is presented; the percentage of hatching flies (D) decreases rapidly at the commencement of the campaign, remains near the zero line for a time and then, during the last phase when the parasites are finally disappearing, shows a tendency to rise again. The proportion of parasites hatching (E) does not show the effects of the insecticides upon them at first, due to their greatly extended pupation period. They reach their peak, therefore, during the months October to November when the insecticides then exert their maximum effect upon them and they become decimated to an extent which causes them to disappear from the picture extremely rapidly.

In other words, the graphs in Fig. 1 indicate that in an area such as the Umfolozi Reserve, which is suitable for aerial operation, the effect of the insecticides upon the tsetse flies is apparent from the commencement of application. The decrease in tsetse fly catches, recorded on a monthly basis, continues inevitably in a steplike progression over a considerable period. There are two reasons for this; (1) in that it is not possible to treat an entire area simultaneously, a small percentage of flies, by virtue of movement from place to place, always has the opportunity of surviving and of depositing larvae, (2) the glossinae cannot be destroyed during the pupal stage so that hatching must be expected to occur between applications of insecticide.

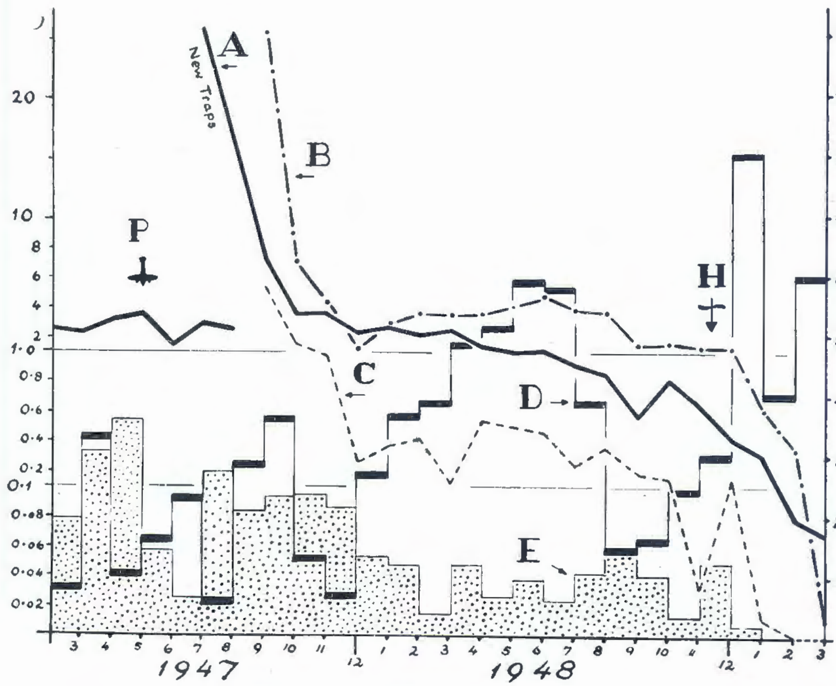

Fig. 2 : Hluhluwe (*G. pallidipes*)

The parasites, on the other hand, respond in a different way to the effects of the insecticide. As the campaign was started in April, at a time when small numbers of parasite imagines are normally present whereas the mass of the new generation are quiescent as larvae or pupae in the pupae of the hosts, the effects upon the parasites were not apparent during the first 4–5 months. The duration of the pupal period of the parasites, which in *Thyridanthrax* may exceed that of the host by over 90 days, has the effect of producing a mass hatching from

September to November, when the insecticide exerts its maximum effect. Accentuated by the ever-decreasing number of tsetse fly pupae available to the parasites at this stage, a precipitous decline in parasite incidence takes place during December to January, so that in place of a normal peak being built up total disappearance results.

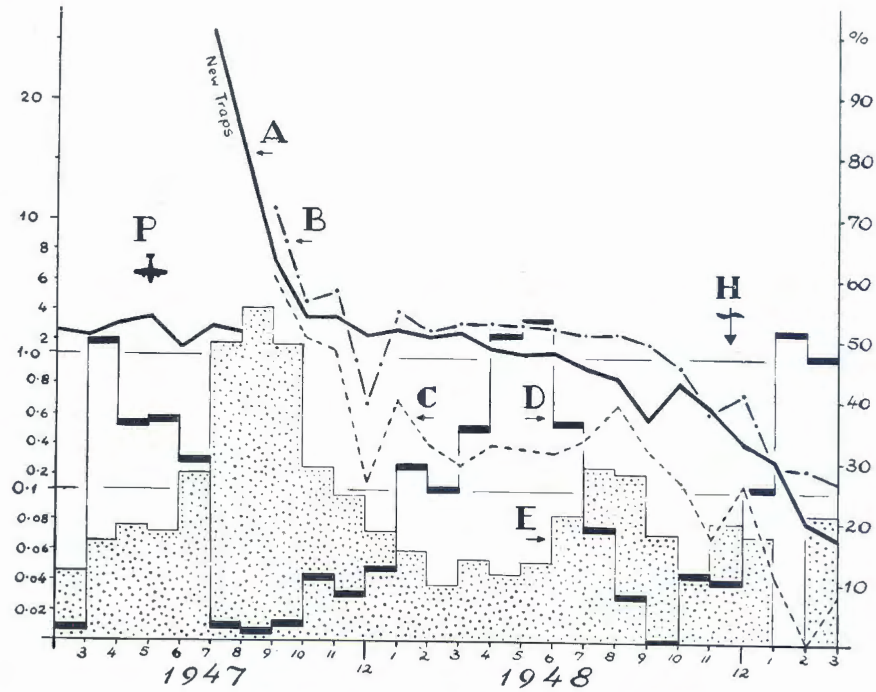

Fig 3 : Hluhluwe (*G. brevipalpis*)

Hluhluwe Reserve.

The course of the campaign in the Hluhluwe Reserve appears in a different light to that in the more open and accessible Umfolozi Reserve. As previously mentioned, the northern portion of this reserve is extremely mountainous and covered with a dense forest-type of vegetation. Expectations for the outcome of the control measures adopted (fixed-wing aircraft application, smoke generators and dusting), of necessity must be less favourable for this section. Whereas the tsetse flies were reduced rapidly to almost elimination point in the more open Hluhluwe Flats or southern portion, they maintained a fairly high density in the northern portion until the introduction of the helicopters. An additional division becomes necessary in this reserve due to the presence of two species of tsetse flies. *G. pallidipes* is distributed more or less evenly throughout the reserve whereas the heavily afforested mountainous area represents the stronghold of *G. brevipalpis*. It follows, therefore, that these two tsetse species as well as their parasites, would respond differently to the campaign started in May 1947.

It must be pointed out, however, that it was not possible to draw a sharp distinction between the course of the campaign in the easily accessible flat portion and the mountainous northern part of the reserve. For this reason the whole area had to be regarded as an entity from the statistical point of view. Furthermore, the catches of the two tsetse species had to be given in a composite curve (A in figs. 2 and 3), as the bait animal survey did not exist at the commencement of the campaign and the response of *G. brevipalpis* to the Harris Fly Traps was so poor compared with that of *G. pallidipes* that these figures alone would confuse the picture. A comparison of the two means of survey at a later stage in the campaign indicated that the method adopted was justified. The break in the curve A represents the introduction of new Harris Traps in July 1947 after which all the traps in the reserve were maintained in a good condition—hence the apparent increase in fly density.

Aftei the commencement of spraying (P), the average monthly catches decreased rapidly. This was readily apparent when the new traps were introduced. The reason for this is the very rapid reduction in flies in the southern, flatter, portion of the reserve following the use of the fixed-wing aircraft. From October 1947 the restricting influence of the mountainous section upon the rate of decrease in fly catches, from about three per trap per month, became noticeable. Even with intensive application of insecticide by smoke generators and dusting it was possible to reduce the fly catches to only 0·6 flies per trap per month over the ensuing 12 months. The introduction of the helicopters (H) in December 1948 increased the rate of decline of the monthly catches, as is reflected in the sharp drop of the curve.

In comparison with the results obtained in the Umfolozi Reserve, the slow progress made in the northern mountainous parts of Hluhluwe until the advent of the helicopters, was responsible for a stagnation of the campaign of almost twelve months. Whereas virtual elimination had occurred in the Umfolozi Reserve, this stage could not be expected in Hluhluwe for approximately another twelve months.

As was the case in the Umfolozi Reserve, the curve of the monthly findings of unhatched pupae (B) more or less follows the fly catches (A). The indirect retarding influence of the terrain in Hluhluwe makes itself felt even when the effects of the helicopters bring about an accelerated decline in catches. It will be noted that the decrease in pupal findings in the case of *G. brevipalpis* (B) is not as rapid as is the case with *G. pallidipes*. The reason for this may be sought in certain ecological peculiarities governing this species. *G. brevipalpis* occurs in fair density even up to the tops of the high heavily-forested ridges where air currents adversely influence the maximum efficiency of the helicopters. Fortunately the number of such sites, where a good smoke cover is seldom obtained and where the flies are able to escape complete destruction, are limited.

The monthly percentage of parasitized pupae (C) shows the same correlation with the fly catches (A) as do the total pupal findings (B). As observed in the Umfolozi Reserve, a fairly precipitous decrease down to the zero point took place (C) at any rate in the case of *G. pallidipes*, some time before the flies themselves were approaching elimination.

This fact becomes clearer when a comparison is drawn between the relative percentages of flies (D) and parasites (E) emerging from pupae collected in the reserve. The higher, more or less undisturbed rate of parasitism in the case of *G. brevipalpis* is clearly demonstrable in Fig. 3, in contrast with the more accentuated effect of the campaign upon parasitism in the case of *G. pallidipes*, distributed over the level country (Fig. 2). Parasitism in the case of *G. pallidipes* decreases slowly but surely and disappears suddenly after the introduction of the helicopters. A slight peak in parasitism is apparent, however, even in the second year (1948). This is due to the retardation in fly destruction due to geophysical factors in this reserve. In the case of *G. brevipalpis* (Fig. 3, E) the rate of parasitism shows even less disturbance and a well-defined seasonal peak can be seen clearly although the effect of the campaign upon the height of this peak is evident. When the helicopters were brought into operation the rate of parasitism merely showed an irregularity. This may be explained possibly by the difficulties experienced in combating the host species in certain areas.

The hatching of tsetse flies from the pupae collected in the Hluhluwe Reserve during the initial stage of the campaign did not follow the pattern experienced in the Umfolosi Reserve. This is probably due to the inability of bringing about a steady sustained reduction in the incidence of the flies.

The fact that *G. brevipalpis* was the least affected by the campaign, as already described, accounts for the relative percentage of hatchings (Fig. 3, D) remaining at the same levels in 1948 and the beginning of 1949, whilst the seasonal peaks in hatchings are still clearly visible. The explanation for the continuance of the seasonal peaks of hatchings of the flies is to be found partly in the relatively slight effect of the insecticides upon *G. brevipalpis* and partly in the original high relative index of parasitism.

In the case of *G. pallidipes* (Fig. 2, D) the effects of the insecticidal applications upon the relative percentage of hatchings become more apparent at a later stage in the campaign. This state of affairs more closely approaches that occurring in the Umfolozi Reserve. Here the remaining tsetse fly pupae were able to complete their development undisturbed due to the ever-decreasing degree of parasitism. This means, that with the disappearance of parasitism, the relative number of hatchings of flies increased.

Conclusions.

In normal years the development of tsetse flies is influenced by two factors, namely the lethal effects of exposure to sunlight and to parasitism. The effects of sunlight are influenced by telluric and vegetational factors, and remain within certain limits, whereas the effects of parasitism show a clearly-defined fluctuation, seasonal in nature. For parasite and host, therefore, the undulating graph of the parasites follows a quarter of a phase behind that of the hosts. The peak of incidence for the tsetse flies falls in August-September, whereas that for the parasites follows in October-November. If this natural cycle is disturbed, as has been the case with the campaign in Zululand, there follows a resultant difference in the reactions of the host and the parasites.

The degree of efficiency with which a campaign is conducted is of the very greatest importance. In general it may be said that the direct effect of the insecticides D.D.T. and B.H.C. is very marked upon both the host and the parasites. It may appear that at the commencement of a campaign the parasites are not severely affected, but this is not true, as in the case under discussion, the campaign was instituted at a time when the parasites were for the most part unassailable—in the pupae of their hosts (Fig. 1, E). The continued insecticide applications which followed resulted in a subsequent wholesale destruction of the adult parasites. This led to their disappearance before the tsetse flies were themselves eliminated. It follows, therefore, that as the numbers of parasites decrease, the surviving tsetse flies, which themselves are also decreasing, have an ever increasing chance of reproducing themselves unimpeded by parasitism.

The experience gained with *G. pallidipes* in the Hluhluwe Reserve (Fig. 2), during the period of reduced reduction prior to the advent of the helicopters, showed that it was uneconomical and perhaps even dangerous, to attempt eradication with a means that was not entirely and rapidly effective.

During the period October 1947 to October 1948 the flies caught monthly were reduced fivefold whereas the reduction in parasites was tenfold. This resulted in the relative percentage of flies emerging during the peak months of 1948 being twice as high as that during the previous year, on account of this disproportionate rate of reduction.

When the parasites have almost disappeared it would seem that a very critical stage is reached in any campaign directed towards the eradication of tsetse flies by means of the contact insecticides. Such a campaign, should at this stage, be continued to finality for the reason that should operations cease when the flies have reached a very low density and the parasites have reached elimination point, a rapid build up in fly density is likely to occur by virtue of the absence of parasites. This may jeopardize the entire undertaking.

It follows, therefore, that a thoroughly efficient and extensive survey should be maintained for a considerable time after the apparent eradication of the fly to detect any possible surviving flies.

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