The role of "Glossina" in the transmission of sleeping sickness

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Sleeping Sickness Survey in Musoma District, Tanzania

II. The Role of *Glossina* in the Transmission of Sleeping Sickness

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Abstract

A survey to determine the role of local *Glossina* species on the transmission of human sleeping sickness has been carried out in the Ikoma/Seronera/Kilimafedha triangle. Three different tsetse species were encountered; they were *G. swynnertoni, G. pallidipes* and *G. brevipalpis*. Out of 6,348 *G. swynnertoni* and 623 *G. pallidipes* examined not a single carried salivary gland infection. *G. swynnertoni* had a wide range of vertebrate hosts including bovids, suids, elephant, hippopotamus, primates, carnivores, aardvark and avians, of which buffalo, warthog and giraffe were the hosts most generally favoured. Comparison of the feeding patterns of this species showed that *G. swynnertoni* is readily adaptable. The local tsetse species are primarily zoophilic and, since game was abundant, they attacked man only through chance meeting.

Introduction

Transmission of the human sleeping sickness was studied from the point of view of the local *Glossina* species acting as vectors of *T. rhodesiense*. Since the time at our disposal was limited, it was not possible to survey a very large area of the District. Consequently, six study sites were selected within the Ikoma/Seronera/Kilimafedha triangle which is the centre of human activity in the Serengeti National Park and Ikoma, and where game and tsetse were abundant. To evaluate the problem of human trypanosomiasis, the following investigations were undertaken: (i) distribution of the local *Glossina species;* (ii) the incidence of salivarian trypanosome infections; (iii) feeding habits of the vector; (iv) the nature of man-fly contact.

Survey Area, Materials and Methods

The six sites examined are shown on the map (Fig. 5). The numbers refer to the order in which the areas were surveyed, that is Area 1 was studied in the first week of the 6-week survey period and Area 6 in the last.

Vegetation

The habitat is for the most part gently undulating, though hilly in places. It has good drainage. In many places beneath the surface of the

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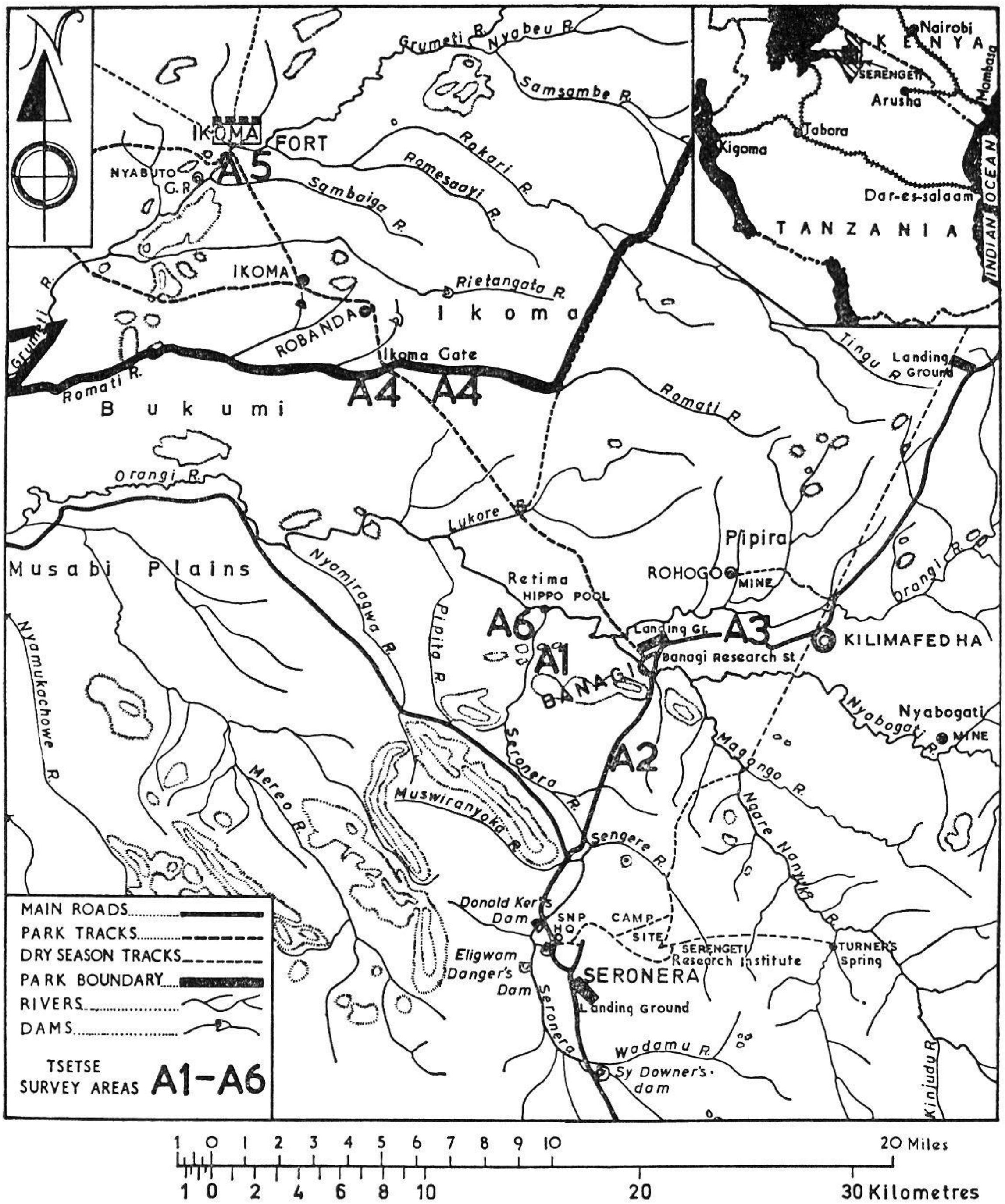

Fig. 5. A map of the part of Musoma District showing locations of tsetse survey areas.

soil there is a cement-like material which binds soil and decomposed rock into a hard pan. Rocky granite kopjes are scattered here and there.

Dry thorn-bush or nyika of one type or another occupies much of the area. The trees and shrubs belong to a great variety of genera but among them Acacia, Euphorbia, Sansevieria and Balanites communities often predominate. The common characteristic of the genera which dominate the nyika is thorniness, with a few important exceptions such as the tree-Combretums and the sparsely scattered baobab (Adansonia). In the greater part of the thorn-bush there is no general canopy. Shrubs which often form thickets are in the main small and evenly scattered throughout the area of grass. Shrubs fringing the banks of rivers and streams form continuous and in places, particularly in Ikoma (Area 5), dense thickets. Areas of open grassland with black cotton soil and patches of hard pan are also features of the habitat. It is characteristic that, except in extreme conditions of dryness, grasses are usually closer and taller than that which commonly grows under "miombo" (see MULLIGAN 1970, p. 294).

Distribution of game

The approximate frequency distribution of different game species for Areas 1–4 and 6 for October are given in Table 1 (JARMAN 1970). The data for Area 5 were not available. It should be mentioned that the frequency of some species such as wildebeest, zebra, gazelles and eland can fluctuate from day to day.

Contents of Table 1 and the observations made during the survey are summarized below. Although as complete as practicable, these data

Table 1. Frequency distribution of game animals in the survey areas in October 1970

Hosts	Areas				
	1	2	3	4	6
Impala	190–200	115–125	235–245	155–165	190–200
Thomson's gazelle	175–185	260–270	5–15	5–10	175–185
Zebra	55–65	–	1–5	305–315	55–65
Wildebeest	–	–	–	280–290	–
Topi	40–50	15–25	25–35	25–35	40–50
Buffalo	20–30	5–10	105–115	5–10	20–30
Hartebeest	15–25	80–90	20–30	5–10	15–25
Giraffe	20–30	10–20	5–15	5–15	20–30
Warthog	20–30	5–15	5–15	5–15	20–30
Dik-dik	20–30	1–5	5–15	5–10	20–30
Grant's gazelle	15–25	–	1–5	10–20	15–25
Hyaena	5–15	5–10	5–10	5–10	5–15
Lion	1–5	1–5	1–5	5–10	1–5
Reedbuck	1–5	–	1–5	5–10	1–5
Leopard	1–5	1–5	1–5	–	1–5
Bushbuck	1–5	–	5–15	–	1–5
Waterbuck	1–5	1–5	1–5	–	1–5
Steinbok	–	1–5	1–5	5–10	–
Duiker	1–5	1–5	–	–	1–5
Elephant	1–5	–	1–5	–	1–5
Rhinoceros	1–5	–	1–5	1–5	1–5
Eland	–	–	–	5–10	5–10

on game possibly do not include some of the rarer animals which were not seen.

Area 1. – This area contained a variety of game. Among the most common animals and in the order of apparent frequency were: impala, Thomson's gazelle, zebra, topi, buffalo/giraffe/warthog/dikdik, hartebeest (kongoni), Grant's gazelle and hyaena. Other animals present included elephant, rhinoceros, waterbuck, reedbuck, bushbuck, duiker, lion and leopard. Hippopotami were seen in restricted places.

Area 2. – The order of apparent frequency of common animals was Thomson's gazelle, impala, hartebeest, topi, giraffe and warthog. Buffalo, hyaena, waterbuck, duiker, dikdik, steinbok, lion, leopard and ostrich were also present.

Area 3. – Impala, buffalo, topi, hartebeest and Thomson's gazelle/giraffe/warthog/dikdik/bushbuck was the order of apparent frequency of common animals present. The fauna also included zebra, Grant's gazelle, lion, reedbuck, leopard, waterbuck, steinbok, elephant and rhinoceros, but these were less frequent.

Area 4. – In this area game was abundant but restricted in variety compared to the other areas. The following was the order of apparent frequency of common game animals: zebra, wildebeest, impala, topi, Grant's gazelle and giraffe/warthog. Other less frequent animals included hyaena, Thomson's gazelle, buffalo, hartebeest, dikdik, lion, reedbuck, steinbok, eland, aardvark and ostrich.

Area 5. – The animals seen or their presence suspected were giraffe, buffalo, zebra, lion, hyaena, impala, topi, bushbuck, waterbuck, hartebeest, dikdik, warthog, wildebeest, Thomson's gazelle, leopard, duiker, aardvark and ostrich.

Area 6. – In view of their close proximity, this area contained a variety of game species similar to that in Area 1. The order of apparent frequency of common animals was impala, Thomson's gazelle, zebra, topi, warthog/giraffe/buffalo/dikdik, hartebeest/Grant's gazelle, hyaena and, in restricted places, hippopotamus and crocodile. The less common animals present included rhinoceros, elephant, lion, reedbuck, leopard, bushbuck, waterbuck, eland and duiker.

Methods of catching Glossina

The following sampling methods were used with a view to determine the distribution of *Glossina* species. The flies caught by these methods were dissected to find trypanosome infections.

(a) Trapping. – Two Langridge traps (modification of single-screen Swynnerton trap, SWYNNERTON (1933)) were used. Each was suspended from a pole between two trees with wires in order to allow free move-

ment in breeze and so enhance its conspicuousness. The flies were trapped for 3–5 days in each area and the traps emptied at 08.00, 10.00, 14.00 and 18.00 hours.

(b) Random catch. – Two groups of three field assistants each using hand-nets caught flies which were attracted to them. Catches were made between 08.00 and 14.00 hours. The catching parties covered about 8 km² in each of the Areas 1, 2, and 4–6.

(c) Landrover catch. – A landrover was driven through the open woodland and beside thickets, stopping from time to time to catch flies which had entered the vehicle and those that alighted on the body.

(d) Fly-round. – This method was employed in Area 3 alone. A transect footpath of 500×200 yd. was cut and divided into 50 yd. sections. The transect traversed thorn-bush woodland and thicket patches. A group of 6 field assistants caught flies from 08.00 to 14.00 hours for a period of four days, six rounds per day.

(e) Bait-animal catch. – Two field assistants caught flies that had alighted on a black cow which was tethered to a tree in Area 2. Catches were made between 06.00 and 18.00 hours over a period of three days.

Trypanosome infections in Glossina

Proboscis, midgut and salivary glands of non-teneral *G. swynnertoni* and *G. pallidipes* were examined under phase-contrast optics. In some cases, the organs containing infective trypanosomes were preserved in liquid nitrogen by the method of DAR & WILSON (1970).

Blood meals

Two catching parties of 2 field assistants each covered about 8 km² in each of the six areas. Flies in Hunger Stage I (JACKSON 1933) were caught from their resting sites and their gut contents expressed on to filter papers. These feeds were dried in a dessicator over calcium chloride and then stored at –20°C. The main groups of hosts were identified by precipitin tests (WEITZ 1952) and the individual species of each group was determined subsequently by the inhibition test (WEITZ 1956). Weak feeds derived respectively from the family *Bovidae* and *Suidae,* which failed to react in the tests specifically, were classed as unidentified species of the groups concerned. "Cat" feeds could be derived from any member of the *Felidae* family including lion and leopard. Feeds which were assigned as "Carnivore" were members of the order *Carnivora* excluding the cat, dog, hyaena and mongoose families. It is possible that these feeds were derived from zorilla and/or honey badger.

Man-fly contact

Observations were made on the reaction of tsetse to the presence of field assistants in all six areas as well as to the men working in the Park.

Results

Distribution of Glossina

The results of sampling methods given in Table 2 are intended to show the relative distribution of the three tsetse species encountered. The local distribution of *G. swynnertoni, G. pallidipes* and *G. brevipalpis* is described below.

Area 1. – *G. swynnertoni* were numerous and were caught in open woodland as well as along thickets close to drainage. *G. pallidipes* were also present but in low numbers confined to riverine thickets.

Area 2. – This area of open woodland with widely scattered small thickets supported a large number of *G. swynnertoni. G. pallidipes* was not encountered.

Area 3. – *G. swynnertoni* were numerous throughout this area of open woodland with riverine thickets. The latter also supported small populations of *G. pallidipes.*

Table 2. Average numbers of tsetse caught per day by four methods

Area	Species	Flies caught per day							
		Random catch		Trap		Bait catch		Fly-round	
		♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
1	*G. swynnertoni*	174	3	46	45	–	–	–	–
	G. pallidipes	1 *	0	2	3	–	–	–	–
2	*G. swynnertoni*	181	22	45	37	122	31	–	–
	G. pallidipes	0	0	0	0	0	0	–	–
3	*G. swynnertoni*	–	–	51	35	–	–	285	4
	G. pallidipes	–	–	2	4	–	–	0	0
4	*G. swynnertoni*	168	10	43	36	–	–	–	–
	G. pallidipes	0	0	4	4	–	–	–	–
5	*G. swynnertoni*	231	16	23	24	–	–	–	–
	G. pallidipes	27	13	57	52	–	–	–	–
	G. brevipalpis	0	0	0	1 *	–	–	–	–
6	*G. swynnertoni*	194	12	48	50	–	–	–	–
	G. pallidipes	1	2	2	4	–	–	–	–

* Caught in five days.
– Catching method not used.

Area 4. – Large numbers of *G. swynnertoni* were encountered in this area of open woodland with thicket patches. Langridge traps caught a few *G. pallidipes* close to large thickets of *Euphorbia candelabra.*

Area 5. – *G. swynnertoni* and *G. pallidipes* were both numerous. The latter were encountered mainly in and around thickets which were numerous and close. One *G. brevipalpis* female was trapped adjacent to dense thicket.

Area 6. – Numerous *G. swynnertoni* were encountered throughout the area while a few *G. pallidipes* found were confined mainly to continuous thickets fringing the river and the Retima Hippo Pool.

Infection rates

The incidence of trypanosome infections in *G. swynnertoni* and *G. pallidipes* are given in Table 3. Although the infection rates in flies from all the six areas were high, not a single salivary gland infection was found. All the mature infections belonged to the *vivax* and *congolense* groups.

Table 3. Rates of trypanosome infection in *G. swynnertoni* and *G. pallidipes*

Area	Species	Number examined		Overall infections %			Mature infections
		♂♂	♀♀	♂♂	♀♀	♂♂+♀♀	%
1	*G. swynnertoni*	939	134	17.2	17.9	17.3	13.7
2	*G. swynnertoni*	777	237	15.2	15.6	15.3	12.3
3	*G. swynnertoni*	789	277	15.6	18.8	16.4	14.8
4	*G. swynnertoni*	893	123	15.3	14.6	15.3	12.2
5	*G. swynnertoni*	1,217	223	11.5	17.5	12.4	10.2
	G. pallidipes	359	264	10.6	10.2	10.4	8.7
6	*G. swynnertoni*	580	159	15.3	19.5	16.2	12.9

Hosts of Glossina

The sample of *G. pallidipes* blood meals is too small – eight squashes in all – to draw valid conclusions from it. Of these, 2 were from warthog, 2 from buffalo, 1 from elephant and 3 from unidentified suids.

The results of identification tests of blood meals of *G. swynnertoni* from all the six areas from which they were collected are shown in Tables 4/5 and Fig. 6. These results are summarized as follows:

Area 1. – Hippopotamus, giraffe, buffalo and elephant each contributed 19.8 % of all feeds. Only 7.9 % were from warthog. Con-

Hosts	Sex	Areas 1			2			3			4			5			6			Total		
Man	♂																1	**1**	0.5 %	1	**1**	0.1 %
	♀																					
Baboon	♂				1	**1**	0.8 %													1	**1**	0.1 %
	♀																					
Carnivore	♂										3	**3**	2.3 %		**1**	0.4 %				3	**4**	0.5 %
	♀													1						1		
Hyaena	♂				2	**2**	1.6 %				1	**1**	0.8 %							3	3	0.3 %
	♀																					
Cat	♂	2	**2**	2.0 %	2	**2**	1.6 %								**1**	0.4 %	1	**1**	0.5 %	5	**6**	0.7 %
	♀													1						1		
Aardvark	♂				3	**3**	2.5 %				2	**2**	1.6 %	1	**1**	0.4 %				6	**6**	0.7 %
	♀																					
Elephant	♂	20	**20**	19.8 %													27	**32**	17.6 %	47	**52**	6.0 %
	♀																5			5		
Elephant and unidentified bovids	♂																2	**2**	1.1 %	2	**2**	0.2 %
	♀																					
Rhinoceros	♂										2	**2**	1.6 %				5	**7**	3.9 %	7	**9**	1.0 %
	♀																2			2		
Unidentified suids	♂				12	**12**	9.8 %	1	**1**	1.0 %	4	**4**	3.1 %	20	**32**	14.0 %				37	**49**	5.7 %
	♀													12						12		
Warthog	♂	7	**7**	6.9 %	33	**34**	27.9 %				26	**34**	26.6 %	118	**144**	63.2 %	2	**2**	1.1 %	186	**221**	25.6 %
	♀				1						8			26						35		
Warthog and unidentified bovids	♂	1	**1**	1.0 %	2	**2**	1.6 %							1	**1**	0.4 %				4	**4**	0.5 %
	♀																					

Hippopotamus	♂	20	**20**	19.8 %														25	**28**	15.4 %	45	**48**	5.6 %
	♀																	3			3		
Unidentified bovids	♂	10	**10**	9.9 %	15	**18**	14.8 %	5	**11**	10.9 %	6	**8**	6.3 %	5	**6**	2.6 %	6	**12**	6.6 %	47	**65**	7.5 %
	♀				3			6			2			1			6			18		
Giraffe	♂	20	**20**	19.8 %	24	**24**	19.7 %	1	**2**	2.0 %	19	**19**	14.8 %	17	**17**	7.5 %	19	**23**	12.7 %	100	**105**	12.2 %
	♀							1									4			5		
Giraffe and buffalo	♂	1	**1**	1.0 %				1	**1**	1.0 %	3	**3**	2.3 %				1	**2**	1.1 %	6	**7**	0.8 %
	♀																1			1		
Buffalo	♂	20	**20**	19.8 %	5	**5**	4.1 %	72	**86**	85.1 %	34	**47**	36.8 %	14	**16**	7.0 %	45	**55**	30.2 %	190	**229**	26.6 %
	♀							14			13			2			10			39		
Waterbuck	♂																1	**1**	0.5 %	1	**1**	0.1 %
	♀																					
Eland	♂																7	**9**	4.9 %	7	**9**	1.0 %
	♀																2			2		
Bushbuck or eland	♂																3	**5**	2.7 %	3	**5**	0.6 %
	♀																2			2		
Topi	♂											**1**	0.8 %								**1**	0.1 %
	♀										1									1		
Topi or hartebeest	♂										2	**2**	1.6 %		**1**	0.4 %				2	**3**	0.3 %
	♀													1						1		
Impala	♂										1	**1**	0.8 %	1	**1**	0.4 %	2	**2**	1.1 %	4	**4**	0.5 %
	♀																					
Avian	♂				19	**19**	15.6 %					**1**	0.8 %	7	**7**	3.1 %				26	**27**	3.1 %
	♀										1									1		
Total meals	♂	101	**101**		118	**122**		80	**101**		103	**128**		184	**228**		147	**182**		733	**862**	
	♀				4			21			25			44			35			129		

Fig. 6. Feeding patterns of *G. swynnertoni* in the six survey areas.

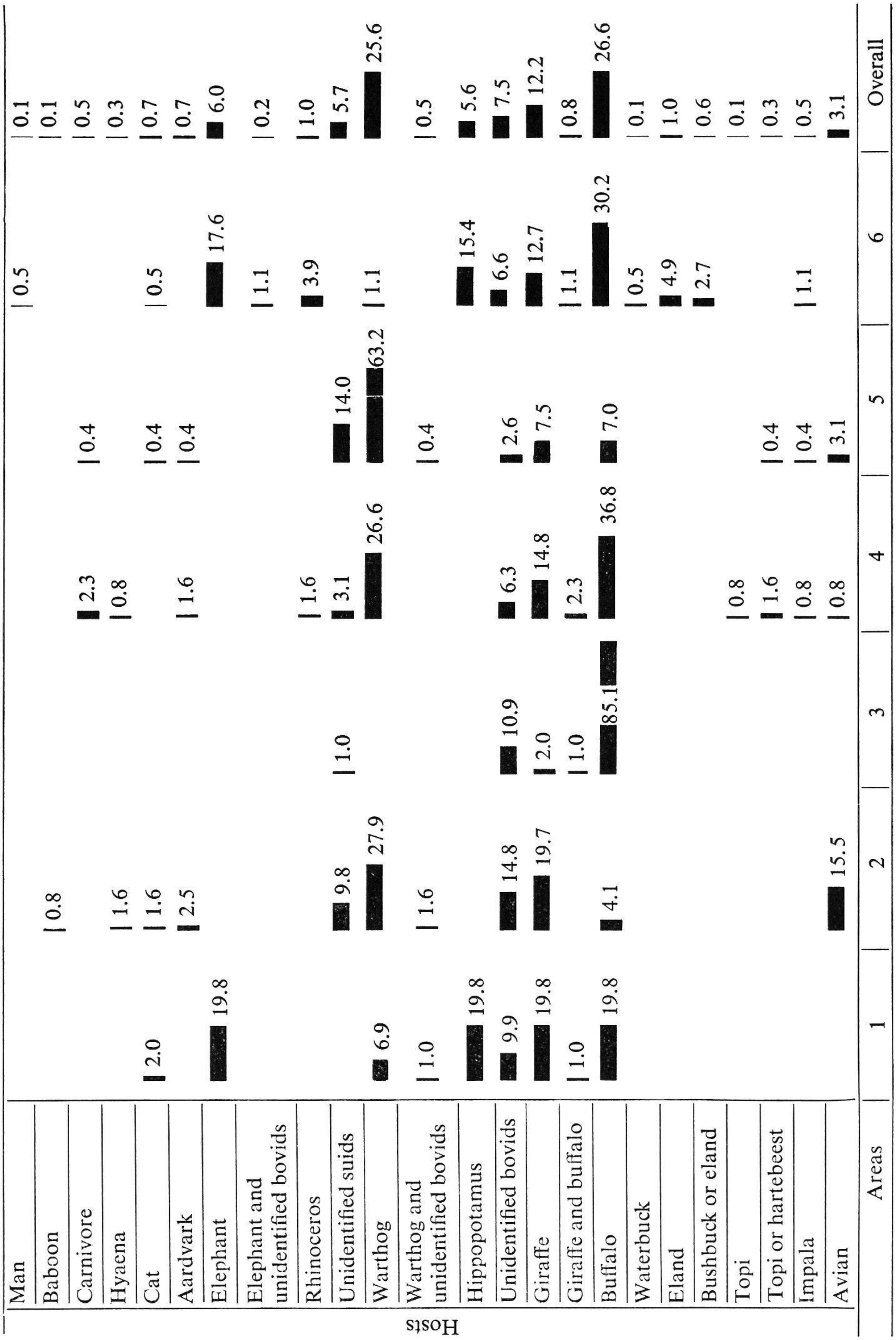

Table 5. Hosts of *G. swynnertoni* in the six survey areas

Hosts	Areas					
	1	2	3	4	5	6
	%	%	%	%	%	%
Primates	–	0.8	–	–	–	0.5
Bovids	51.5	39.5	99.0	64.1	18.3	60.8
Suids	7.8	38.7	1.0	29.0	77.3	1.1
Carnivores	1.9	3.2	–	3.1	0.9	0.5
Elephant	19.4	–	–	–	–	18.3
Rhinoceros	–	–	–	1.5	–	3.8
Hippopotamus	19.4	–	–	–	–	15.1
Aardvark	–	2.4	–	1.5	0.4	–
Avian	–	15.3	–	0.8	3.1	–

tribution from cat was 2 % while of the two double feeds, one came from giraffe/buffalo and the other from warthog/unidentified bovid.

Area 2. – The order of preferred hosts was warthog (27.9 %), giraffe (19.7 %) and birds (15.6 %), most probably ostrich which were present in the area. The less favoured hosts included buffalo (4.1 %), aardvark (2.5 %), hyaena (1.6 %), cat (1.6 %) and baboon (0.8 %). The two double feeds were from warthog/unidentified bovids.

Area 3. – The feeding pattern of the tsetse in this locality showed very strikingly that buffalo was the host most commonly fed on. Including the giraffe/buffalo double feed, 86.1 % of all feeds were from this host. Giraffe contributed 2 % of feeds and suids only 1 %.

Area 4. – The order of favoured hosts was buffalo (39.1 %), warthog (26.6 %) and giraffe (17.1 %). Carnivore (2.3 %), rhinoceros (1.6 %), aardvark (1.6 %), topi or hartebeest (1.6 %), topi (0.8 %), impala (0.8 %) and avian (0.8 %) contributed altogether 10.3 % of all feeds. Three double feeds found were from giraffe/buffalo.

Area 5. – Warthog, which contributed 63.6 % of all feeds, was the most favoured host in this area. Giraffe and buffalo provided only 7.5 % and 7.0 % of all feeds, respectively. Birds, possibly ostrich, contributed 3.1 % of the total feeds. Single feeds were from cat, topi or hartebeest, impala and aardvark. One double feed was from warthog/unidentified bovid.

Area 6. – In view of the proximity of Areas 6 and 1, and hence their similarity in fauna, the feeding pattern of the tsetse in this locality was similar to that in Area 1. The order of favoured hosts was buffalo (31.3 %), elephant (18.7 %), hippopotamus (15.4 %) and giraffe (13.8 %). Eland contributed 4.9 %, rhinoceros 3.9 %, eland or bushbuck 2.7 %, warthog 1.1 %, impala 1.1 %, cat 0.5 % and waterbuck

0.5 % of all feeds. Two double feeds were from elephant/unidentified bovids while a third from giraffe/buffalo. One feed was derived from man.

The overall results for the entire survey area are given in the last column of Table 4. Of 875 identified meals (double feeds included), 442 (50.5 %) came from bovids and nearly a third (31.3 %) from suids, possibly all warthog. Of the bovid feeds, 53.4 % were from buffalo and 25.3 % from giraffe. The other important hosts were elephant, hippopotamus and avians, which provided 6.2 %, 5.5 % and 3.1 % of all feeds, respectively. Contributions from carnivores were 1.5 %, rhinoceros 1.0 %, aardvark 0.7 % and primates 0.2 % of all feeds.

Man-fly contact

The local tsetse species were mostly dependent on game for food and little on man. Contact between man and fly was therefore "impersonal". However, of the three species encountered, *G. swynnertoni* was attracted most to man and attacked the fly-catching parties as well as other human beings in the area quite freely; in some cases even managing to draw blood undetected by their human hosts. Hence, the probability of man-fly contact for this species could be high. In Ikoma (Area 5) where *G. swynnertoni* and *G. pallidipes* were both present in equally high numbers, the latter seldom attacked the catching parties, thus man-*G. pallidipes* contact was negligible.

Discussion

Three different tsetse species were present within the Ikoma/Seronera/Kilimafedha triangle; they were – *G. swynnertoni,* Aust., *G. pallidipes,* Aust. and *G. brevipalpis.* Newst. *G. swynnertoni* was the most widely distributed species and occurred in high numbers in all the six areas surveyed. *G. pallidipes,* on the other hand, had restricted distribution; apart from Area 5 in Ikoma where they were quite numerous, the populations of this species encountered were small and confined largely to riverine vegetation. *G. brevipalpis* was restricted to a small localised area in Ikoma. The distribution of these three tsetse species was closely related to their vegetational requirements. The dry thorn-bush or nyika forms the main vegetation type in the area and is one to which *G. swynnertoni* is well adapted; hence its wide distribution. *G. pallidipes* too is adapted to life in the savannah but requires dense thickets. This latter type of vegetation was encountered mainly close to drainage, while in Ikoma (Area 5), continuous thickets favoured by *G. pallidipes* were quite extensive. The localised distribution of *G. brevipalpis* was due to its requirement of dense thickets providing heavy shade (SWYNNERTON 1936). Of the areas surveyed, Area 5 (Ikoma) provided vegetational requirement for all the three tsetse species while Area 2, having open woodland with sparsely scattered small thickets, supported only *G. swynnertoni*. The remaining four areas afforded in the main the vegetational requirements for *G. swynnertoni* and, in restricted places, for *G. pallidipes* also.

Out of 6,384 *G. swynnertoni* dissected, 796 (12.5 %) contained mature trypanosome infections, as against 54 (8.7 %) of the 623 *G. pallidipes* examined. It is noteworthy that not a single fly showed salivary gland infection, indicating that the incidence of mature *brucei* type infection in the survey area must be very low indeed. It is known that in nature the incidence of positive salivary gland infections is generally very low. For example, in a Rhodesian sleeping sickness area in Tanzania, VANDERPLANK (1947) dissected 35,112 *G. swynnertoni* and *G. pallidipes*; infections attributed to *T. brucei* were under 0.1 %. In an endemic area in South Busoga, Uganda, the corresponding figures for the dissections made by WILSON and his colleagues (1971) were 0.09 % in 13,240 *G. pallidipes*. The same team, working in Mara Region, Kenya, from April, 1969 to October, 1970 found this type of infection in 0.07 % each of 10,375 *G. pallidipes* and 5,928 *G. swynnertoni* examined. It is noteworthy that of the total of four *G. swynnertoni* found carrying *brucei* infections, three were from a single batch caught in Talek area (WILSON et al. 1971). During an outbreak due to *T. rhodesiense* in the Lake Province, Tanzania, DUKE (1923) dissected a total of 2,206 *G. swynnertoni* caught from three different areas and obtained the following rates of *T. brucei* infection: (i) 0.24 % of 819 flies from the locality where the inhabitants were heavily infected; (ii) 0.1 % of 772 flies from villages where fly-man transmission was relatively low; and (iii) 0 % of 665 flies from uninhabited localities.

G. swynnertoni had a wide range of vertebrate hosts including bovids, suids, elephant, hippopotamus, primates, carnivores, aardvark and avians, of which buffalo, warthog and giraffe were the hosts most generally favoured. WEITZ (1963) has shown that various species of *Glossina* exhibit selective feeding patterns. The work on this subject carried out by WEITZ & GLASGOW (1956), GLASGOW et al. (1958) and WEITZ et al. (1958) has shown that the main host of *G. swynnertoni* is warthog. The present study indicates that the feeding habits of this tsetse species varied according to locality. For example, while warthog was the favoured host in Area 2 and 5, buffalo provided the bulk of the feeds in Area 3. In Area 4 and 6, buffalo was again found to have contributed more feeds than warthog. It is noteworthy that hippopotamus, elephant, buffalo and giraffe each provided 19.8 % of the feeds in Area 1 and, even in Area 6 the number of feeds from hippopotamus and elephant were large. A high proportion of bird feeds, possibly ostrich, in Area 2 and 5 is also notable. Clearly, *G. swynnertoni* is adaptable in its feeding habits.

The blood of zebra, gazelles, wildebeest or dikdik was not found in any meal although these animals were present in large numbers in at least some of the areas surveyed. Reedbuck, steinbok and duiker were also present, though in small numbers, but provided none of the feeds. Impala, topi and hartebeest were common in many areas, but contributed only 0.9 % of the total feeds. In some areas gazelle and impala were present practically throughout the day and yet ignored by tsetse. It is probable that these animals which are highly active can avoid tsetse attacks very efficiently. A proportion of feeds from topi is of interest. Although WEITZ et al. (1958) found some *G. swynnertoni* meals derived from hartebeest, topi or wildebeest, a specific topi feed has never before been identified from any *Glossina* species.

It should be noted that this is the first time a study of the tsetse feeding habits has been carried out in six areas within a given locality and within a few days of each other. The results show striking differences between areas and this seems to correspond very well to the availability of hosts. For example, in Areas 2 and 5 with low buffalo populations (5–10) the number of feeds on suids were 37.7 % and 77.2 %, respectively, whereas in Area 4 with a high frequency of buffalo (105–115), 85.1 % of the feeds were from this host. Again, a large number of feeds from warthog (77.2 % of all feeds) in Area 5 corresponds to high warthog and low buffalo populations. Another example of *G. swynnertoni* feeding on a host readily available is given by the giraffe feeds. Giraffe were present in large numbers in Area 1, 2 and 6, and the number of feeds on this host were likewise high in these areas: 19.8, 19.7 and 12.7 %, respectively. The high percentage of giraffe feeds in Area 4 (17.8 %) are probably related to small numbers of buffalo present in the area. Furthermore, large herds of giraffe were observed in this area during the period of the survey. The high percentage of Avian feeds in Area 2 is also noteworthy. This is almost certainly due to the greater number of ostrich present in this area compared with other areas.

Weak feeds derived respectively from the family *Bovidae* and *Suidae,* which failed to react in the tests for the species, were classed as unidentified species of the groups concerned. "Cat" feeds were tested for members of the *Felidae* family including lion and leopard. Feeds which were assigned as "Carnivore" were members of the older Carnivore excluding the cat, dog, hyaena and mongoose families. It is possible that these feeds were derived from zorilla or honey badger.

In addition to furnishing the bulk of the blood meals for tsetse, game provides a reservoir for the causative agent of Rhodesian sleeping sickness (WILLETT & FAIRBAIRN 1955; HEISCH et al. 1958). The correlation of the animals on which *G. swynnertoni* feeds with the incidence of *T. brucei* infections in such hosts (ASHCROFT 1959; GARNHAM 1960; GUILBRIDE et al. 1962; BAKER 1968; GEIGY et al. 1971) and with the degree of their susceptibility to experimental infection with these trypanosomes (ASHCROFT et al. 1959) indicates quite strikingly that the favourite hosts are not efficient reservoirs of *T. rhodesiense* and thus confirm a similar suggestion made by ASHCROFT et al. (1959). The data compiled by ASHCROFT (1959) show that only one of the 26 buffaloes examined harboured *brucei* trypanosomes while, in the 150 warthogs, 68 giraffes and 11 elephants, the corresponding rates were 2 %, 1.5 % and 0 %, respectively. GARNHAM (1960) and GUILBRIDE et al. (1962) examined altogether 424 hippopotami, none of which showed *T. brucei* infection. In the less favoured waterbuck, hartebeest, eland, bushbuck, and impala, the incidence of this type of infection was as high as 24 %, 9 %, 5 %, 5 % and 1.3 %, respectively (ASHCROFT 1959). Studies on the reservoir potential of the game animals have shown that warthog and some ruminants, possibly buffalo and giraffe, usually become infected with *T. rhodesiense* and *T. brucei* but are resistent, the parsitaemia being scanty and not persisting for long. On the other hand, bushbuck, eland, hyaena and impala, which were rarely fed on by *G. swynnertoni,* are noted for their tolerance to such infections, nearly always become infected and show a blood positive period of considerable duration (ASHCROFT et al. 1959). Aardvark, which provided a small proportion of *G. swynnertoni* feeds (0.7 % of total feeds), is highly susceptible to *T. rhodesiense* and usually killed by it (VANDERPLANK 1941; BURTT 1946b). It is conceivable that such animals might in certain circumstances function, though, temporarily, as reservoirs of the parasite.

It is known that under the condition of game scarcity, *G. pallidipes* will attack man but not as readily as *G. swynnertoni,* which shows remarkable attraction to man. Owing to its confinement to dense thickets, *G. brevipalpis* seldom comes into contact with man and does not readily attack him (SWYNNERTON 1923b). This would explain the predominance of *G. swynnertoni* in the random and fly-round catches. It has been pointed out by SWYNNERTON (1923a) that even when cattle are present, this species attacks man quite freely. Study on the reaction of flies to the simultaneous presence of bait cow and man in Area 2 has confirmed his observation. In order or readiness to attack man, the three species of tsetse encountered may be ranged as follows: (1) *G. swynnertoni,* (2) *G. pallidipes* and (3) *G. brevipalpis. G. swynnertoni* is a clandestine tsetse and gentle "biter" (SWYNNERTON 1923a) as indicated by their several successes in drawing blood off the catching parties undetected.

The results of the random and fly-round catches show that, although in nature the two sexes occur in approximately equal numbers, the proportions of females caught in all the survey areas were exceedingly low. This indicates a "non-hungry" picture (Fiske 1920; Nash 1948). The local tsetse species are primarily zoophilic and, since game was abundant, the flies attacked man only through chance meeting.

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