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THE NATURAL HOSTS OF SOME SPECIES OF *GLOSSINA* IN EAST AFRICA

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A great deal of work has been aimed at discovering the sources of food of various species of *Glossina*, both by field observations and by laboratory tests, but in general the results are confusing and, in most cases, unrewarding. This is due to the great difficulties of accurate field observations and to the lack of suitable techniques for the identification of blood meals originating from such a wide fauna. The admirable review of this subject by BUXTON (1955) covers the work most extensively, and the reader is referred to it for further information.

It was not until more sensitive and particularly more specific methods of identifying the origin of blood meals became available, that the reliable study of the feeding habits of tsetse flies was possible. The test, using the inhibition of the agglutination of tanned and sensitized erythrocytes (WEITZ and JACKSON, 1955) is suitable for the routine identification of the serum proteins and the distinction between the blood meals from closely related animals (WEITZ, 1956).

THE IDENTIFICATION OF BLOOD MEALS

Blood meals which were obtained from flies in Hunger Stage I and from some in Stage II (JACKSON, 1933), were immediately smeared on to good quality filter paper and dried for dispatch to the laboratory. In most specimens the digestion of the blood meal had not proceeded beyond that expected at the end of Hunger Stage I, but as the collections were made from different species of flies and by different collectors, the assessment of the hunger stage was not completely uniform.

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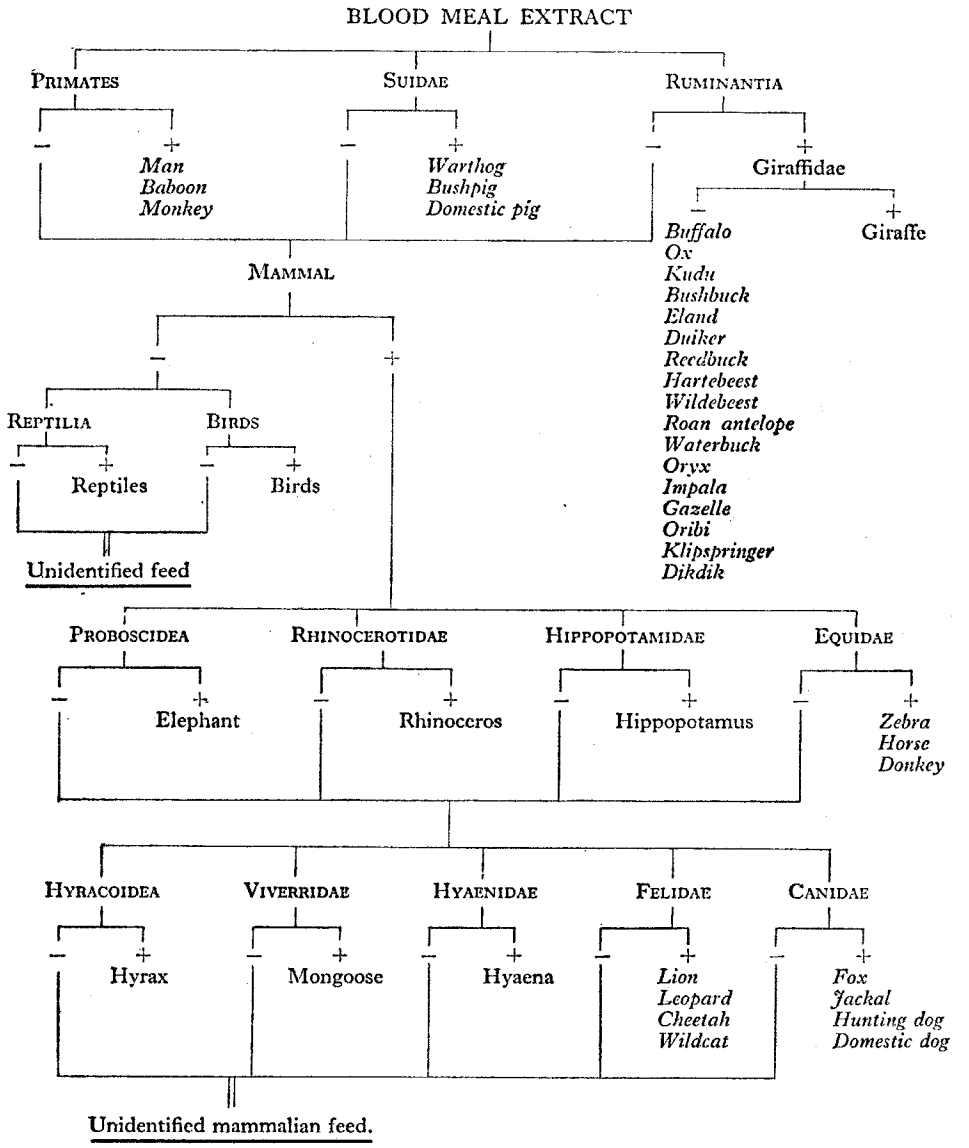

FIG. 1. The order of testing for the identification of blood meals of *G. morsitans*, showing how the species most commonly fed on, are tested first in order to save material.

\+ = positive result of test

− = negative „ „ „

Groups identified by the precipitin test are shown in roman type.

Species identified by the inhibition test are italicized.

The blood smears were kept dry for varying periods before testing, in some cases for as long as 5 years, and the results showed clearly that no deterioration had occurred over even such long periods. The smears were extracted overnight in a varying amount of 0.85 per cent. saline solution (1.5 ml. to 2.5 ml.) according to the estimated concentration of the feed. Extracting was continued for at least 12 hours at 4° C and the extracts were then held frozen at −15°C until required for testing.

Procedures

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 (Fig. 1). The specimens were tested for the presence of the blood of all the hosts known to be in the area unless the amount of material available was not sufficient for tests for all possible hosts. When these could be made, the results strongly confirmed the identification based on positive tests. For example, if a blood smear was found to contain bovid blood and this was subsequently identified as buffalo, the fact that the same blood meal failed to react positively when also tested for ox, bushbuck or kudu, strongly reinforces the identification as buffalo. Feeds which were assigned to one of the main groups by the precipitin test, but which failed to react in the tests for the species, were classed as an unidentified species of the group concerned (e.g. " unidentified bovid ") ; it was assumed that the failure to identify the species of origin was due to the digestion of the blood meal in the fly. Although the origin of a feed was usually found without using all the material in the smear, it may be noted that there are at least 17 identifiable species of Bovidae, and the material available was not always sufficient for this number of inhibition tests. Fortunately, the list of possible bovids present in any given area rarely exceeded six or seven, and the required six or seven tests could usually be made. Poorer blood smears sometimes contained enough for only one or two species tests and as a result the species of host could not always be determined.

Recording of results

Results are recorded by the vernacular names of the host, which may indicate sometimes more than one species. These, and the significance of the term " unidentified " are set out in Table I. For example, identifications recorded as " warthog " indicate that the blood meal was derived from *Phacochoerus aethiopicus* and not from bushpig (*Potamochoerus koiropotamus*) or domestic pig (*Sus scrofa*) ; blood meals identified as warthog might, in fact, have been from a related species, e.g. the giant forest hog (*Hylochoerus* spp.), and such distinctions were not made because no serum of *Hylochoerus* was available. In Table I, species from which no serum was available for checking the specificity of the identification tests, are indicated by an asterisk ; but in most instances these species were not present in the areas studied.

Validity of testing methods

Preliminary estimates of the validity of the identifications by the inhibition test and the precipitin tests, were made on the blood meals of *G. swynnertoni* Austen fed on known hosts (WEITZ and JACKSON, 1955). A more comprehensive check was made with tsetse flies fed under natural conditions. This experiment was planned by the late Dr. C. H. N. JACKSON and carried out by Mr. R. JEWELL. Captive animals were taken to the habitat of *G. swynnertoni*. Tsetse were fed, given individual marks and released. A day later

some of them were recaptured and some wild unmarked flies which had fed on the natural hosts in the bush were also collected. Thus, 55 flies in Hunger Stage I were collected, consisting of 34 marked and 21 unmarked flies. The blood smears were numbered at random and sent for test with the information that among the possible hosts only the Proboscidea and the Hyracoidea were excluded, and that among the Bovidae the possibilities (not all of which were necessarily included) were kudu, roan antelope, impala, reedbuck, duiker, dikdik, gazelle and cattle. No indication was given of which blood meals were from artificially fed flies and which from unmarked flies fed in the bush.

The results of the identification of these blood meals (Table II) were in most respects satisfactory. The marked flies had in fact been fed on man, domestic pig, ox, reedbuck, duiker, Thompson's gazelle and domestic fowl. The unmarked flies might have fed on giraffe, kudu, roan antelope, dikdik, rhinoceros, impala, warthog, bushpig, baboon or monkey, all of which were present in the bush. All the five human feeds were identified as such and not as baboon or monkey. All the Suidae feeds were correctly identified as seven domestic

TABLE I. The interpretation of the identifications of the blood meals : list of possible species to which the vernacular name refers.

(1) *Identification*	(2) *Interpretation*
I. PRIMATES	
Man	Man (*Homo sapiens*) or chimpanzee (*Pan troglodytes*).
Baboon	Species of *Papio*.
Monkey	Species of *Cercopithecus* or *Erythrocebus* or *Colobus*.
" Unidentified Primate "	Feed is insufficient for species differentiation but could only include any of the species above, but not species of Lorisidae.
II. SUIDAE	
Warthog	*Phacochoerus aethiopicus* (could possibly include **Hylochoerus* if present).
Bushpig	*Potamochoerus koiropotamus* (could include **P. porcus*).
Domestic pig	*Sus scrofa*.
" Unidentified pig "	Feed insufficient for species differentiation but could only include any of the species above.
III. RUMINANTIA	
Giraffe	*Giraffa camelopardalis* or *G. reticulata*.
Buffalo	*Syncerus caffer*.
Kudu	*Strepsiceros strepsiceros* or *S. imberbis*.
Bushbuck	*Tragelaphus scriptus* (possibly also **Limnotragus spekii*).
Eland	*Taurotragus oryx*.
Ox	*Bos taurus* (includes *Bubalus bubalis*).
Duiker	*Sylvicapra grimmia* (may include **Cephalophus* spp. and **Guevei* spp.).
Reedbuck	*Redunca redunca, R. fulvorufula, R. arundinum*.
Roan antelope	*Hippotragus equinus* (does not include *H. niger*).
Hartebeest	*Alcelaphus buselaphus* (Jackson's or Coke's spp.) *A. lichtensteinii, Gorgon taurinus*, or *Damaliscus korrigum*.
Dikdik	*Rhynchotragus* spp.
Impala	*Aepyceros melampus*.
Gazelle	*Gazella thomsonii, G. granti*.
Goat	*Capra hircus*.
Sheep	*Ovis aries*.
" Unidentified Ruminant "	Feed unsuitable for species differentiation, but could include one of the species above.

TABLE I (*continued*)

IV. OTHER MAMMALS	
Horse	*Equus caballus.*
Zebra	*Equus burchellii, E. grevyi.*
Donkey	*Equus asinus.*
" Unidentified equid "	Feed unsuitable for species differentiation but could only be one of the species of *Equus.*
Rhinoceros	*Diceros bicornis* (?probably includes *Rhinoceros simus*).
Elephant	*Loxodonta africana.*
Hyrax	*Dendrohyrax* spp. or *Heterohyrax* spp. or *Procavia* spp.
Cats	*Felis catus, Panthera pardus, P. leo,* or *Acinonyx jubatus* (other species of *Felis*).
Dogs	*Canis familiaris, C. aureus* (and probably also †*C. adustus* and †*C. mesomelas*) †*Lycaon pictus, Octocyon megalotis.*
Mongoose	*Ichneumia albicauda, Atilax paludinosus* (other genera and species of Herpestinae are also most probably included).
Hyaena	*Crocuta crocuta* (also most probably *Hyaena hyaena*).
" Unidentified Mammal "	Feed possibly unsuitable for species differentiation or some mammal for which no test was applied.
BIRD	Avian species including wide range of birds from ostrich to crow.
REPTILE	No specific test available.
" Unidentified "	Feed unsuitable for testing, i.e. not mammal or bird (could be reptile).

* Indicates that no serum was obtained from this animal and that the specificity of identification tests was therefore not confirmed for the species.

(1) The identification is given in the vernacular for the sake of simplicity.

(2) Species for which no identification tests were made have been omitted from this list.

† Indicates that no specificity tests for this species was possible but that the species is, in all probability, included under the vernacular identification given.

pig feeds from the marked flies and 13 warthog feeds, all from unmarked flies. Of the seven reedbuck feeds, six were identified and one feed which presumably contained insufficient material was reported " unidentified mammal " ; another of the reedbuck feeds was found to contain rhinoceros blood also, probably the result of a feed after release in the bush and another feed appeared to be reedbuck and/or dikdik. Of three ox feeds, two were identified correctly, and one contained bovid blood which was insufficient for species differentiation. Three of four fowl feeds were identified as avian and one was negative. There were therefore no errors with these 26 feeds. Of five feeds on duiker one was reported as ox and another as dikdik ; one was identified correctly and two were reported as unidentified ruminant. Of three feeds from Thomson's gazelle, one was identified correctly and two incorrectly as dikdik. Thus, four of 34 feeds were identified incorrectly and three of them as dikdik.

Failures in specific identification (i.e. five feeds unidentified bovids and one negative), were attributable to the scarcity of antigenic material in the blood meal. This was to be expected as even by the precipitin test only 50 per cent. of meals can be identified when flies are recaptured approximately 24 hours after feeding (WEITZ and BUXTON, 1953). Three of the four incorrect identifications were largely due to technical difficulties with the reagents used for the identification of dikdik, which were suspected of being unreliable, as is also indicated by the identification of one of the reedbuck feeds as either reedbuck or dikdik. One of the unknown feeds was identified as a dikdik feed, the validity of this result being questionable in view of these findings. More reliable reagents for the identification of dikdik blood have since been used. The observations in this paper relating to this species may

TABLE II. Results of identification tests on a mixed sample of 55 smears of " known and unknown " blood meals of *G. swynnertoni*.

Fly meal No.	Origin of feed if known	Result by identification tests	Remarks
1.	*Unknown*	*Warthog*	
2.	*Unknown*	*Unidentified ruminant*	
3.	Man	Man	
4.	*Unknown*	*Warthog*	
5.	Domestic pig	Domestic pig	
6.	*Unknown*	*Warthog*	
7.	Man	Man	
8.	Ox	Unidentified ruminant	
9.	*Unknown*	*Warthog*	
10.	Thomson's gazelle	Dikdik	Incorrect identification
11.	Reedbuck	Unidentified mammal	Probably poor feed
12.	*Unknown*	*Dikdik*	*Questionable identification*
13.	Ox	Ox	
14.	Domestic pig	Domestic pig	
15.	Man	Man	
16.	Reedbuck	Reedbuck	
17.	Duiker	Duiker	
18.	Domestic pig	Domestic pig	
19.	Domestic fowl	Domestic fowl	
20.	Reedbuck	Reedbuck	
21.	Reedbuck	Reedbuck	
22.	Man	Man	
23.	*Unknown*	*Kudu**	
24.	Domestic fowl	Domestic fowl	
25.	Domestic fowl	Negative	Feed too poor for identification
26.	Domestic pig	Domestic pig	
27.	*Unknown*	*Warthog*	
28.	*Unknown*	*Warthog*	
29.	Domestic fowl	Domestic fowl	
30.	*Unknown*	*Unidentified ruminant*	
31.	*Unknown*	*Warthog*	
32.	Reedbuck	Reedbuck and rhinoceros	Double feed (see text)
33.	Domestic pig	Domestic pig	
34.	*Unknown*	*Unidentified ruminant*	
35.	Ox	Ox	
36.	Domestic pig	Domestic pig	
37.	Thomson's gazelle	Thomson's gazelle	
38.	Reedbuck	Reedbuck and/or dikdik	
39.	Domestic pig	Domestic pig	
40.	Duiker	Dikdik	Incorrect identification
41.	*Unknown*	*Warthog*	
42.	*Unknown*	*Warthog*	
43.	*Unknown*	*Ox*	*Possibly correct (see text)*
44.	*Unknown*	*Warthog*	
45.	*Unknown*	*Ox*	*Possibly correct (see text)*
46.	*Unknown*	*Warthog*	
47.	Thomson's gazelle	Dikdik	Incorrect identification
48.	Man	Man	
49.	Duiker	Unidentified ruminant	
50.	Duiker	Ox	Incorrect identification or clerical error
51.	*Unknown*	*Warthog*	
52.	*Unknown*	*Warthog*	
53.	Duiker	Unidentified ruminant	
54.	Reedbuck	Reedbuck	
55.	*Unknown*	*Unidentified ruminant*	

* Freshly fed fly obtained in the immediate neighbourhood of a herd of kudu.
Feeds of unknown origin (i.e. from unmarked flies) are in italics.

therefore be regarded as correct although no field tests were made to check. The incorrect identification of a duiker feed as ox is inexplicable. Moreover, two among the unknown feeds were identified as ox, although it had been believed that wild flies in that area could not have fed on ox ; further laboratory tests however confirmed this identification. It was later ascertained that these flies could have had access to this host. The results with unknown feeds otherwise support the validity of the identification technique. Unfortunately, giraffe was not indicated as a possible host, and no tests for giraffe were made. In fact, giraffe were present in the area in fairly large numbers and it must be assumed that among the feeds reported as " unidentified ruminant " a large proportion were giraffe feeds that could easily have been identified if the requisite test had been applied. Finally, it should be noted that all the feeds were tested also for a large number of hosts which were not involved, and that these tests were negative.

It is clear that with the improvement of the test for dikdik, the identification of blood meals from flies caught in the field could now be accepted with the confidence that the greatest possible error would be in the order of 5 per cent. In fact, the error is likely to be much smaller in practice since many improvements in the technique were introduced in the course of the work.

Collection of blood meals in the field

Between 1950 and 1955 a number of collections of blood meals were made from seven species of *Glossina*. Although some of these surveys were made as part of special projects to be reported elsewhere, the results are added here to those of surveys made primarily to determine food sources of tsetse flies under various conditions. Altogether 1,590 blood smears were collected. The species of *Glossina* were : *G. swynnertoni*, Aust., *G. morsitans* West., *G. pallidipes* Aust., *G. austeni* Newst., *G. palpalis fuscipes* Newst., *G. brevipalpis* Newst., and *G. longipennis* Corti, collected from areas in the Sudan, Uganda, Kenya, Tanganyika, Zanzibar and Southern Rhodesia. The animals in these areas varied widely both in the density and the variety of species, and in one district or another all the species listed in Table I were contained. The areas can be considered as fairly representative of the tsetse habitat in East Africa, and the results are on the whole representative of the sources of food for the tsetse.

In describing the fauna of the districts from which these collections originated, no attempt was made to estimate the populations or densities of the game or other animals ; the possible hosts are listed from the observations made by the collectors themselves who in most cases have an intimate knowledge of the area.

AREA I. *Kariangwe-Sebungwe.* (17° 54′ S, 27° 30′ E). The area described by LOVEMORE (1955) contains a variety of game. Among the most common animals were elephants, rhinoceros, buffalo, zebra, impala, kudu, roan and sable antelopes ; warthog and baboon were numerous. Waterbuck and bushbuck occurred frequently along the rivers especially, and duiker and reedbuck on the hills surrounding the valley. Other animals present included, vervet monkey, bushpig, lion, hyaena, jackal and wild dog. Mr. D. F. LOVEMORE[1] collected 200 blood meals of *G. morsitans* in this area, representing a fairly evenly distributed sample covering various climatic conditions. Tests were applied for all the animals mentioned except sable antelope.

AREA II. *Lokila and Galual.* (Bahr-el-Ghazal Province, Southern Sudan, 8° 42′ N, 28° 35′ E). From these two places, which are grouped together not only on account of their propinquity but also because they contain a similar variety of hosts, 50 *G. morsitans* feeds were collected by Mr. E. T. M. REID [2]. The order of apparent frequency of animals was buffalo, rhinoceros, baboon,

giraffe, roan antelope, tiang (*Damaliscus korrigum*), waterbuck, warthog, oribi, Uganda kob, bushbuck, duiker, reedbuck, elephant, dog, goat and sheep, cattle, man, the Hussar monkey, and in restricted places, hippopotamus. Bushpig was absent from the area (REID, 1955). Tests were applied for all the species mentioned. The quality of the feeds was, on the whole, very poor, and by visual examination only about half appeared to contain sufficient blood for identification.

AREA III. *Kakoma area.* (5° 45′ S, 32° 20′ E). Described by JACKSON (1937). Seven feeds of *G. morsitans* from Kakoma, two from the Wala river and eight from the Ugalla river collected by Dr. JACKSON[3] are considered together. VESEY-FITZGERALD (1954) has published one of the very few estimates of the relative abundance of game, based on a traverse of the Ugalla river area. Animals present included giraffe, roan and sable antelopes, hartebeest, eland, elephant, buffalo, oribi, southern reedbuck, warthog, bushpig, man, baboon and greater kudu.

AREA IV. *Kingolwira.* (6° 40′ S, 37° 45′ E) is an area where game is abundant but restricted in variety. A prison farm has been carved out of the woodland, and in the area in which the collections were made there were usually working parties of prisoners. One of the fly-rounds, which produced about half of the specimens, was done with a bait ox, and all the specimens identified as ox came from this round. Lichtenstein's hartebeest is particularly common ; warthog and bushpig are frequent. Elephant, bushbuck, duiker, reedbuck, baboon and monkey also occur. The fly is the eastern race of *G. morsitans* of which 157 fed specimens were collected by Mr. J. R. WELCH[3].

AREA V. *Gedamara.* (4° 17′ S, 35° 53′ E) was the scene of studies of JACKSON (1953), who collected 26 *G. morsitans* feeds from this area to establish the significance of the presence of large numbers of impala, hartebeest and zebra, all of which were abundant in the area. Warthog, greater kudu, giraffe, roan antelope, reedbuck, were also present. Baboon has been seen and the presence of monkey was suspected.

AREA VI. *Daga-Iloi.* (4° 10′ S, 35° 40′ E). The collection of 378 feeds was made by Dr. JACKSON in the course of a study of the bionomics of *G. morsitans* in an area which was under constant observation. The fly-round was on a spiral (JACKSON, 1955), and an intimate knowledge of the fauna was acquired which has been already described (WEITZ and JACKSON, 1955). On the basis of observed spoor, the relative frequency with which herds of animals were seen on the fly-round was :

Duiker	42
Hartebeest	21
Roan antelope	10
Bushbuck	8
Warthog	8
Reedbuck	5
Buffalo	2
Zebra	2
Waterbuck	1
	99

Duiker were more often seen than bushbuck which live in dense thicket, or reedbuck, which like long grass. Rhinoceros, elephant and bushpig were also present although not seen. Impala was present on the perimeter but was unlikely to be available as an important source of food. More details of this area are given by JACKSON (1955) and WEITZ and JACKSON (1955).

AREA VII. *Butambara.* (3° 30′ S, 31° 50′ E). Two collections of *G. morsitans* totalling 120 feeds were made, in May and June, 1955 by Mr. G. R. JEWELL[3]. A fairly high concentration of game was present including : warthog, bushpig, elephant, hartebeest, giraffe, roan antelope, duiker, and some buffalo, topi, kudu and eland. Sable antelope was present in the area but was not tested for specifically. Numerous baboons and some monkeys were also present.

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(1) Tsetse Fly Operations, Southern Rhodesia.
(2) Sudan Veterinary Service, Khartoum, Sudan.
(3) Central Tsetse Research Laboratory, Shinyanga, Tanganyika.
(4) Sleeping Sickness Inspector, Kampala, Uganda.
(5) Tsetse Control Dept., Kampala, Uganda.

AREA VIII. *Shinyanga, Block 10B.* (3° 30′ S, 33° 20′ E). The collection by Mr. G. R. JEWELL of 102 *G. swynnertoni* feeds is of interest since the distribution and nature of the fauna is very well known. There is a single giraffe and two greater kudu. Herds of impala are frequent and both bushpig and warthog are present. Small game such as steinbok, duiker and dikdik also inhabit the area. Man and his domestic animals frequent the district. Baboon and monkey both occur.

AREA IX. *Shinyanga, Block* 9. (3° 30′ S, 33° 20′ E). This area, from which another collection of 134 *G. swynnertoni* was made by Dr. E. BURSELL[3] was more densely populated with game than Block 10B (VIII) and included : giraffe, rhinoceros, reedbuck, duiker, Thomson's gazelle, greater and lesser kudu, baboon, monkey, bushpig, warthog, roan antelope, dikdik, impala, carnivores, eland, zebra and steinbok. There were also a few elephants.

AREA X. *Sikiri.* (0° 30′ S, 34° 25′ E) is a peninsula in Lake Victoria, near Kisumu. Bushbuck and bushpig were the most abundant animals ; waterbuck, duiker, leopard, and hippopotamus were also present. Mr. D. L. JOHNS[3] collected 36 *G. pallidipes* feeds here.

AREA XI. *Ruma.* (0° 40′ S, 34° 15′ E). Another collection of 35 *G. pallidipes* was made by Mr. JOHNS[3] in this isolated inland area of low forest not far from Sikiri. The fauna included bushpig, bushbuck, buffalo, waterbuck, duiker, reedbuck, topi, oribi, roan antelope and Jackson's hartebeest.

AREA XII. *Port Victoria.* (0° 7′ N, 34° E) described by GLASGOW and WILSON (1953), and *Waturi* (0° 30′ S, 34° 15′ E). Two collections by Mr. F. WILSON[3] and Mr. J. M. B. HARLEY[3] of only 22 blood meals from *G. palpalis fuscipes* are pooled here. The feeds were of very poor quality ; this is regrettable in the case of Port Victoria where the number of hosts is accurately known. In both areas reptiles, birds, bushpig, bushbuck, hippopotamus, duiker and waterbuck occurred, and in Waturi, eland as well. No tests for reptile blood were made.

AREA XIII. *Lake Victoria.* (West shores, Uganda). In this area *G. palpalis* was collected by Mr. W. A. HARSTON[4] from selected but typical places where apart from small lizards, birds and perhaps snakes, the most likely host of the fly was the monitor lizard. Crocodile was believed to have been exterminated from the area.

AREA XIV. *Jozani Forest, Zanzibar.* (6° 15′ S, 39° 25′ E). 192 blood meals of *G. austeni* were collected by Mr. D. L. JOHNS[3]. Bushpig was the only member of the Suidae present. Other animals were pygmy antelope (*Nesotragus moschatus*), duiker (*Cephalophus adersi*) and leopard. There were some experimental cattle kept in the area, and these may have contributed some meals in addition to those coming from the bait oxen.

AREA XV. *Bugerere.* (0° 45′ N, 33° E). 56 blood meals were collected from *G. brevipalpis* by Mr. A. G. ROBERTSON[5]. Possible hosts were : hippopotamus, bushpig, bushbuck, duiker and oribi ; waterbuck and reedbuck were rare or absent. In addition to man (the collecting fly boys) and ox (used as bait), goats and sheep occurred outside the fly focus.

AREA XVI. *Bugerere.* A comparable collection of blood meals from *G. brevipalpis* was obtained from a place further away from the Nile than Area XV. The fauna included buffalo, baboon and monkey, in addition to those mentioned above. Hippopotamus was probably not so common in this place and there were no bushbuck. Crocodile and varanus were also present.

AREA XVII. *Mluza.* (4° 5′ S, 34° 20′ E). The first recorded blood meals of *G. longipennis* were collected here by Mr. G. R. JEWELL. Three specimens were taken in February, 1953 and seven in August, 1954. The possible hosts include rhinoceros, eland, impala, dikdik, wildebeest, zebra, man, baboon, carnivora, ox, buffalo, Thomson's gazelle and hyrax, roughly in that order of abundance.

RESULTS

Of the total of 1,590 blood smears collected from the seven species of tsetse mentioned, and from 17 different places (see Tables III, and IIIa), 152 smears did not contain sufficient material for identification. The species of host was identified in 1,213 blood smears and the main group of hosts in the remaining 225. There were 29 " multiple feeds " bringing the number of meals identified to 1,242. The results of all the tests are grouped under

TABLE III. Identification of blood meals of various species of *Glossina*.

Host		Species of *Glossina*													
		G. morsitans		*G. swynnertoni*		*G. pallidipes*		*G. palpalis*		*G. austeni*		*G. brevipalpis*		*G. longipennis*	
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
SUIDAE :	Warthog	308	36	97	42	—	—	—	—	—	—	—	—	0	0
	Bushpig	28	3	7	3	8	12	0	0	164	88	10	20	—	—
	Unidentified	30	4	13	6	—	—	0	0	0	0	3	6	0	0
	TOTAL	366	43	117	51	8	12	0	0	164	88	13	26	0	0
RUMINANTS :	Giraffe	16	2	17	7	—	—	—	—	—	—	—	—	—	—
	Ox	24	3	12	5	—	—	—	—	23	12	2	4	0	0
	Buffalo	43	5	—	—	0	0	—	—	—	—	0	0	0	0
	Bushbuck	23	3	—	—	43	63	5	7	—	—	1	2	—	—
	Kudu	29	3	21	9	—	—	—	—	—	—	—	—	0	0
	Eland	7	1	5	2	—	—	1	1	—	—	—	—	0	0
	Duiker	10	1	0	0	0	0	1	1	0	0	0	0	—	—
	Waterbuck	6	1	—	—	0	0	0	0	—	—	0	0	—	—
	Reedbuck	20	2	0	0	0	0	—	—	—	—	0	0	—	—
	Roan antelope	36	4	0	0	0	0	—	—	—	—	—	—	—	—
	Impala	3	1	4	2	—	—	—	—	—	—	0	0	0	0
	Sheep/Goat	—	—	5	2	—	—	—	—	—	—	0	0	—	—
	Unidentified	103	12	13	6	16	24	6	8	0	0	2	4	0	0
	TOTAL	320	38	77	33	59	87	13	17	23	12	5	10	0	0
PRIMATES :	Man	51	6	10	4	1	1	1	1	—	—	0	0	—	—
	Baboon	13	2	1	1	—	—	0	0	0	0	0	0	0	0
	Monkey	7	1	0	0	0	0	—	—	—	—	0	0	0	0
	Unidentified	9	1	5	2	0	0	1	1	0	0	0	0	0	0
	TOTAL	80	10	16	7	1	1	2	2	0	0	0	0	0	0
OTHER MAMMALS :	Elephant	19	2	0	0	—	—	—	—	—	—	—	—	—	—
	Rhinoceros	16	2	10	4	—	—	—	—	—	—	—	—	9	100
	Hippopotamus	—	—	—	—	—	—	0	0	—	—	30	63	—	—
	Dogs	4	0.3	1	1	—	—	—	—	—	—	—	—	0	0
	Cats	2	0.3	0	0	0	0	0	0	—	—	—	—	0	0
	Hyaena	2	0.3	0	0	0	0	—	—	—	—	—	—	0	0
	Porcupine	2	0.3	0	0	0	0	—	—	—	—	0	0	0	0
	Donkey	—	—	2	1	—	—	—	—	—	—	—	—	—	—
	Unidentified	22	2	4	2	0	0	0	0	0	0	0	0	0	0
	TOTAL	67	7	17	8	0	0	0	0	0	0	30	63	9	100
BIRDS :		19	2	1	1	0	0	4	5	0	0	0	0	0	0
REPTILES :		—	—	—	—	—	—	56	75	—	—	—	—	—	—
TOTALS		852	100	228	100	68	100	75	99	187	100	48	99	9	100

Note : *G. morsitans* meals from Maruzi and Ankole, Uganda were tested quite recently and 25-50 per cent. of all feeds came from hippopotamus. This animal does not often occur in the habitat of *G. morsitans* but when it does it seems a favoured host at the expense of warthog.

— indicates the species was absent from the areas.

0 indicates that no feeds were found from this species although present.

TABLE IIIa. The source of food of tsetse flies.

Area No.	*G. morsitans*							*G. swynnertoni*		*G. palli-dipes*		*G. palpalis*		*G. austeni*	*G. brevipalpis*		*G. longipennis*
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII
Hosts																	
Warthog	51	18	38	39	16	55	24	43	53	—	—	—	—	—	—	—	0
Bushpig	0	—	0	8	—	6	3	3	4	0	30	0	—	88	0	36	—
Giraffe	—	0	0	—	26	—	12	0	13	—	—	—	—	—	—	—	—
Ox	—	—	—	24	—	—	—	19	—	—	—	—	—	12	0	7	0
Buffalo	5	18	0	—	—	11	1	—	—	—	0	—	—	—	—	0	0
Bushbuck	9	9	—	6	—	0	—	—	—	96	70	29	—	—	0	3	—
Kudu	5	—	0	—	37	—	15	7	13	—	—	—	—	—	—	—	0
Eland	1	—	0	—	—	—	5	—	4	—	—	6	—	—	—	—	0
Duiker	2	0	—	4	—	1	0	0	0	0	0	6	—	0	0	—	—
Waterbuck	2	9	—	—	—	0	—	—	—	0	0	0	—	—	0	0	—
Reedbuck	2	0	25	2	10	3	3	—	0	—	0	—	—	—	0	—	—
Roan antelope	1	9	25	—	0	6	14	—	0	—	0	—	—	—	—	—	—
Topi	—	0	—	—	—	—	0	—	—	—	0	—	—	—	—	—	—
Hartebeest	—	—	0	0	0	0	0	—	—	—	0	—	—	—	—	—	—
Impala	1	0	—	—	10	—	—	5	1	—	—	—	—	—	—	—	0
Sheep/Goat	—	0	—	—	—	—	—	8	—	—	—	—	—	—	0	0	—
Man	2	32	12	6	—	10	6	7	4	4	0	6	—	—	0	0	—
Baboon	0	0	0	0	0	5	0	2	0	—	—	0	—	0	—	0	0
Monkey	1	0	—	1	0	0	5	0	0	0	0	—	—	—	—	0	0
Elephant	8	0	0	6	—	0	1	—	0	—	—	—	—	—	—	—	—
Rhinoceros	8	5	—	—	—	1	—	—	8	—	—	—	—	—	—	—	100
Hippopotamus	—	0	—	—	—	—	—	—	—	0	—	0	—	—	100	54	—
Zebra	0	—	—	—	0	0	—	—	0	—	—	—	—	—	—	—	0
Dogs	0	0	0	0	0	1	2	1	0	—	—	—	—	—	—	—	0
Cats	0	0	0	0	0	0	2	0	0	0	—	—	—	—	—	—	0
Hyaena	0	0	0	0	0	1	0	0	0	—	—	—	—	—	—	—	0
Porcupine	0	0	0	2	0	0	0	0	0	—	—	—	—	—	—	—	0
Birds	1	0	0	2	0	2	6	2	0	0	0	24	0	0	0	0	0
Reptiles	—	—	—	—	—	—	—	—	—	—	—	29	100	—	—	—	—
No. of feeds	163	22	8	102	19	281	95	62	131	25	27	17	51	187	15	28	9

The figures indicate the percentage of feeds from a host in each area.
0 indicates that this host was not fed on in the area.
— indicates that this host was absent from the area.

Suidae, Primates, Ruminants, other mammals and birds (Table III). The importance of any group for particular species of tsetse is evident from this Table, but it should be borne in mind that the areas from which the different collections were made had different faunas. An attempt to represent the variation of the main hosts is made in Table IIIa. Variations in the incidence of blood meals from different hosts is obviously largely determined by the availability of the animals in the collecting areas. As only very little is known about the numbers of animals in most areas, it is not possible to indicate their density. Table IIIa gives the following information : (1) The species of animals in each area, (2) the animals on which the flies have fed, (3) the intensity of feeding on each species of host as shown by feeds expressed as a percentage of the total feeds in the area, (4) the animals present in the area and on which the flies did not feed.

DISCUSSION OF RESULTS

It is important to consider the factors which may have influenced the results. The greatest difficulty is to assess the effect of the bias in the samples of flies caught ; this is influenced by : (1) the inevitable selection of only fully fed flies, (2) the sex ratio which is always greatly in favour of male flies, (3) the possibility that blood meals from different animals may have different effects on the activity of the fly and consequently affect the probability of its being caught, (4) climatic conditions which affect sampling in various ways.

The availability of hosts to the flies is also most variable and difficult to assess and depends largely on the movements of the game, the density of the hosts and the nature of the country. The influence of such variables on the results is to some extent minimized by the collection of flies from different localities and by the size of the samples. A bird's eye view of the pattern of feeding of tsetse can thus be obtained, particularly as the results from the various places agree. The results of the feeding habits of *G. morsitans* are, in this light, perhaps more significant than those of the other species of *Glossina*, of which fewer samples were collected.

The part played by each species of host as a food source for the flies (Tables III and IIIa) may be summarized as follows : .

I. SUIDAE

Species of the Suidae supply about half the food supply of *G. morsitans*, *G. swynnertoni* and nearly 88 per cent. of the feeds of *G. austeni*. Warthog is by far the most important host of *G. morsitans* and *G. swynnertoni*, a fairly consistent finding in all the surveys of these species. At Daga-Iloi there was a definite excess of warthog feeds over those expected from the relative frequency of the host species, for here Suidae were responsible for 10 per cent. of the spoor, but 60 per cent. of the identified blood meals (WEITZ and JACKSON, 1955). In the South Tabora area warthog were the most abundant hosts, and possibly their habits make them an especially reliable source of tsetse food. Warthog was absent from the areas from which collections of blood meals from other species of tsetse were made, so that its importance cannot be judged. *G. pallidipes* took 24 per cent. of its feeds from bushpig in one area but, surprisingly, none from another nearby where bushpig were apparently just as available. *G. brevipalpis* obtained 26 per cent. of their food from Suidae, chiefly bushpig.

II. RUMINANTS

The remainder of the food supply of *G. morsitans* and *G. swynnertoni* is very largely derived from the ruminants (36 per cent.) consisting of at least a dozen species. In Zanzibar, they constituted the only other source of food of *G. austeni*. Ruminants, more specifically bushbuck, were the main source of food of *G. pallidipes* (63 per cent.) and the bushbuck was the source of at least some of the *G. palpalis* meals and about 10 per cent. of *G. brevipalpis* meals. None of the very few blood meals of *G. longipennis* contained ruminant blood. The species concerned in the surveys are :

(1) *Buffalo* appears to be a sporadic source of food of tsetse, its importance being related to the movements of the herds in the area. At Daga-Iloi (VI) for instance, the feeds corresponded to the appearance of buffalo spoor in the " spiral " on the day preceding the catch. This host supplied 5 per cent. of all the feeds and 18 per cent. of the ruminant feeds of *G. morsitans* and *G. swynnertoni*. Buffalo appears to be an inconsistent but attractive source of food for the game tsetse. *G. palpalis*, *G. pallidipes*, *G. brevipalpis* and *G. longipennis* did not feed on buffalo although it was present in the areas.

(2) *Roan antelope* provided 15 per cent. of the ruminant feeds of *G. morsitans* and *G. swynnertoni*. Thus it was a more reliable source of food than buffalo, although it did not occur in such large numbers. This is doubtless a reflection of its more solitary habits. *G. pallidipes* did not apparently feed on this animal in Sikiri but it was an unlikely host, being present only rarely.

(3) *Reedbuck*, living mainly in long grass, was similarly a consistent source of food of *G. morsitans* and *G. swynnertoni* (8 per cent. of ruminant feeds). Other species of fly did not feed on reedbuck although it was present in Bugerere (XV and XVI) where *G. brevipalpis* were caught.

(4) *Kudu* was a more consistent source of food of *G. morsitans* and *G. swynnertoni* (14 per cent. of total ruminant feeds). It may be noted that there were only two kudus in block 10 B (Shinyanga) and these animals provided four feeds of a total of 19 ruminant feeds of which 12 were on ox. It did not occur in areas where other flies were collected.

(5) *Eland* was not a regular source of food for *G. morsitans*, only six feeds being found (3 per cent. of ruminant feeds). Of 17 feeds of *G. palpalis* meals from Waturi (XII), one was from eland, although bushbuck and duiker were apparently the only ruminants in the area.

(6) *Bushbuck* living in thick bush, is a more important host of tsetse as a whole than any other bovid. It supplied 14 per cent. of the ruminant feeds of *G. morsitans* ; was almost the exclusive source of food of *G. pallidipes* in Sikiri (X) and formed the greater part (70 per cent. of all feeds) of the source of food of this species in Ruma (XI). *G. longipennis* failed to feed on this species.

(7) *Duiker* formed a small proportion of food of *G. morsitans* (4 per cent. of ruminant feeds). A single feed was found in the *G. palpalis* collection. *G. swynnertoni*, *G. pallidipes*, *G. brevipalpis* and *G. austeni* failed to feed on it.

(8) *Waterbuck*, like duiker, was a relatively unimportant host of *G. morsitans* (3 per cent. of total ruminant feeds) ; *G. pallidipes*, *G. palpalis* and *G. brevipalpis* were not found to feed on it.

(9) *Giraffe* was not a consistent source of food and formed 7 per cent. of ruminant feeds of *G. morsitans*. There was only one giraffe in Shinyanga (VIII) where *G. swynnertoni* was collected so that the absence of feeds on this animal is hardly surprising.

(10) *Impala.* The very low feeding rate of the flies on this species is a notable result. For *G. morsitans* and *G. swynnertoni* together it formed only 0.8 per cent. of all the feeds and 3 per cent. of the ruminant feeds. In Lubu-Sebungwe (I) these animals were very numerous and they were expected to provide the main source of ruminant blood of *G. morsitans* in this area. In fact only one feed out of a total of 163 was found, and at Gedamara (V) two out of a total of 19. Four out of 62 *G. swynnertoni* feeds were found in Shinyanga. *G. longipennis* failed to feed on this species.

(11) *Hartebeest.* In view of large numbers of this species in Daga-Iloi (VI) and particularly in Kingolwira (IV) and Gedamara (V) the total absence of blood meals from this host in *G. morsitans* is a most significant finding. There is no reason to suspect the testing methods because both the precipitin and the inhibition tests for this species were applied.

(12) *Topi.* Although present in S. Sudan (II) and in Butambara (VII) there was no feeding on this animal. It may be relevant that, serologically, topi and hartebeest are very closely related.

(13) *Ox, Sheep and Goat.* It is probably unjustified to stress the value of the feeds on these domestic animals as in many cases they were derived from ox used as bait. On any occasion where these species were present, they were detected in the blood meal identifications. This result would be expected in view of the well-known usefulness of ox as a bait animal and the high rate of infection of cattle with trypanosomes.

III. PRIMATES

It is difficult to assess the importance of Primates as a whole as a source of food to tsetse because the feeds from the members of this Order are largely derived from man. About 10 per cent. of all the feeds of *G. morsitans* and *G. swynnertoni* were from Primates.

(1) *Man.* Human feeds formed 7 per cent. of the total feeds of *G. morsitans* and *G. swynnertoni.* Usually the catching party was almost the only source of human blood, so that this percentage is surprisingly high, and might be thought to indicate a preference for human blood. There is much evidence against this view, however, which is summarized by BUXTON (1955), and it is striking that at Kingolwira (IV) where men other than catchers were abundant, an abnormally high proportion of flies did not feed on man. It is supposed, therefore, that the human feeds were the result of the catchers following the same fixed route every day. Flies getting an undetected meal off the catching party would rest near the fixed route and be especially liable to capture the next day. *G. austeni, G. brevipalpis* and *G. longipennis* did not contain human blood.

(2) *Baboon.* There is little evidence of feeding on baboon as a whole, although 13 out of 281 *G. morsitans* feeds were recorded in Daga-Iloi (VI) alone and a single feed was recorded from the *G. swynnertoni* collection in Shinyanga (VIII), making a total of 14 feeds out of 750 or nearly 2 per cent. Other species were not found to feed on baboon.

(3) *Monkey* was undoubtedly a very small proportion of the food of all species of tsetse, and occurred at the rate of 1 per cent. of total feeds in Lubu (I) and Kingolwira (IV) but 5 per cent. of feeds in Butambara (VII). Only *G. morsitans* was found to feed on monkey.

IV. EQUIDAE

Although quite numerous in some areas, e.g. Daga-Iloi (VI) and Gedamara (V) and frequent in Lubu-Sebungwe (I), no feeds were recorded from zebra, the only equid available.

This reluctance to feed on zebra confirms the finding of SYMES and MCMAHON (1937). It is of interest that a few donkeys were in or around Block XB at Shinyanga (VIII), and two feeds of *G. swynnertoni* from this host were found here. It thus appears that equid blood is not objectionable to tsetse, a conclusion consistent with the infectivity of horses with trypanosomes. The results again illustrate the curious attraction domestic animals always have for tsetse when present in the area.

V. OTHER MAMMALS

Among the mammals other than Suidae, Ruminants, Equidae or Primates, the large animals are the most important. Rhinoceros was responsible for 2 per cent. of feeds of *G. morsitans*. It is a rare animal, but was fed on in all areas in which it was present. The only other survey in which flies other than *G. morsitans* were captured and where rhinoceros was available was at Mluza. Here all the *G. longipennis* caught had fed on rhinoceros. By contrast, elephants, which live in herds, provided a higher proportion of the total feeds in the collection in which they occur, but elephant feeds were found in only three of the six areas in which there were elephants. The total (2.5 per cent.) was much the same as for rhinoceros.

Hippopotamus was the main food source of *G. brevipalpis* at Bugerere (XV and XVI). No feeds from this animal were found in *G. pallidipes* at Sikiri (XI) nor among the *G. palpalis* feeds. In a recent collection of *G. morsitans* from Maruzi province in Uganda, about half the flies had fed on hippopotamus. *G. morsitans* was also found to feed on hippopotamus in Ankole.

Small animals seemed of little importance, but it may be of interest from an epidemiological point of view that feeds on dogs (which may be the bat eared fox, wild hunting dog or jackals) cats (which may be lion, leopard, cheetah or other felines) and porcupines have been found in *G. morsitans* blood smears.

VI. BIRDS

The proportion of avian feeds is relatively small in *G. morsitans* (2 per cent.) and *G. swynnertoni* (1 per cent.) and none was found in *G. pallidipes*, *G. brevipalpis* or *G. longipennis*. No examination for bird blood was made in the *G. austeni* collection from Zanzibar (XIV). Four out of 19 feeds were avian in *G. palpalis* from Port Victoria.

VII. REPTILES

Feeds of *G. palpalis* were identified as reptilian by establishing the absence of avian blood in the smears which contained nucleated red blood cells. All the feeds of *G. palpalis* from the west shores of Lake Victoria (XIII) and five out of 17 of the *G. palpalis* feeds from Port Victoria and Waturi (XII) were reptilian.

NATURAL HOST PREFERENCES OF TSETSE SPECIES

On the evidence obtained only generalizations can be attempted and these must be accepted with caution, especially where the number in the samples was small.

1. *G. morsitans* and *G. swynnertoni*

These two species are closely related and of similar habits ; the results from them are

so similar (Tables III and IIIa) that it is convenient to examine them together. A total of 1,184 smears were examined from these species, and 1,080 were identified (883 species and 197 to group of hosts). This is an impressive sample, particularly as they were obtained from 10 different areas, and collected at different times of the year. We have therefore considerable confidence in the results, although we are aware of the possible errors due to sampling bias which is discussed below.

TABLE IV. The relative importance of animals as sources of food for *G. morsitans* and *G. swynnertoni* as determined by the †" frequency " and the *" intensity " of feeding.

Host	†Frequency	Per cent.	Host	*Intensity	Per cent.
1. Warthog	9/9	100	1. Warthog	405	45.9
2. Man	8/8	100	2. Man	61	6.9
3. Rhinoceros	4/4	100	3. Kudu	50	5.6
4. Ox	2/2	100	4. Buffalo	43	4.8
5. (Donkey)	1/1	100	5. Roan antelope	36	4.1
6. Kudu	5/6	83	6. Ox	36	4.1
7. Buffalo	4/5	80	7. Bushpig	35	3.9
8. Impala	4/5	80	8. Giraffe	33	3.7
9. Reedbuck	6/8	75	9. Rhinoceros	26	2.9
10. Bushbuck	3/4	75	10. Bushbuck	23	2.6
11. Eland	3/4	75	11. Reedbuck	20	2.3
12. Roan antelope	5/7	71	12. Birds	20	2.3
13. Bushpig	5/7	71	13. Elephant	19	2.2
14. Waterbuck	2/3	66	14. Baboon	14	1.6
15. Birds	5/9	55	15. Eland	12	1.3
16. Giraffe	3/6	50	16. Duiker	10	1.1
17. Sheep	1/2	50	17. Monkey	7	0.8
18. Elephant	3/7	43	18. Impala	7	0.8
19. Duiker	3/7	43	19. Waterbuck	6	0.7
20. Monkey	3/8	38	20. Sheep	5	0.6
21. Dogs-Jackal	3/?9	33	21. Dogs-Jackal	5	0.6
22. Baboon	2/9	22	22. Hyaena	2	0.3
23. Hyaena	1/?5	20	23. Cats	2	0.3
24. Cats	1/8	12	24. Porcupine	2	0.3
25. Porcupine	1/?9	11	25. Donkey	2	0.3
26. Hartebeest	0/5	0	26. Hartebeest	0	
27. Zebra	0/4	0	27. Zebra	0	
28. Topi	0/2	0	28. Topi	0	
29. Hippopotamus	0/1	0	29. Hippopotamus	0	
			Total	883	100

† " Frequency " is the proportion of the number of areas in which the animal was bitten/the number of areas where the animal was present.

* " Intensity " is the proportion of feeds derived from any given animal.

It would be misleading to arrange the natural hosts in order of preference of the tsetse only on the basis of the number of feeds which originated from each species, because this number must be a function of the availability of each host in the area, as well as of tsetse preferences. Some hosts are much sought after by the tsetse, although, because they are rare, they do not contribute very many feeds to the total. This is evident from the observation that some hosts are invariably used when they are present in the area while other potential hosts, although perhaps present in large numbers, are never used. Intermediate preferences, on this basis, are indicated by the number of areas in which the animal acted

as host compared with the total number of areas in which it was available. This simple proportion (number of areas where animal was bitten/number of areas where animal was present) can be used as an index of the " frequency " with which a host is selected by the tsetse. Table IV shows the preferences of *G. morsitans* and *G. swynnertoni* for various animals as indicated by (a) the " intensity " of biting (proportion of feeds derived from any host species) and (b) the " frequency " as defined above. Thus, warthog is the preferred host, both on the basis of the " intensity " (46 per cent.) and of " frequency " (100 per cent.), whereas rhinoceros, though not apparently preferred as judged by " intensity " (3 per cent.) is an attractive host on the basis of " frequency " (100 per cent.), i.e. it was invariably used in the areas in which it was present. Either method of interpretation may be used to estimate the importance of a possible host, depending upon the point of view. It is clear that the " frequency " is a measure of the fly's preferences, while the " intensity " is a measure of its actual diet. The " intensity " of feeding on various hosts, when compared with the relative numbers of those hosts on the ground, will indicate the varying capacity of different hosts to maintain a tsetse population. The search for the reservoir host of parasites transmissible by the fly could be facilitated perhaps by taking account of preferences based on " frequency."

Broadly, the hosts of *G. morsitans* and of *G. swynnertoni* can be summarized as follows :

(*a*) *The animals always bitten* (and which would probably show a high " intensity " of feeding if they were sufficiently available). In this category were included warthog and rhinoceros. Man and domestic animals, although not natural hosts, were always found.

(*b*) *The animals commonly bitten :* roan antelope, reedbuck, buffalo, kudu, bushpig, bushbuck, elephant, giraffe.

(*c*) *Animals rarely bitten :* eland, duiker, waterbuck, impala, baboon, monkey, dogs and cats, hyaena, porcupine and birds.

(*d*) *Animals never bitten :* hartebeest, topi, zebra, and wildebeest.

In any given survey the hosts would fall roughly into these categories, depending always on the availability of hosts and other factors considered later. As hartebeest and zebra were very common in at least two areas, and yet supplied no feeds to *G. morsitans* or *G. swynnertoni*, they were classed as animals which are never bitten.

It is difficult to compare these results with those obtained by previous workers, because the methods they used are in most cases not beyond reproach. The proportion of mammalian feeds (93 per cent.) recorded by LLOYD, JOHNSON, YOUNG and MORRISON (1934) agrees with these findings. These authors identified the host species by the measurements of red blood cells in the fresh feeds, and they found that 76 per cent. of the feeds come from a group which included the " small antelopes and the pigs." Only 12 per cent. were from " large antelopes." These figures are comparable if the distinction which these authors make between the small antelopes and the pigs is ignored. This group contained 62 per cent. with cells measuring 4.7 to 5.6μ which included cells from a number of small antelopes, and 14 per cent. of the cells measuring 5.7 to 6.6μ which included chiefly warthog. In view of the closeness of the two ranges of cell diameters, it is doubtful whether distinctions based on such measurements are justified. SYMES and MCMAHON (1937) examined a large number of *G. swynnertoni* blood meals by the precipitin test ; the interpretation of the results they obtained is so confusing as to make any comparison difficult. The only definite conclusion was the complete absence of zebra feeds, a result which we fully confirmed.

2. *G. pallidipes*

There is clear evidence that bushbuck is much the preferred host in the areas studied and that bushpig is the host of second choice.

3. *G. palpalis*

At Waturi (XII) birds and reptiles were of equal importance and together formed the main food of this species, as far as could be judged by the very few flies examined. The preference for bushbuck is noticeable but it was the only bovid there except for duiker and eland which each provided one feed. All the flies from the West shores of Lake Victoria (XII) had fed on reptiles, there being no other possible hosts except birds. Lungfish (*Protopterus*) might also be a source of food.

4. *G. austeni*

The flies from Zanzibar appear to be completely dependent on bushpig for their food supply, apart from some cattle feeds which were in flies caught on the fringe of the forest.

5. *G. brevipalpis*

About 60 per cent. of the flies had fed on hippopotamus. The areas from which the feeds were collected had been hunted, and other animals were relatively scarce. It would not be justified to accept these findings as representative of the feeding habits of *G. brevipalpis* elsewhere in undisturbed areas. PIRES (1950) greatly reduced the numbers of *G. brevipalpis* on the Maputo river by removing hippopotamus, but there were no other wild mammals. *G. brevipalpis* is certainly not obligatorily dependent upon hippopotamus as it is abundant in the Busoga forest of Uganda, several miles from the Lake and where these animals rarely come.

6. *G. longipennis*

No conclusion can be drawn from the results of the few feeds of *G. longipennis*, as the specimens had all fed on rhinoceros. The collections were made at the same place at two different periods (in February and September of the following year).

SOME FACTORS LIKELY TO AFFECT NATURAL USE OF VARIOUS HOSTS BY TSETSE FLIES

1. *Availability of hosts*

This depends not only on the numbers but also on the habits of the animals. Animals which run in herds, such as buffalo, may impress a human observer as abundant, and yet will be available to tsetse only in the near neighbourhood of the herd. It is not surprising, for instance, that *G. morsitans* should feed more on warthog than on bushpig, since *G. morsitans* and warthog are both diurnal. *G. austeni*, facultatively a crepuscular species, may be supposed to be able to find bushpig more easily than does *G. morsitans* (there were no warthog, however, in the area in which *G. austeni* was studied). Seasonal differences in the vegetation may well be of importance for the " savannah species " (*G. morsitans* and *G. swynnertoni*), since small animals may be easily found in the dry season when the grass is short, but during the rains may be concealed by long grass and therefore much less available to tsetse. We are now exploring this point by collecting samples of blood meals in one place throughout the year.

2. *Tolerance of the host*

There is little real evidence of tolerance differences between different host species. Monkeys and baboons are reputed to eat tsetse which attempt to feed on them : if this is true, such animals should be preserved in an anti-tsetse operation. HARRISON (1940) wrote :

" Using powerful Zeiss binoculars with a magnification of ten by fifty, many observations were made on giraffe at a range of eighty yards and tsetse were always seen to be feeding or trying to feed on them. The long lashing tail is constantly in motion, hind hooves are scraping tsetse from their forelegs and above all, the shudder of a giraffe, which must be seen to be believed, would dislodge the most tenacious insect. From these observations it was concluded that tsetse must follow for a considerable distance before they are finally satisfied. Warthog were continually observed at a range of twenty-five yards and they were always swarming with tsetse. Zebra were watched at a range of forty to fifty yards and on three occasions when tsetses were swarming around the observer, none was seen on the zebra, neither were there any movements or indications to show that unobserved tsetses were annoying them, so that further observations on zebra were considered unnecessary."

The absence of zebra feeds from our samples may not be due to an intolerance of the zebra to tsetse as much as to an aversion to zebra on the part of tsetse. Yet horses and mules are quickly infected with trypanosomiasis when brought into a fly-belt ; donkey blood was among the blood meals from Shinyanga, and both *G. morsitans* and *G. swynnertoni* have been found on freshly shot zebra (WEITZ and JACKSON, 1955). The matter is difficult to explain as also is the absence of hartebeest feeds from areas where these animals appeared to be important. This observation is quite at variance with that of JACKSON (1937) who observed a " catastrophic " fall in a population of *G. morsitans* associated with emigration of hartebeest.

If a host is intolerant, in the sense that it was especially adept at dislodging a feeding tsetse by tail lashing or other means, or if its blood was distasteful, then it would be likely to be a party to multiple feeds in tsetse. By " multiple feeds " is meant cases where two kinds of blood were detected in one fly, implying that a feed was interrupted and completed on another host. Though 29 multiple feeds were observed, no one species of host seemed to be especially involved.

It would also be expected that, if host intolerance really existed, game animals would sometimes be driven away from places where tsetse were especially numerous. No such movement has ever been observed and would not make for the survival of the host species (since African mammals are apparently unharmed by trypanosomes) until the tsetse became so numerous as to take an appreciable quantity of blood. GLASGOW and WILSON (1953) have calculated that an animal supporting a thousand tsetses (a high number) would lose about half an ounce of blood a day. The view that this is a negligible quantity has been challenged by FAIRBAIRN (1954).

3. *Digestion of blood of various animals*

SHUTE and MARYON (1955) showed that mosquitoes respond differently to feeding on different artificial hosts. They found that, unlike *Anopheles atroparvus*, *A. stephensi* cannot satisfactorily digest the blood of guinea-pigs although it appears to have no difficulty in digesting rabbit blood. The result is that, in the laboratory, *A. stephensi* cannot be maintained on guinea-pig but is satisfactorily maintained on rabbit, whereas *A. atroparvus* will thrive equally well on either. No such effect has so far been observed with tsetses, but we intend to compare the nutritive qualities of warthog and zebra blood for various species of tsetse.

If the activity of the tsetse were considerably and regularly changed by a feed on a particular host, in such a way as to affect the liability of the fed fly to be caught, a very definite sampling bias would result. It may be that the apparent importance of warthog for *G. morsitans* is due to such an effect. There is at present no evidence for this view, but we are well aware that our samples, though in some cases large, are not statistically " adequate," since in any one catch, only a small proportion (about one-thirtieth) of the fed flies that one knows to be present are captured. It is reasonable, too, to postulate a bias in favour of palatable, tolerant species, for such hosts would presumably give larger feeds which have a better chance of being detected.

SUMMARY

(1) The natural hosts of seven species of *Glossina* have been studied by the identification of 1,433 blood meals of flies caught in different areas. The identification was made by the combination of the precipitin test and the inhibition of agglutination test which gave specific and reliable results.

(2) A significant preference for blood from Suidae was observed with *G. morsitans*, *G. swynnertoni* and *G. austeni* which derived nearly or more than half their food supply from pigs.

(3) No flies fed on hartebeest, zebra or topi ; only very few feeds were found from impala which were very numerous in some areas.

(4) *G. palpalis* fed mainly on reptiles in one area but a large proportion of feeds were of avian origin in another ; bushbuck formed the greater part of the food of *G. pallidipes*. *G. brevipalpis* were feeding chiefly on hippopotamus in an area from which the game had been partially eliminated. A few feeds of *G. longipennis* were all from rhinoceros.

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