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Sleeping Sickness Survey in the Serengeti Area (Tanzania) 1971

II. The vector role of *Glossina swynnertoni* Austen

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Abstract

The paper reports an epidemiological survey of populations of *Glossina swynnertoni* Austen in the Serengeti National Park. Tsetse flies were sampled from different areas supporting different densities of flies, and their infection rates were determined by dissection. Although, as in a previous survey, no mature *T. brucei* subgroup infections were encountered, it appeared that the *T. vivax* subgroup infection rate was highest in areas of high tsetse density. Infection rate figures are analysed to show that, as previously found during laboratory studies, not all infected blood meals eventually give rise to mature trypanosome infections in the flies. The feeding conditions of populations of flies in the study areas were assessed, and the differences are explained in terms of food availability. The importance is stressed, of considering both the feeding preferences of the flies and the natural incidence of trypanosome infections in the wild game, in assessing the reservoir potential of any particular game species.

In addition to the work on tsetse, a few *Hippobosca longipennis* Fabricius were collected from darted lions and hyaenas. From over 200 dissected none carried live trypanosomes.

Introduction

The entomological survey carried out in 1970 in the Serengeti region did not discover a single tsetse fly, out of a total of over 7,000 dissected, with salivary gland infections of the *Trypanosoma brucei* subgroup (MOLOO et al., 1971). In contrast, 10 % of 115 wild animals and 3.5 % of 798 domestic cattle were found to be carrying *T. brucei* subgroup organisms (GEIGY et al., 1971; MWAMBU & MAYENDE, 1971). Thus in the Serengeti area the vector role of the tsetse fly in the transmission cycle of this trypanosome was not established.

In the survey reported here attention was concentrated on the tsetse fly *Glossina swynnertoni* Austen, by far the most widespread and abundant of the tsetse species in the area. In addition the hippoboscid *Hippobosca longipennis* Fabricius, associated with lions and hyaenas, was studied to determine whether it might be involved in non-cyclical transmission of trypanosomes. Populations of tsetse were sampled as in the previous year and flies dissected to determine the rates of infection with the three trypanosome subgroups.

In an attempt to find tsetse flies infected with *T. brucei,* particular attention was paid to those areas in which flies were heavily infected with the animal trypanosomes, *T. vivax* and *T. congolense.* This was because it is apparent from

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the survey of ASHCROFT (1959) that many more of the wild animal hosts of *Glossina* are doubly infected with either of these trypanosome species and with the *T. brucei* subgroup than would be expected assuming that the infections occurred at random. It should follow from this that areas in which the tsetse population is heavily infected with *T. vivax* and *T. congolense* (indicating a high infection rate of host animals) are more likely sources of *T. brucei* infected tsetse than areas in which the infection rate of flies with the animal trypanosomes is low.

Eventually, three study areas were chosen and samples of *G. swynnertoni* collected in each. The flies were used mainly to determine infection rates, but small samples were also taken for the purposes of determining the age, weight and feeding condition of the populations in the three areas. A number of engorged flies were encountered, and their blood meals later identified.

The samples of hippoboscids caught off darted lions and hyaenas were also dissected, to see if they were capable of supporting trypanosome infections.

The survey areas

The three survey areas are shown in Fig. 1 (Part I). The nature of the Serengeti region and the dominant vegetations are described by GREENWAY (1962) and more briefly by MOLOO et al. (1971). In all three areas the small-leaved *Acacia* and *Commiphora* species predominated. Broader leaved trees and shrubs, *Cordia, Grewia, Lannea* and *Pavetta* spp. were found along drainage lines that, during the present survey, were mostly dry.

Area I, situated on the edge of the Serengeti Plains, was completely open except for trees and shrubs along dry river courses, and the sometimes large kopjes with their characteristic vegetation. In this area, the standard catch referred to below was taken on a N.W. S.E. transect parallel and close to one of the dry river beds. Animals seen in the area during the survey included Thomson's gazelle, topi, Coke's hartebeest, giraffe, warthog, zebra, ostrich, bat-eared fox, hyaena and lion.

Area II was along a N.W. S.E. transect approximately half a mile North of the Banagi Ikoma track, and ended at the Orangi River. *Acacia* and *Commiphora* species were quite abundant and the transect crossed a number of dry water courses. Animals seen during the survey included Thomson's and Grant's gazelles, topi, buffalo, impala, warthog, giraffe, hartebeest, hyaena and cheetah.

Area III was a transect along the Kyabaratero Valley. This carried by far the most abundant vegetational cover and supported the widest range of animal species. Both can be attributed to the tendency for this valley to retain surface water after the previous two regions have dried out, a fact emphasized by the presence in this area only of *Kigelia africana* (Lam.) Benth., the 'sausage tree', and *Acacia polycantha* Willd. ssp. *campylacantha* (A. Rich.) Brenan, the 'falcon's claw acacia'. Animals seen in the valley itself included impala, warthog, elephant, baboon, topi, giraffe, buffalo, eland, leopard and lion. Hartebeest, zebra and Thomson's gazelle were seen at the mouth of the valley, near the Musabi Plains.

Materials and methods

In each of the three areas flies were sampled by use of a Land Rover. In addition in Area II flies were sampled by short fly rounds. Flies, caught in hand nets, were placed individually in small, numbered polythene tubes and kept alive in a cooled 'Thermos' flask for dissection in the laboratory. Dissections were

carried out in saline mostly within six hours of being caught, but occasionally up to eighteen hours after collection.

Trypanosome infections in the tsetse flies were identified according to the site of infection in the flies (LLOYD & JOHNSON, 1924). Infections in the proboscis alone were recorded as *T. vivax* and in the proboscis and midgut as *T. congolense*. The salivary glands were carefully examined for mature *T. brucei* infections. The wing fray method of JACKSON (1946) provided an estimate of the age of each fly.

The tsetse samples for fat and residual blood meal estimation consisted of flies attracted to and resting on the outside of a Land Rover. It is important to distinguish between flies caught inside and outside a vehicle since there may be important differences between them. The flies were kept alive for return to the laboratory, where only the proboscis was removed for inspection. They were then immediately killed by freezing, and later placed in opened tubes over a desiccant. In such samples, therefore, only *T. vivax* infection rates could be determined with any certainty. The *T. congolense* infection rates recorded below are based on samples of slightly fewer flies than the corresponding *T. vivax* rates.

The processes of fat extraction and estimation of the residual blood meal of tsetse flies are described in detail by FORD et al. (1972), and were followed here. Drying to constant weight provides the 'dry weight' of each fly which, after chloroform extraction of the lipids and re-drying, becomes the 'reduced dry weight'. The difference between the two weights is referred to as the 'fat' content. The unexcreted haematin in the gut of each fly was estimated spectrophotometrically, and is referred to below as the 'haematin' content (the PHC of FORD et al., 1972). The wing fray of each fly and the length of the vein along the 'cutting edge' of the hatchet cell in the wing were also recorded.

A number of resting and engorged flies were captured, mainly during the survey of game animals (see Part I), either near to darted animals or in their immediate vicinity. The recorded frequency of tsetse feeds from those species studied during the game survey is therefore probably biased and represents an over-estimate of the average frequency of feeding from such hosts. The blood meals were prepared, stored and later identified in the way described by MOLOO et al. (1971).

The standard catch was introduced in order to assess the relative abundance of *G. swynnertoni* in the three study areas. At the start of the catch all flies were caught from inside and outside the Land Rover, and discarded. The vehicle was driven for one minute at about 10 m.p.h. (16 k.p.h.) and then stopped, all the approaching flies being caught and counted. The sum of the males and females captured during ten such stops represents the standard catch for each area.

The samples of hippoboscids were treated in a similar way to the tsetse samples. They were collected by hand from darted lions and hyaenas, and all flies from one animal kept separately. It proved impracticable to dissect these flies in the field so that, as with the tsetse flies, they were dissected in the laboratory, again mainly within six hours of collection. Both the mouthparts and gut were examined for living trypanosomes.

Results

The standard catches from the three areas are given in Table 6 together with a visual estimate of the tree cover. The catch increased from Area I to III, whilst the percentage of females in the catch decreased.

Table 6. Result of the standard catches in the three study areas, and mature *T. vivax* infection rates

Area	Tree cover %	Standard Catch Males	Females	Total	Female %	*T. vivax* infections Males	Females
I	< 5 %	16	13	29	45 %	6.8 %	7.3 %
II	10 %	59	23	82	28 %	11.1 %	13.5 %
III	20 %	405	101	506	20 %	20.0 %	25.9 %

During the survey a total of over 3,500 *G. swynnertoni* were dissected completely (2,421 males and 1,129 females). Not one carried a mature *T. brucei* infection in its salivary glands. Thus once again this tsetse fly is not a proven vector of *T. brucei* in the Serengeti area.

Of over 200 hippoboscids dissected none carried live trypanosomes, although during the survey dead trypanosomes were seen in the partly digested blood meal within the gut (JENNI, pers. comm.).

The infection rates of *G. swynnertoni* with mature *T. vivax* and *T. congolense* organisms are given in Table 8. Flies in Area III are much more heavily infected with *T. vivax* than flies in Area I, whilst Area II flies are intermediate. In each area females of any particular wing fray category tend to be more heavily infected than the corresponding males, probably because of the slower rate of wing fraying in females.

Table 7. A comparison of the feeding condition of non-teneral *G. swynnertoni* caught outside a Land Rover during standard catches. Means with standard errors of the populations in the three study areas. Vein lengths in micrometer units and haematin in optical density units

Male flies

Area	Wing Fray	Vein Length	Reduced Dry Weight mgms.	Fat mgms.	Haema-tin	Sample Size
I	2.66	57.00±0.37	6.95±0.10	1.60±0.11	0.090	35
II	2.67	57.88±0.38	7.16±0.18	1.62±0.14	0.148	26
III	3.17	56.61±0.26	6.83±0.10	1.81±0.09	0.055	46

Female flies

Area	Wing Fray	Vein Length	Weight mgms. Reduced Dry	Fat mgms.	Haema-tin	Sample Size
I	2.34	64.83±0.31	10.22±0.52	3.31±0.38	0.285	29
II	2.85	64.29±0.56	11.22±0.45	3.71±0.40	0.350	24
III	2.76	64.14±0.33	10.17±0.27	4.80±0.38	0.177	29

Table 8. The incidence of mature trypanosome infections in *G. swynnertoni* in the three study areas of the Serengeti National Park (for sites see Fig. 1)

		Wing Fray	I	%	II	%	III	%	IV	%	V	%	VI	%	Total	%
Males	Area I	*T. vivax*	2/48	4.2	4/53	7.5	4/41	9.8	1/29	3.4	1/10	10.0	1/10	10.0	13/191	6.8
		T. congolense	0/34	–	0/42	–	0/32	–	0/25	–	0/8	–	0/9	–	0/150	–
	Area II	*T. vivax*	4/162	2.5	15/135	11.1	17/115	14.8	12/94	12.8	12/69	17.4	7/26	26.9	67/601	11.1
		T. congolense	1/102	1.0	1/80	1.3	3/46	6.5	0/47	–	1/42	2.4	2/15	13.3	8/332	2.4
	Area III	*T. vivax*	11/175	6.3	26/183	14.2	34/142	23.9	43/141	30.5	26/85	30.6	10/23	43.5	150/749	20.0
		T. congolense	0/168	–	5/166	3.0	3/129	2.3	5/134	3.7	4/77	5.2	1/21	4.8	18/695	2.6
		Wing Fray	I	%	II	%	III	%	IV	%	V	%	VI	%	Total	%
Females	Area I	*T. vivax*	0/36	–	4/33	12.1	0/22	–	3/20	15.0	0/5	–	2/7	28.6	9/123	7.3
		T. congolense	0/20	–	1/25	4.0	1/12	8.3	0/14	–	0/4	–	0/5	–	2/80	2.5
	Area II	*T. vivax*	2/66	3.0	4/38	10.5	12/44	27.3	1/18	5.6	5/17	29.4	2/10	20.0	26/193	13.5
		T. congolense	0/28	–	1/14	7.1	0/15	–	0/5	–	0/10	–	0/4	–	1/76	1.3
	Area III	*T. vivax*	15/153	9.8	25/128	19.5	36/113	31.9	34/96	35.4	30/65	46.2	7/12	58.3	147/567	25.9
		T. congolense	1/143	0.7	3/119	2.5	2/105	1.9	1/89	1.1	7/63	11.1	0/11	–	14/530	2.6

The results of the laboratory analysis of samples of males and females from outside a Land Rover in the three areas are given in Table 7. The values represent the means together with their standard errors for samples of the observed size of the populations from which the means are derived. Standard errors are not given for wing fray and haematin averages because the distributions of values for these two characters are not normal. None of the differences recorded in the Table is statistically significant except that between the vein length of male flies in Areas II and III (for which $t = 2.85$, $p < 0.01$). However, the trend in the results is discussed below.
and III (for which $t = 2.85$, $p < 0.01$). However, the trend in the results is discussed below.

Forty-seven out of a total of 59 *G. swynnertoni* blood meals were identified. Of these, 40 % (19) were from warthog, 36 % (17) from buffalo, 8.5 % (4) from 'cat', 4 % (2) each from giraffe and hartebeest or topi and 2 % (1) from an avian. In addition there were two identified double feeds: one from warthog and an unidentified bovid and the other from giraffe and hartebeest or topi. The 'cat' feeds were most probably derived from lion since they were collected near to darted lions. However, they may have been derived from any other member of the Felidae family.

Analysis

The laboratory analysis of flies from the three study areas shows that it is unlikely that the flies belong to three distinct populations with different susceptibilities to trypanosome infection. The differences between the samples can be explained in terms of differences in the availability of food in the three areas. Flies from an area with an abundant supply of host animals (Area III) are longer lived (higher wing fray), contain more fat and are of slightly smaller size (shorter vein length) than flies from areas where food is scarce. Teneral flies tend to have a smaller average vein length than non-tenerals (GLASGOW, 1963) probably because of a higher mortality in smaller flies.

It would be expected from this analysis that flies from Area I (low fat content) are 'hungrier' than flies from the other two areas. This appears to be the case. The standard catch from Area I gave the highest percentage of females of any of the areas (see Table 6) – a characteristic of 'hungry' populations (JACKSON, 1933).

The difference in the *T. vivax* infection rates of the flies from the three areas is probably due to a difference in their feeding pattern. MOLOO et al. (1971) showed that *G. swynnertoni* in the Serengeti area is a reasonably opportunistic feeder. More recently MOLOO (in prep.)

has reviewed the literature and demonstrated a positive correlation between the infection rate of *G. swynnertoni* with *T. vivax* and the percentage of the blood meals of the flies that were derived from Bovidae. He suggests that bovids act as the main source of *T. vivax* infections, because warthogs, the other main hosts of *G. swynnertoni,* are refractory to such infections.

The pattern of *T. congolense* infections is different. Both Suidae and Bovidae can support such infections and MOLOO (in prep.) did not find a similar correlation between the percentage of flies infected with *T. congolense* and their feeding pattern. In the present study there is little difference between the *T. congolense* infection rates in Areas II and III (no infections were found in Area I) and the results from these two areas have been combined for the analysis below.

The difference in the *T. vivax* infection rates of flies in the three areas presumably reflects a difference in the rates at which flies take infected blood meals. In a paper to be published separately it will be shown that on the assumptions of i) an equal infectability of flies of all ages to trypanosome infections and ii) no differential mortality between infected and uninfected flies, the expectation is that the logarithm of the percentage (or proportion) of flies uninfected with trypanosomes will be inversely and linearly related to the age of the flies. The present results for the infections in male flies have been treated as suggested above, and the results are shown in Fig. 2, where age is expressed in terms of wing fray. The combined results for *T. congolense* are shown in the upper part of the figure, whilst the *T. vivax* infections in the three areas are treated separately in the lower part of the figure. Flies of wing fray category six are of indeterminate age, and their infections have not been considered in the calculations of the regressions shown in Fig. 2.

The results follow the predictions of the model – an inverse linear relationship. The slopes of the regression lines shown in the figure are determined by the percentage of blood meals that gives rise to infections in the flies – a figure which presumably varies with the infection rate of the wild animal hosts of tsetse. For example, the relationship shown in Fig. 2 for the *T. vivax* infections of Area III would be predicted assuming that flies of wing fray category 5 are 45 days old and have taken 10 blood meals (values derived from the work of JACKSON, 1946, 1933) and that 7.7 % of all blood meals eventually give rise to infection in the flies. The corresponding figures for Area II and Area I are 3.4 % and 0.8 %, respectively. For the combined *T. congolense* results the graph suggests that only 0.8 % of blood meals eventually give rise to infections in the flies.

The results of the analysis of tsetse fly infection rates can be compared with the infection rates of the wild hosts of the flies. Laboratory

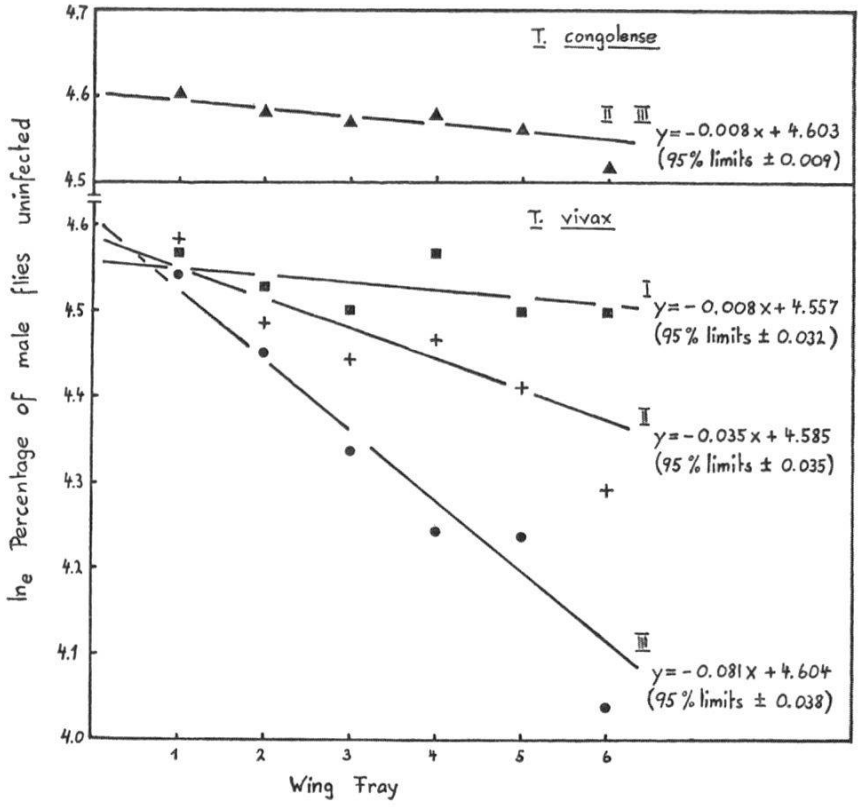

Fig. 2. Relationship between the logarithm of the percentage of male *G. swynnertoni* uninfected with trypanosomes, and the wing fray (i.e. age) of the flies. Upper: *T. congolense* infections for Areas II and III combined. Lower: *T. vivax* infections for the three areas separately (see text). The figures in parentheses represent the 95 % confidence intervals of the respective regression coefficients.

studies have demonstrated that not all infected blood meals manage to infect the tsetse flies taking them (FAIRBAIRN & WATSON, 1955; ELCE, 1971; GRAY & ROBERTS, 1971) but the precise extent of this barrier to infection in field flies has not been determined. The survey of 1970 carried out in the Serengeti region (GEIGY et al., 1971) estimated the incidence of trypanosome infections in the wild mammals and can be used for comparison with the results of the present tsetse survey. Although the game survey by no means provides a random sample of the total variety of tsetse hosts present, there is no reason to believe that animal species particularly prone to *T. congolense* or *T. vivax* subgroup infections were selected in preference to those species not so susceptible. The survey recorded 11.3 % (13/115) of animals infected with *T. vivax* and 15.7 % (18/115) with *T. congolense* (in some cases the infections were mixed). A comparison with the previous figures derived from the analysis of the infections in the flies shows that in the field situation not all infected blood meals can give rise to mature infections in the flies. The comparison further suggests that a smaller proportion of *T. congolense* infected blood meals establish themselves in the tsetse flies than do *T. vivax* infected blood meals. This coincides

with laboratory experience and may result from the more complicated developmental cycle of the former trypanosome species in the vector host. It seems probable that an even lower proportion of *T. brucei* infected blood meals eventually establish infections in the flies. The game survey of 1970 (GEIGY et al., 1971) recorded an overall *T. brucei* infection rate of 10.4 % (12/115: probably an over-estimate of the percentage of tsetse fly blood meals infected with this trypanosome), whilst no such infections were detected in any of the tsetse flies examined, both in 1970 and 1971 (a total of over 10,000 individuals).

The pattern of *G. swynnertoni* host selection as indicated by the blood meal results is similar to that recorded in the much more extensive collection of MOLOO *et al.* (1971) for the same tsetse species in the same area. Once again warthog and buffalo are by far the most favoured hosts. The favoured hosts found in the present sample in order of selection are compared with their ranking in the previous survey (MOLOO et al., 1971; Fig. 6) as follows: 1) Warthog (2nd), 2) Buffalo (1st), 3) 'Cat' (11th), 4) Giraffe (3rd), 4) Hartebeest or topi (17th) and 6) Avian (8th). 'Cat' and hartebeest or topi feeds are more frequent in the present survey, probably for the reason mentioned above (Materials and Methods) that the flies were mostly collected in the vicinity of animals darted during the game survey.

In any analysis of the transmission of trypanosome species it is important to consider both the behaviour of the fly in relation to the game, and the susceptibility of each game species to infection. Those animals that were found during the 1970 survey to harbour *T. brucei* infections were not (with the single exception of warthog) those hosts favoured by the tsetse fly. Thus hyaena, lion, waterbuck and hartebeest, in which the overall *T. brucei* infection rate was 31.4 % (11/35), together provided only 1.4 % of the identified blood meals of tsetse (infection rate figure from GEIGY et al., 1971; Table 10: blood meal figure from MOLOO et al., 1971; Fig. 6). Warthog, with only a 7.7 % (1/13) *T. brucei* infection rate, alone provided 25.6 % of the identified blood meals of *G. swynnertoni*. It is possible to show that warthog may be a much more important source of *T. brucei* infections in *G. swynnertoni* than the other game species, by making use of what ASHCROFT (1959) has termed the 'index of importance' of any particular animal species as a reservoir of trypanosomiasis. The probability that any particular fly ingests a blood meal from a *T. brucei* infected member of the group (lion, hyaena, waterbuck and hartebeest) is equal to the product of the probability that the fly will feed on a member of the group (in this case 0.014 since 1.4 % of blood meals are derived from this group) and the probability that that particular member is harbouring a *T. brucei* infection (in this case 0.314 since 31.4 % of the group are infected with *T. brucei*). Changing this product (0.004) to a percentage

it is concluded that 0.4 % of *G. swynnertoni* blood meals contain *T. brucei* subgroup organisms derived from lion or hyaena or waterbuck or hartebeest. In the case of the warthog the comparable figure is 2.0 % (= $0.256 \times 0.077 = 0.0197$, or 2.0 %). Thus it is clear that warthog is five times more likely to be the source of *T. brucei* infections in *G. swynnertoni* than all the other *T. brucei* infected host animals put together, simply because of the avidity of this tsetse fly for feeding on warthog. ASHCROFT (1959) has previously shown how the host selection pattern of the tsetse fly and the rate of infection in the wild animal hosts must be considered together in establishing the epidemiological importance of a range of animal species.

Discussion

The present survey has suggested that high population densities of tsetse fly are associated with high infection rates of the flies with the animal trypanosome *T. vivax*. Populations of flies will tend to build up in areas where favoured hosts are abundant and relatively stationary, such areas usually being associated with the presence of permanent water and vegetation. Trypanosome infections, once introduced, have a better chance of being maintained since the vectors live for longer periods. The break in any transmission cycle is most likely to occur at that point at which the individuals carrying the infection live for the shortest period of time. In many cases of insect-borne diseases this must involve the insect vector.

Low fly densities and low infection rates of flies with the animal trypanosomes were encountered in more open habitats. Generally, apart from warthog, only the less favoured hosts of tsetse were to be seen in such places: hartebeest and topi, impala. Some of the lowest infection rates of the whole survey were found in samples of tsetse flies taken from the vicinity of animals darted during the game survey – an operation necessarily performed in rather open country.

It is perhaps more than a coincidence that that area which produced the highest *T. vivax* infection rate in the flies (Area III) is the only one of the three from which human sleeping sickness cases have been recorded. It is also the only one of the three in which men have stayed for any period of time. The men were attempting to drill a borehole for a permanent supply of water, whilst the animals remain because surface water is available for longer periods than elsewhere. Although epidemics of sleeping sickness are not necessarily associated with high densities of tsetse flies, but rather with close man-fly contact (MORRIS, 1952), the casual infection of individual humans from any wild game reservoir is much more likely in areas such as Area III with a large and

static game population and a well-fed and therefore relatively immobile and long-lived fly population.

The identification of double feeds during the present blood meal survey raises the interesting possibility of non-cyclical transmission of trypanosomiasis. This result shows that tsetse, possibly interrupted during feeding from one animal, are prepared to continue feeding on another within a fairly short period of time (i.e. before digestion of the first partial feed). Such interrupted feeds may well occur when the animal on which the flies are feeding is itself disturbed, perhaps by the appearance of predators or humans, which may then provide the second partial feed. Tourists have the habit of disturbing animals such as lions – known reservoirs of *T. brucei* subgroup infections. And they do so in motor vehicles, which appear to function as quite efficient traps for the more hungry section of the tsetse population. In such a situation the possibility of mechanical transmission of sleeping sickness to humans cannot be ruled out.

Since this paper was prepared a further survey in the Serengeti region has been carried out under the auspices of E.A.T.R.O. Dr. S. K. Moloo has kindly allowed us to mention here that trituration of samples of *G. swynnertoni* and subsequent inoculation into mice has revealed the presence of *T. brucei* strains in samples of tsetse flies taken near to Banagi at Ikoma gate, and in the Kyabaratero Valley. This work is still in progress, and will be published later.

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