Bull. Org. mond. Santé
Bull. Wld Hlth Org. } 1963, **28**, 711-729

The Feeding Habits of *Glossina**

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The feeding habits of 15 species of Glossina *have been studied by the identification of their blood meals. Representative samples of the blood meals from each of these species of tsetse fly and from different habitats were collected and 22 640 blood meals were identified. The feeding patterns are characteristic for each species of tsetse fly and do not appear to depend entirely on the availability of different hosts, suggesting that the feeding habits of* Glossina *are genetically determined. However, a broad grouping can be made into five categories : species feeding mainly on suids, those feeding on suids and bovids, those feeding mainly on bovids, those feeding mainly on mammals other than suids and bovids, and those feeding on most available hosts and on man.*

The possibility of control by selective elimination of the main hosts of these groups is discussed.

Since Buxton (1955) surveyed the knowledge of the feeding habits of tsetse flies improved techniques for the identification of blood meals (Weitz, 1952, 1956) from blood-sucking insects have yielded precise and reliable facts about the sources of food of most species of *Glossina*. Most of these facts were related to particular problems in the field and have been reported individually. Many limited surveys have been reported and subsequently reviewed by Weitz (1960). The first (Weitz & Jackson, 1955) indicated that *Glossina* showed surprisingly selective feeding patterns which were confirmed in a survey of 1242 blood meals from seven species of tsetse flies (Weitz & Glasgow, 1956). The collated results, from both published and unpublished works, from 1953 to 1962 inclusive, total over 22 000 blood meal identifications from more than 15 species of *Glossina* from many areas within many different regions, and yield general information about the feeding habits of tsetse flies and about the relative importance of different species of hosts, which cannot be appreciated by the study of individual published reports. The object of this report is to assemble and evaluate in one publication all the available information.

The field collections range from fairly extensive collections over several seasons and from areas containing a wide variety of game animals to rather specialized collections, perhaps made with a particular objective and thus not fully representative of the species of fly or of the range of possible hosts. The gorged flies were collected in East Africa (Kenya, Uganda, Tanganyika, Zanzibar), Northern and Southern Rhodesia, and West Africa (mainly Nigeria).

MATERIALS AND METHODS

Collection of blood meals

The conditions of capture of the blood-fed flies are as published elsewhere (see Table 1). The blood-fed flies were captured in various ways: by collecting blood-fed specimens in their resting-places (see Isherwood, 1957), or from live baits such as oxen, or from screens carried by the searching party. Flies containing visible blood, or their stomach contents after dissection, were squashed on to filter paper discs. The discs were dried, usually in the air, and usually, but not always, kept in a desiccator over calcium chloride. The discs of filter paper were sent to the laboratory for identification after varying periods.

Identification procedures

Identification tests were made after the samples had been kept in the laboratory for periods varying from a few days up to 12 months. There was no evidence that deterioration of the samples occurred when kept, and identifications made on duplicate samples were similar after six months. Essentially, the methods of identification were as previously reported (see Weitz & Glasgow, 1956; Weitz, 1956). Every effort was made to identify a sample before

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it was used up; to this end tests were made for the more likely hosts first. The procedure may have biassed unfavourably the chances of identification of unusual hosts of the smaller feeds, because of insufficient material for tests for all possible hosts.

Each blood meal was cut out of the filter paper and extracted with physiological saline solution in varying volumes depending on the quality of the feed. The extracts were kept at 4°C for 12-18 hours and gently shaken before testing. The better extracts were diluted as necessary, the aim being a final concentration of the blood meal equivalent to about 1/1000 dilution of normal mammalian serum. From 1956 to 1959 the concentration was estimated by spectrophotometric absorption at 280 Å in comparison with standard absorption curves of normal serum. After 1959 the dilutions of the blood meal were made according to the colour of the extract and the concentration was checked by testing with anti-mammal serum (see below).

Group identification was first established by the precipitin test with the following group antisera: anti-primate (positive with sera of man, baboons and monkeys), anti-suid (reacting with sera of warthog, bushpig, giant forest hog, red river hog and domestic pig), anti-bovid (reacting with all bovids and

TABLE 1

SUMMARY OF DETAILS RELATING TO THE COLLECTIONS OF BLOOD SMEARS EXAMINED FOR IDENTIFICATION

Species	No. of smears identified	Origin and references (if previously reported)
G. swynnertoni Aust.	5 531	Tanganyika (Weitz & Glasgow, 1956; Glasgow et al., 1958; Lamprey et al., 1962). Kenya (Weitz et al., 1958; MacOwen, 1962).
G. austeni, Newst.	394	Zanzibar (Weitz & Glasgow, 1956). Kenya.
G. fuscipleuris, Aust.	553	Nigeria (Jordan et al., 1962). Uganda.
G. tabaniformis, West.	253	Nigeria (Jordan et al., 1961).
G. morsitans morsitans West.	3 778	Tanganyika (Weitz & Jackson, 1955; Weitz & Glasgow, 1956; Glasgow et al., 1958; Harley & Jewell, 1958; Pilson & Harley, 1959). Uganda.
G. morsitans orientalis Vanderpl.	2 367	Tanganyika, Northern and Southern Rhodesia (Weitz & Glasgow, 1956).
G. morsitans submorsitans Newst.	1 342	Nigeria (Jordan et al., 1962). Uganda.
G. pallidipes Aust.	2 688	Tanganyika (Weitz & Glasgow, 1956; Glasgow et al., 1958). Kenya (Weitz & Glasgow, 1956; Weitz et al., 1958; Isherwood et al., 1961). Uganda.
G. longipalpis, Wied.	1 069	Nigeria (Jordan et al., 1961, 1962).
G. fusca, Walker	707	Nigeria (Jordan et al., 1961).
G. longipennis, Corti	1 422	Tanganyika and Kenya (Weitz & Glasgow, 1956; Weitz et al., 1958; MacOwen, 1962; Langridge, 1960).
G. brevipalpis, Newst.	1 151	Uganda (Weitz & Glasgow, 1956). Kenya (Weitz et al., 1958; MacOwen, 1962; Isherwood et al., 1961).
G. palpalis fuscipes, Newst.	590	Tanganyika, Kenya, Uganda (Weitz & Glasgow, 1956).
G. palpalis palpalis, Rob.-Desv.	371	Nigeria (Jordan et al., 1961; 1962).
G. tachinoides, Westw.	424	Nigeria (Jordan et al., 1962).
Total	22 640	

giraffe). Feeds positive with any of these group antisera were further tested for the individual species within the group concerned by the inhibition test (see Weitz, 1956). Feeds which did not react with the group antisera were then tested with anti-mammalian serum (reacting with all known mammals), anti-avian serum (reacting with all common species of birds, including ostrich) and anti-reptilian serum (reacting with the sera of crocodiles, monitor lizards, tortoise and a variety of snakes). All the meals positive with anti-mammalian serum were tested by the precipitin test with group antisera covering the carnivores, rodents and equids; if positive, they were then tested for the individual species of this group, either by the precipitin test (e.g., for dogs and cats) or by the inhibition test. Non-reacting feeds were finally tested with species-specific precipitating antisera for the remaining mammals, e.g., elephant, hippopotamus, aardvark, porcupine.

Interpretation of tests

Blood meals which failed to react in all test systems are not included in this summary. The proportion of negative results with each consignment largely depended on the collectors. From experienced and selective collectors it was seldom more than 5%. Many blood meals contained the blood of two or sometimes even more different species of host. In the present survey these are allocated individually to each contributing host and, as a result, the total number of identifications exceeds the number of blood smears examined, but by not more than 1%-2%.

Sources of blood meals

The 22 640 blood meals identified between 1954 and 1961 from each of 15 species of *Glossina* and the main areas from which they were collected are shown in Table 1. The numbers of blood meals of each species of tsetse fly are contributed partly by samples as yet unreported and partly by published material to which references are given. The species of host was identified in 18 243 blood meals and group identifications only were made in the remainder.

RESULTS

In Tables 2-6 the results are arranged under each main group of hosts: Primates, Suidae, Bovidae, other mammals, birds and reptiles. Within each group are recorded the number of species-identified blood meals and the number of group-identified meals and the percentage they represent of all feeds examined. It is reasonable to assume that the group-identified feeds were derived from the hosts within the group in similar proportions to the meals from which the host species were identified.

Fig. 1-5 record the percentage distribution of each group of hosts and of the main species contributing to each of the groups. The main group identifications include the " unidentified " meals of each group, but the percentages of the individual species are calculated from the species-identified meals.

The systematic names of the hosts shown in Tables 2-6 are listed below for convenience in identification:

1. PRIMATES:

   Baboon: *Papio* spp.
   Monkey: *Cercopithecus*, *Erythrocebus* or *Colobus* spp.

2. SUIDS:

   Warthog: *Phacochoerus aethiopicus*
   Bushpig: *Potamochoerus koiropotamus*
   Red river hog: *Potamochoerus porcus*
   Giant forest hog: *Hylochoerus* sp.

3. BOVIDS:

   Giraffe: *Giraffa camelopardalis* or *G. reticulata*
   Buffalo: *Syncerus caffer*, *S. nana*
   Kudu: *Strepsiceros strepsiceros*, *S. imberbis*
   Eland: *Taurotragus oryx*
   Bushbuck: *Tragelaphus scriptus* or *Limnotragus spekii*
   Duiker: *Cephalophus*, *Philantomba* and *Sylvicapra* .spp.; also ? *Guevei* sp.
   Waterbuck: *Kobus defassa*, *K. ellipsiprymnus*
   Reedbuck: *Redunca redunca*, *R. arundinum*, *R. fulvorufula*
   Hartebeest: *Alcelaphus buselaphus*, *A. lichtensteinii*
   Impala: *Aepyceros melampus*
   Oribi: *Ourebia ourebi*
   Roan antelope: *Hippotragus equinus*, *H. niger*
   Gazelles: *Gazella thomsonii*, *G. granti*
   Steinbok: *Raphicerus campestris* or *R. sharpei*
   Kob: *Adenota kob*
   Sheep/Goat: *Ovis aries*, *Capra hircus*
   Ox: *Bos taurus*

4. OTHER MAMMALS:

   Elephant: *Loxodonta africana*
   Rhinoceros: *Diceros bicornis*
   Hippopotamus: *Hippopotamus amphibius*
   Dogs: *Canis*, *Lycaon* and *Octocyon* spp.
   Cats: *Felis*, *Panthera*, *Acinonyx*, *Leptailurus* spp.

Hyaena: *Hyaena hyaena, Crocuta crocuta*
Other carnivores: Includes *Mustelidae, Viverridae*
Porcupine: *Atherurus africanus, Hystrix africae-australis*
Aardvark: *Orycteropus afer*

5. BIRDS:
Ostrich: *Struthio camelus*

FIG. 1
BLOOD MEALS OF *GLOSSINA* SPECIES FEEDING MAINLY ON SUIDS

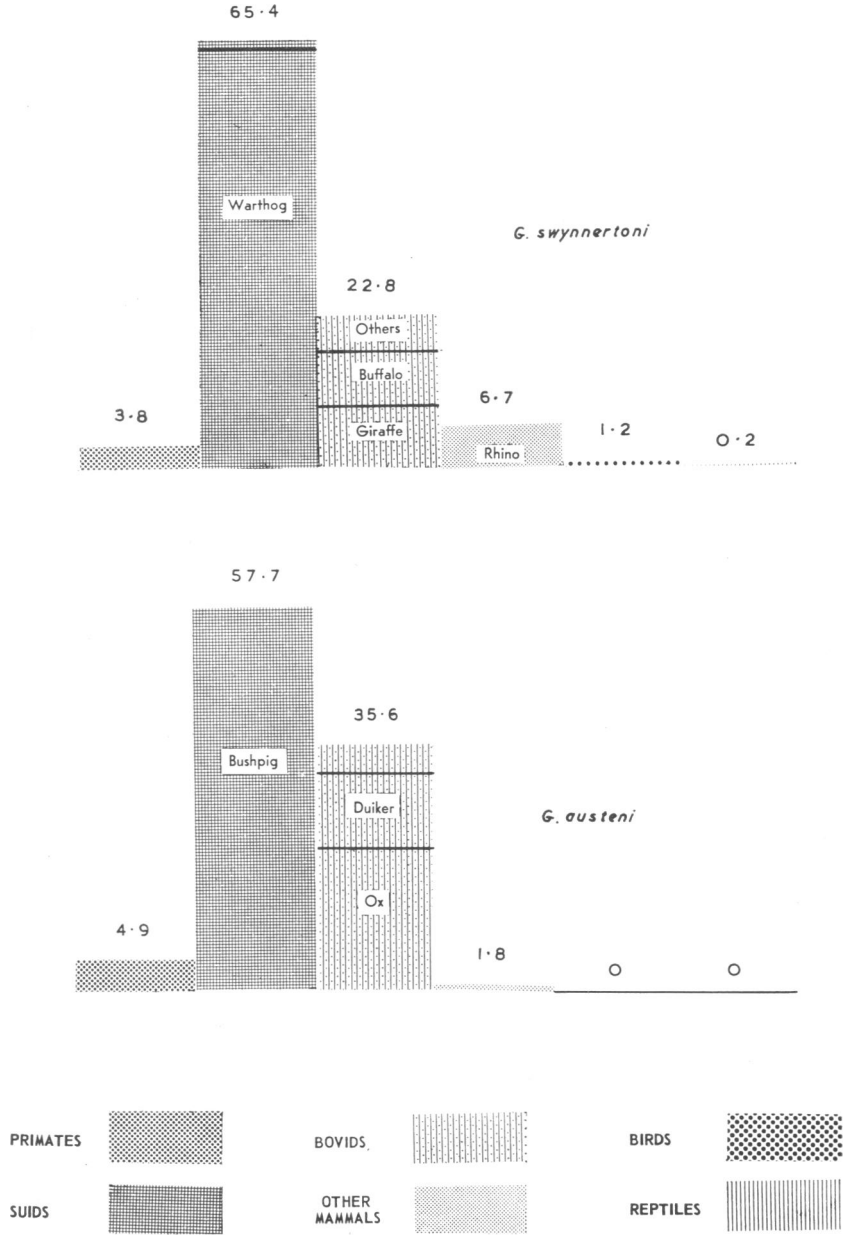

TABLE 2

BLOOD MEALS OF *GLOSSINA* SPECIES FEEDING MAINLY ON SUIDS

Host	*G. swynnertoni*				*G. austeni*			
	No. identified		Percentage		No. identified		Percentage	
			Group	Species			Group	Species
1. PRIMATES								
Man	162			3.4	18			5.9
Baboon	9			0.2	—			
Monkey	6			0.1	—			
Total species identified	177				18			
Unidentified primates		34				1		
Total Primates		211	3.8			19	4.9	
2. SUIDS								
Warthog	3 179			67.7	—			
Bushpig	52			1.1	188			61.8
Red river hog	—				—			
Giant forest hog	—				—			
Total species identified	3 231				188			
Unidentified suids		386				37		
Total Suids		3 617	65.4			225	57.7	
3. BOVIDS								
Giraffe	417			8.9	—			
Buffalo	386			8.2	4			1.3
Kudu	2			0.04	6			1.9
Eland	67			1.4	1			0.3
Bushbuck	5			0.1	4			1.3
Duiker	9			0.2	29			9.5
Waterbuck	1			0.02	—			
Reedbuck	1			0.02	—			
Hartebeest	9			0.2	—			
Impala	25			0.5	—			
Oribi	—				—			
Roan antelope	34			0.7	—			
Gazelles	1			0.02	—			
Steinbok	2			0.04	—			
Kob	—				—			
Sheep/Goat	19			0.4	—			
Ox	21			0.4	56			18.4
Total species identified	999				100			
Unidentified bovids		261				43		
Total Bovids		1 260	22.8			143	35.6	
4. OTHER MAMMALS								
Elephant	45			1.0	1			0.3
Rhinoceros	140			3.0	—			
Hippopotamus	—				—			
Dogs	4			0.09	—			
Cats	6			0.1	—			
Hyaena	6			0.1	—			
Other carnivores	17			0.4	—			
Porcupine	—				1			0.3
Aardvark	—				—			
Total species identified	218				2			
Unidentified mammals		152				5		
Total Other Mammals		370	6.7			7	1.8	
5. BIRDS								
Ostrich	—				—			
Others	64			1.4	—			
Total Birds		64	1.2					
6. REPTILES	9			0.2	—			
		9	0.2					
TOTALS	4 698	5 531	100.1	99.9	308	394	100.0	101.0

FIG. 1 *(continued)*
BLOOD MEALS OF *GLOSSINA* SPECIES FEEDING MAINLY ON SUIDS

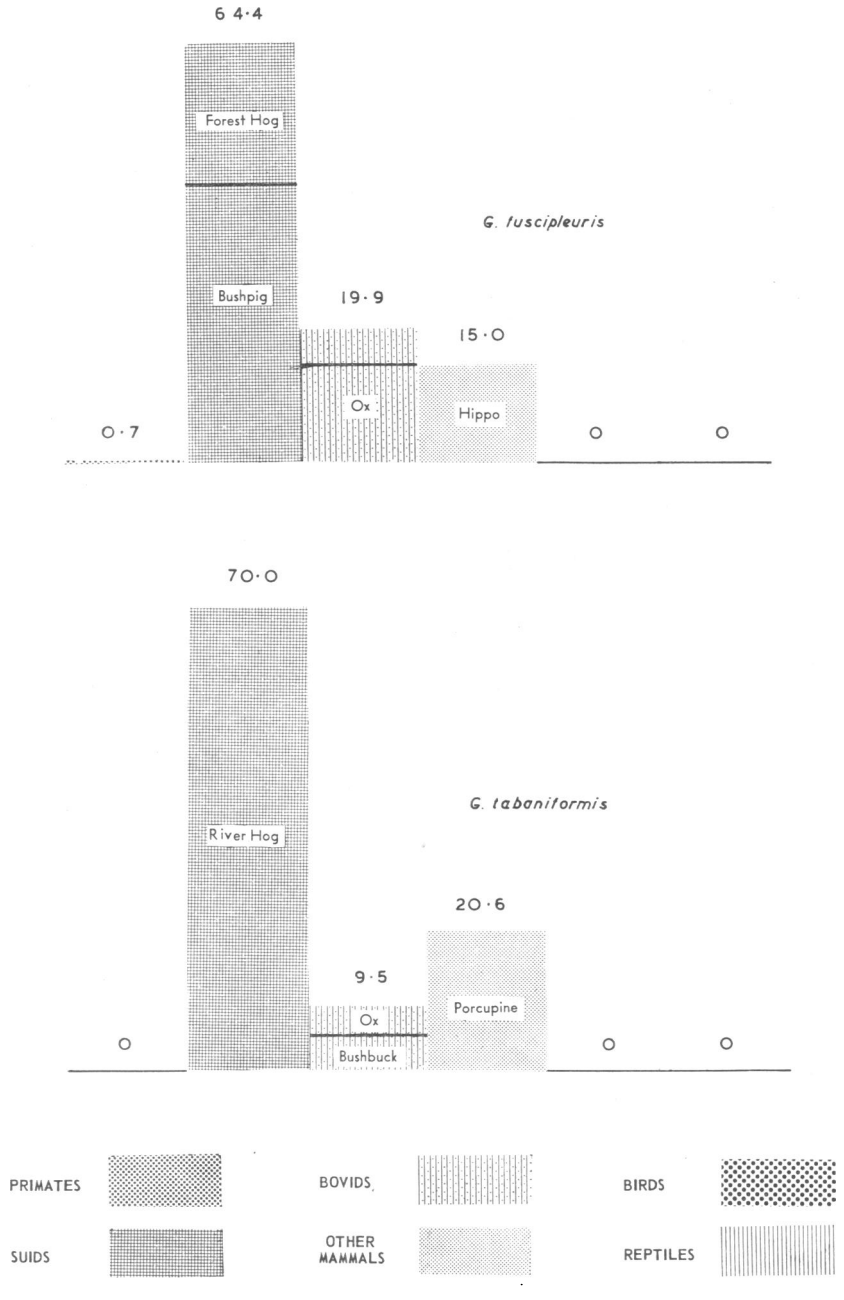

TABLE 2 *(continued)*

BLOOD MEALS OF *GLOSSINA* SPECIES FEEDING MAINLY ON SUIDS

Host	*G. fuscipleuris*				*G. tabaniformis*			
	No. identified		Percentage		No. identified		Percentage	
			Group	Species			Group	Species
1. PRIMATES								
Man	2			0.5	—			
Baboon	1			0.2	—			
Monkey	—				—			
Total species identified	3				—			
Unidentified primates		1				0		
Total Primates		4	0.7			0		
2. SUIDS								
Warthog	2			0.5	—			
Bushpig	175			41.2	—			
Red river hog	—				158			69.6
Giant forest hog	90			21.2	—			
Total species identified	267				158			
Unidentified suids		89				19		
Total Suids		356	64.4			177	70.0	
3. BOVIDS								
Giraffe	—				—			
Buffalo	12			2.8	1			0.4
Kudu	—				—			
Eland	—				—			
Bushbuck	9			2.1	10			4.4
Duiker	—				—			
Waterbuck	—				—			
Reedbuck	—				—			
Hartebeest	—				—			
Impala	—				—			
Oribi	—				—			
Roan antelope	—				—			
Gazelles	—				—			
Steinbok	—				—			
Kob	—				—			
Sheep/Goat	—				—			
Ox	55			12.9	8			3.5
Total species identified	76				19			
Unidentified bovids		34				5		
Total Bovids		110	19.9			24	9.5	
4. OTHER MAMMALS								
Elephant	—				—			
Rhinoceros	—				—			
Hippopotamus	79			18.6	—			
Dogs	—				—			
Cats	—				—			
Hyaena	—				—			
Other carnivores	—				—			
Porcupine	—				50			22.0
Aardvark	—				—			
Total species identified	79				50			
Unidentified mammals		4				2		
Total Other Mammals		83	15.0			52	20.6	
5. BIRDS								
Ostrich	—				—			
Others	—				—			
Total Birds		0				0		
6. REPTILES	—				—			
TOTALS	425	553	100.0	100.0	227	253	100.1	99.9

FIG. 2
BLOOD MEALS OF *GLOSSINA* SPECIES FEEDING MAINLY ON SUIDS AND BOVIDS

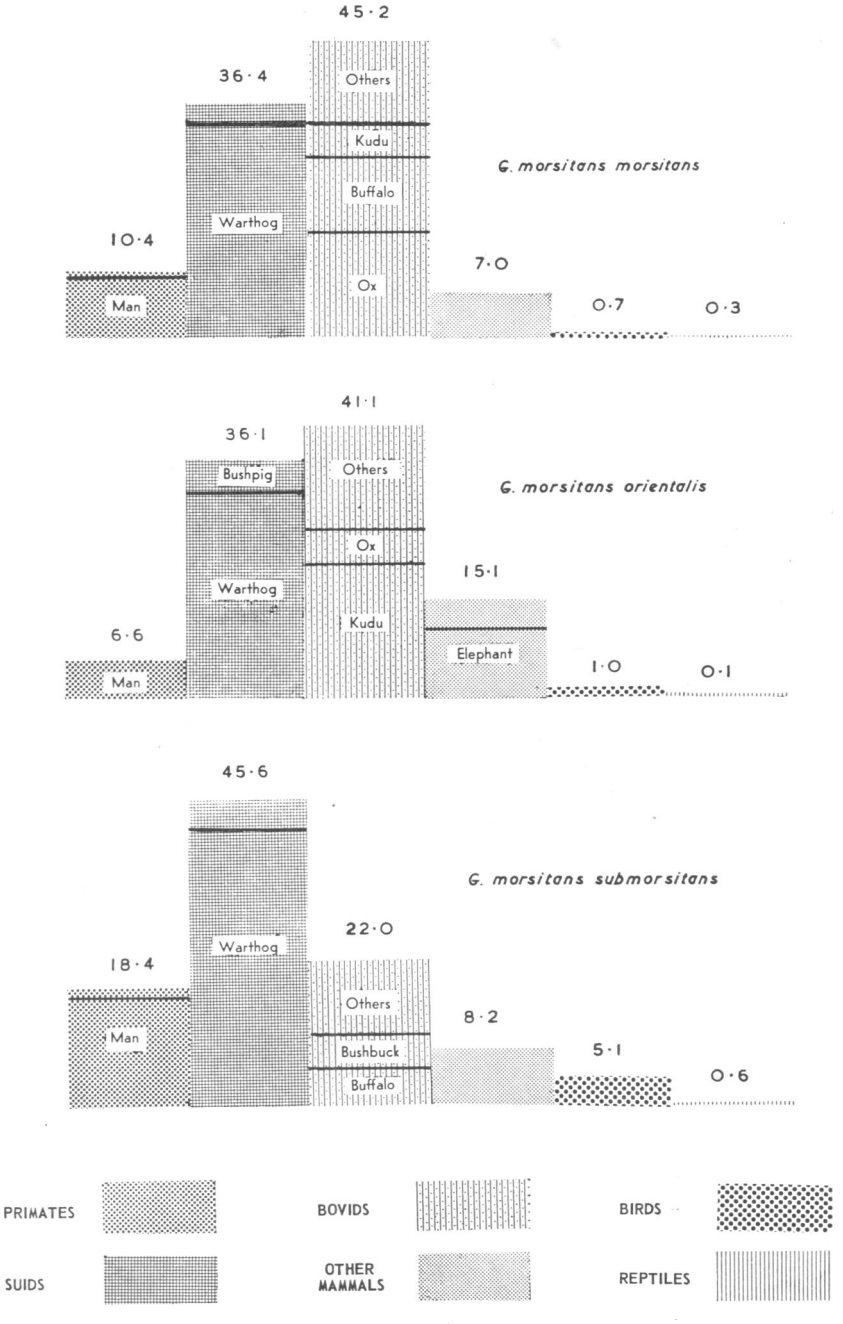

TABLE 3

BLOOD MEALS OF *GLOSSINA* SPECIES FEEDING MAINLY ON SUIDS AND BOVIDS

Host	*G. morsitans morsitans*				*G. morsitans orientalis*				*G. morsitans submorsitans*			
	No. identified		Percentage Group Species		No. identified		Percentage Group Species		No. identified		Percentage Group Species	
1. PRIMATES												
Man	305			11.1	95			5.8	198			18.3
Baboon	14			0.5	17			1.0	11			1.0
Monkey	3			0.1	5			0.3	11			1.0
Total species identified	322				117				220			
Unidentified primates		70				40				27		
Total Primates		392	10.4			157	6.6			247	18.4	
2. SUIDS												
Warthog	929			33.9	487			29.5	493			45.5
Bushpig	78			2.8	77			4.7	7			0.6
Red river hog	—				—				—			
Giant forest hog	—				—				—			
Total species identified	1 007				564				500			
Unidentified suids		370				291				112		
Total Suids		1 377	36.4			855	36.1			612	45.6	
3. BOVIDS												
Giraffe	46			1.7	15			0.9	4			0.4
Buffalo	318			11.6	39			2.4	53			4.9
Kudu	139			5.0	413			25.0	5			0.5
Eland	77			2.8	46			2.8	3			0.3
Bushbuck	87			3.2	25			1.5	51			4.7
Duiker	32			1.2	8			0.5	5			0.5
Waterbuck	14			0.5	1			0.06	—			
Reedbuck	81			3.0	15			0.9	1			0.1
Hartebeest	—				—				21			1.9
Impala	9			0.3	2			0.1	1			0.1
Oribi	—				—				12			1.1
Roan antelope	35			1.3	3			0.2	38			3.5
Gazelles	1			0.04	—				—			
Steinbok	—				—				—			
Kob	—				—				—			
Sheep/Goat	1			0.04	1			0.06	3			0.3
Ox	368			13.4	82			5.0	15			1.4
Total species identified	1 208				650				212			
Unidentified bovids		500				324				84		
Total Bovids		1 708	45.2			974	41.1			296	22.0	
4. OTHER MAMMALS												
Elephant	32			1.2	219			13.3	2			0.2
Rhinoceros	43			1.6	46			2.8	20			1.8
Hippopotamus	41			1.5	—				—			
Dogs	17			0.6	4			0.2	14			1.3
Cats	6			0.2	7			0.4	11			1.0
Hyaena	2			0.07	—				—			
Other carnivores	4			0.1	4			0.2	4			0.4
Porcupine	14			0.5	9			0.6	21			1.9
Aardvark	5			0.2	6			0.4	2			0.2
Total species identified	164				295				74			
Unidentified mammals		101				62				36		
Total Other Mammals		265	7.0			357	15.1			110	8.2	
5. BIRDS												
Ostrich	—				—				—			
Others	26			0.9	23			1.4	69			6.4
Total Birds		26	0.7			23	1.0			69	5.1	
6. REPTILES	10			0.4	1			0.06	8			0.7
		10	0.3			1	0.1			8	0.6	
TOTALS	2 737	3 778	100.0	99.9	1 650	2 367	100.0	100.0	1 083	1 342	99.9	100.0

FIG. 3
BLOOD MEALS OF *GLOSSINA* SPECIES FEEDING MAINLY ON BOVIDS

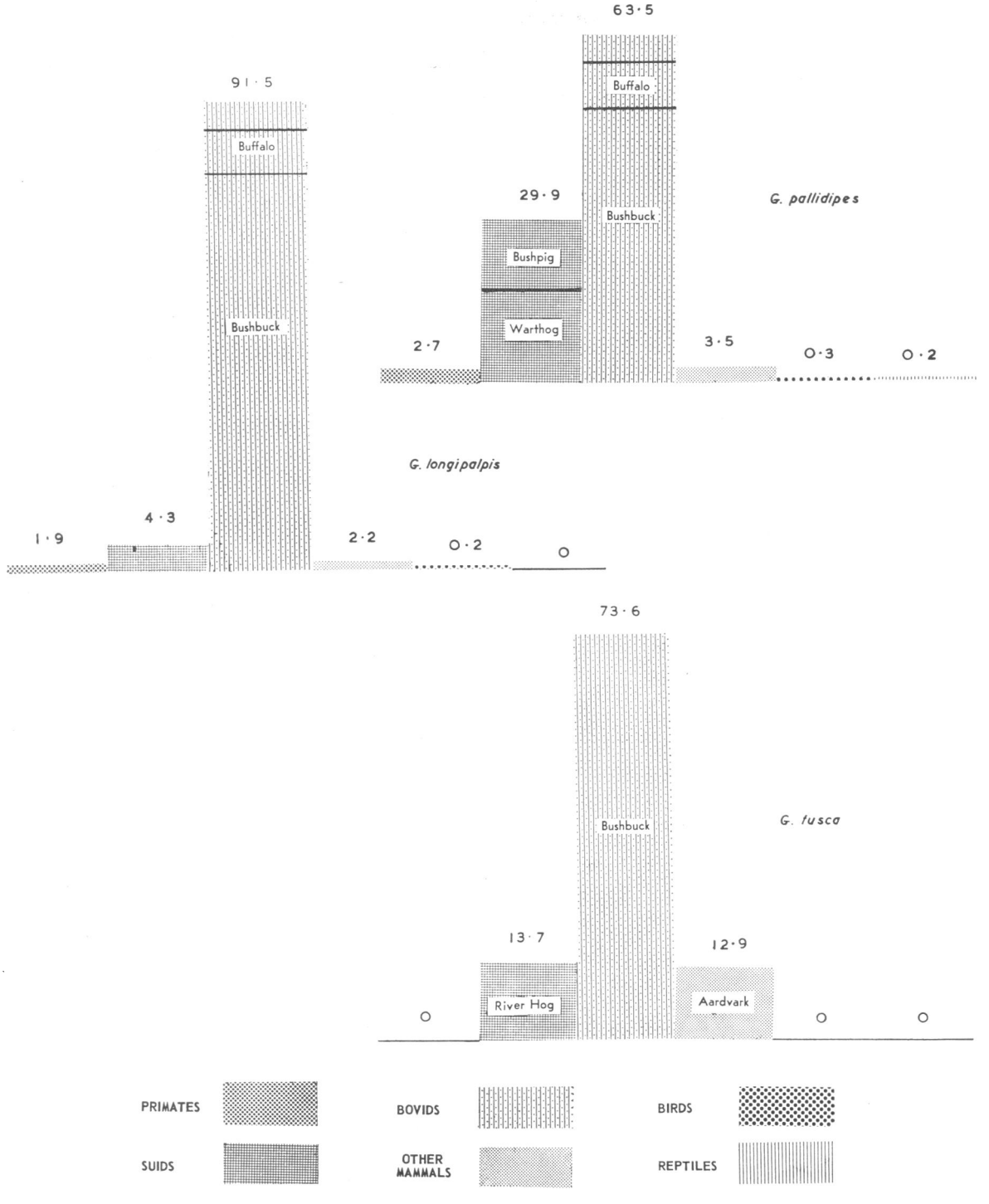

TABLE 4

BLOOD MEALS OF *GLOSSINA* SPECIES FEEDING MAINLY ON BOVIDS

Host	*G. pallidipes*				*G. longipalpis*				*G. fusca*			
	No. identified		Percentage		No. identified		Percentage		No. identified		Percentage	
			Group	Species			Group	Species			Group	Species
1. PRIMATES												
Man	62			2.8	14			1.6	—			—
Baboon	—				—				—			
Monkey	—				2			0.2	—			
Total species identified	62				16				—			
Unidentified primates		11				3						
Total Primates		73	2.7			19	1.9			0		
2. SUIDS												
Warthog	430			19.2	1			0.1	—			
Bushpig	301			13.4	—				—			
Red river hog	4			0.2	33			3.8	89			14.4
Giant forest hog	—				—				—			
Total species identified	735				34				89			
Unidentified suids		68				12				7		
Total Suids		803	29.9			46	4.3			96	13.7	
3. BOVIDS												
Giraffe	10			0.4	—				—			
Buffalo	180			8.0	142			16.3	2			0.3
Kudu	9			0.4	—				—			
Eland	4			0.2	—				—			
Bushbuck	1 099			49.0	649			74.4	452			73.4
Duiker	2			0.09	10			1.1	6			0.9
Waterbuck	1			0.04	—				—			
Reedbuck	10			0.4	—				—			
Hartebeest	1			0.04	—				—			
Impala	—				—				—			
Oribi	—				—				—			
Roan antelope	18			0.8	—				—			
Gazelles	1			0.04	—				—			
Steinbok	—				—				—			
Kob	—				—				2			0.3
Sheep/Goat	3			0.1	—				—			
Ox	35			1.6	15			1.7	1			0.2
Total species identified	1 373				816				463			
Unidentified bovids		332				162				57		
Total Bovids		1 705	63.5			978	91.5			520	73.6	
4. OTHER MAMMALS												
Elephant	28			1.2	2			0.2	1			0.2
Rhinoceros	13			0.6	—				—			
Hippopotamus	14			0.6	—				—			
Dogs	—				—				—			
Cats	—				—				—			
Hyaena	—				—				—			
Other carnivores	3			0.1	—				—			
Porcupine	2			0.09	1			0.1	8			1.3
Aardvark	—				1			0.1	55			8.9
Total species identified	60				4				64			
Unidentified mammals		34				20				27		
Total Other Mammals		94	3.5			24	2.2			91	12.9	
5. BIRDS												
Ostrich	—				—				—			
Others	7			0.3	2			0.2	—			
Total Birds		7	0.3			2	0.2			0		
6. REPTILES	5			0.2	—				—			
		5	0.2									
TOTALS	2 242	2 687	100.1	99.8	872	1 069	100.1	99.8	616	707	100.2	99.9

FIG. 4

BLOOD MEALS OF *GLOSSINA* SPECIES FEEDING MAINLY ON MAMMALS OTHER THAN SUIDS AND BOVIDS

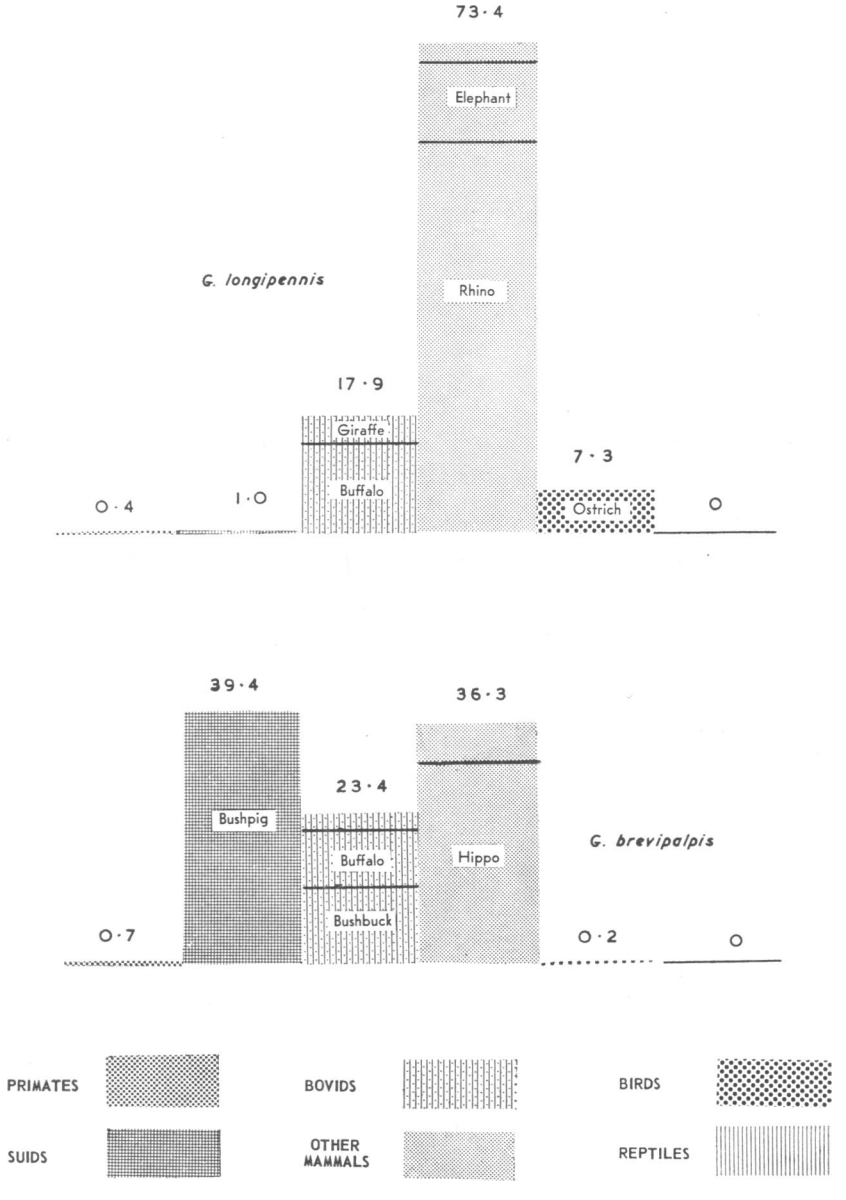

TABLE 5

BLOOD MEALS OF *GLOSSINA* SPECIES FEEDING MAINLY ON MAMMALS OTHER THAN SUIDS AND BOVIDS

Host	*G. longipennis*				*G. brevipalpis*			
	No. identified		Percentage		No. identified		Percentage	
			Group	Species			Group	Species
1. PRIMATES								
Man	4			0.3	7			0.7
Baboon	—				—			
Monkey	—				—			
Total species identified	4				7			
Unidentified primates		1				1		
Total Primates		5	0.4			8	0.7	
2. SUIDS								
Warthog	6			0.4	—			
Bushpig	—				417			40.7
Red river hog	—				—			
Giant forest hog	—				—			
Total species identified	6				417			
Unidentified suids		8				36		
Total Suids		14	1.0			453	39.4	
3. BOVIDS								
Giraffe	46			3.4	1			0.1
Buffalo	192			14.1	119			11.6
Kudu	—				—			
Eland	—				2			0.2
Bushbuck	—				83			8.1
Duiker	—				2			0.2
Waterbuck	—				1			0.1
Reedbuck	—				—			
Hartebeest	—				—			
Impala	—				—			
Oribi	—				—			
Roan antelope	—				1			0.1
Gazelles	—				—			
Steinbok	—				—			
Kob	—				—			
Sheep/Goat	—				—			
Ox	—				11			1.1
Total species identified	238				220			
Unidentified bovids		17				51		
Total Bovids		255	17.9			271	23.4	
4. OTHER MAMMALS								
Elephant	174			12.8	37			3.6
Rhinoceros	816			60.0	18			1.8
Hippopotamus	—				319			31.1
Dogs	1			0.07	—			
Cats	9			0.7	—			
Hyaena	1			0.07	1			0.1
Other carnivores	1			0.07	3			0.3
Porcupine	—				2			0.2
Aardvark	5			0.4	—			
Total species identified	1 007				380			
Unidentified mammals		37				37		
Total Other Mammals		1 044	73.4			417	36.3	
5. BIRDS								
Ostrich	} 104			7.7	—			
Others					2			0.2
Total Birds		104	7.3			2	0.2	
6. REPTILES	—				—			
TOTALS	1 359	1 422	100.0	100.0	1 026	1 151	100.0	100.2

FIG. 5
BLOOD MEALS OF *GLOSSINA* SPECIES FEEDING ON MOST AVAILABLE HOSTS AND MAN

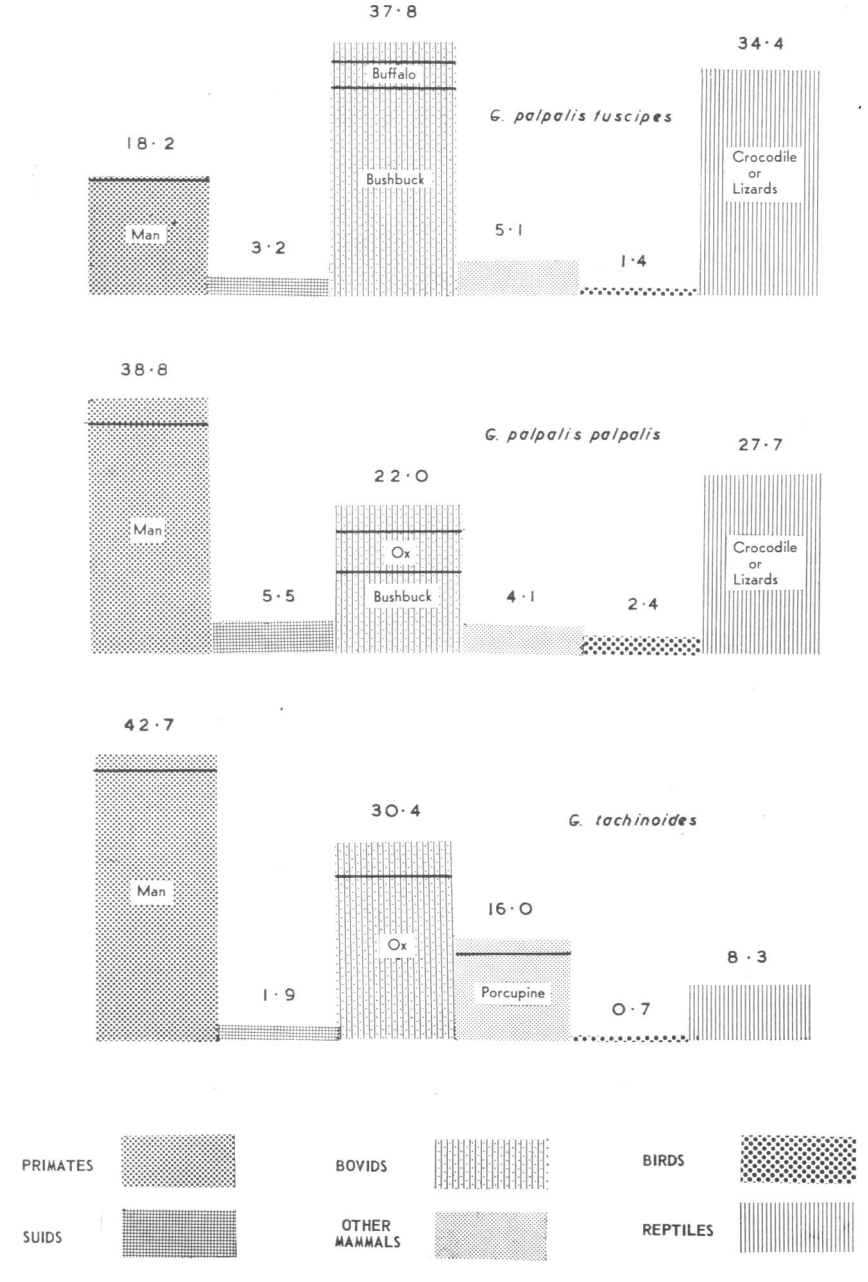

TABLE 6

BLOOD MEALS OF *GLOSSINA* SPECIES FEEDING ON MOST AVAILABLE HOSTS AND MAN

Host	*G. palpalis fuscipes*				*G. palpalis palpalis*				*G. tachinoides*			
	No. identified		Percentage		No. identified		Percentage		No. identified		Percentage	
			Group	Species			Group	Species			Group	Species
1. PRIMATES												
Man	99			21.1	106			35.8	126			54.1
Baboon	1			0.2	2			0.7	5			2.1
Monkey	1			0.2	10			3.4	—			
Total species identified	101				118				131			
Unidentified primates		6				25				50		
Total Primates		107	18.2			143	38.8			181	42.7	
2. SUIDS												
Warthog	—				2			0.7	3			1.3
Bushpig	18			3.8	2			0.7	—			
Red river hog	—				8			2.7	—			
Giant forest hog	—				—				—			
Total species identified	18				12				3			
Unidentified suids		1				10	5.5			5		
Total Suids		19	3.2			22				8	1.9	
3. BOVIDS												
Giraffe	—				—				—			
Buffalo	12			2.6	6			2.0	1			0.4
Kudu	—				—				—			
Eland	—				—				—			
Bushbuck	103			22.0	30			10.1	3			1.3
Duiker	—				1			0.3	3			1.3
Waterbuck	—				—				—			
Reedbuck	—				—				—			
Hartebeest	—				—				—			
Impala	—				—				—			
Oribi	—				1			0.3	—			
Roan antelope	—				1			0.3	—			
Gazelles	—				—				—			
Steinbok	—				—				—			
Kob	—				—				—			
Sheep/Goat	—				—				—			
Ox	8			1.7	17			5.7	34			14.6
Total species identified	123				56				41			
Unidentified bovids		100				25				88		
Total Bovids		223	37.8			81	22.0			129	30.4	
4. OTHER MAMMALS												
Elephant	—				—				—			
Rhinoceros	—				—				—			
Hippopotamus	—				—				—			
Dogs	—				—				—			
Cats	—				—				1			0.4
Hyaena	—				—				—			
Other carnivores	16			3.4	2			0.7	2			0.8
Porcupine	—				—				17			7.3
Aardvark	—				—				—			
Total species identified	16				2				20			
Unidentified mammals		14				13				48		
Total Other Mammals		30	5.1			15	4.1			68	16.0	
5. BIRDS												
Ostrich	—				—				—			
Others	8			1.7	9			3.0	3			1.3
Total Birds		8	1.4			9	2.4			3	0.7	
6. REPTILES	203			43.3	101			34.1	35			15.0
		203	34.4			101	27.7			35	8.3	
TOTALS	469	590	100.1	100.0	298	371	100.5	100.2	233	424	100.0	99.9

FEEDING PATTERNS OF DIFFERENT SPECIES OF *GLOSSINA*

The general feeding pattern of each species is evident from the tables and figures. Although it is appreciated that variations from the main pattern occur in some localities, some general trends are apparent. Some species of fly, though apparently using certain species of host preferentially, nevertheless feed on a wide range of hosts of all main groups of animals except birds and reptiles. Others are distinctly more selective, choosing only a few hosts. The feeding habits of the tsetse fly are divisible into five main patterns, which are the basis of the distributions in Fig. 1-5.

Group 1 : Flies feeding mainly on suids (Fig. 1 and Table 2)

G. swynnertoni. Of 5531 identified meals, 3617 (65.4%) came from suids, mostly warthog (67.7% of identified species), a proportion consistently found in all the areas in Tanganyika and Kenya sampled. The bovids contributed only 22.8% of all the feeds of this species, largely giraffe and buffalo (8% each of species-identified feeds), the only other important host being rhinoceros (3% of species-identified feeds).

G. austeni. The contribution from suids is 57.7%, all originating from bushpig (61.8% of all identified species). Of the 308 blood smears, 187 came from Zanzibar, where a relatively high proportion of feeds was obtained from cattle in a marginal tsetse fly area (total ox feeds 18.4% of species identified for all areas). The duiker was an important host in Kenya (9.5% of all identified feeds), making the total contribution from bovids 35.6%.

G. fuscipleuris. The sources of food reflect the habitat of this species. The giant forest hog and the bushpig together contribute 64.4% of all feeds. No other fly is known to feed on the giant forest hog. A rather high percentage of ox feeds (12.9% of identified species) is largely due to the fact that these flies were caught near the forest, where cattle were grazing. Hippopotamus constitutes a larger source of food (18.6%) for *G. fuscipleuris* than for any other fly except *G. brevipalpis*, a finding consistent with the riverine habitat of *G. fuscipleuris.*

G. tabaniformis. This West African forest species feeds very largely (70% of all groups) on the local suid, the red river hog. The relatively large number (50 of 227 feeds identified) of feeds from porcupine indicates the relatively limited fauna available to this species in the forest.

The pattern of feeding of this group of tsetse fly is not all a reflection of the available fauna. Jackson (1940) suspected that some species of tsetse fly had a physiological need for suid blood, a suggestion consistent with these results, since each species of tsetse fly obtained its food from whatever suid was available, although the habitats of the suids varied considerably. This suggests that these tsetse flies display a real preference for suids.

Group 2 : Flies feeding mainly on suids and bovids (Fig. 2 and Table 3)

The three subspecies of *G. morsitans* are ecologically very similar, living generally in open woodland or *miombo* containing a variety of large and small antelopes in fairly large numbers and herds of buffalo and other migratory mammals, such as elephant, which are present sporadically. It is thus not surprising that *G. morsitans*, having a wide choice of bovid hosts obtains a large proportion of its food from some species of this group.

G. morsitans morsitans. A third of the feeds of this subspecies was from warthog, and nearly half from bovids. Of the bovids, 30% were from ox, which may be regarded as an adventitious host, since herds of cattle were often present (e.g., in Ankole) and diverted the fly from its natural food sources. The other bovid feeds were mostly from buffalo (26% of bovid feeds) and kudu (11.5% of bovid feeds). Buffalo were not always present and the variations of their numbers at different times was indicated by the number of feeds on them. At Ulyampiti, Tanganyika, kudu was the main host (70% of all feeds; see Glasgow et al., 1958). The relatively large proportion of human feeds indicates a certain attraction of this fly for man, but in many cases these feeds were obtained from the catching party.

G. morsitans orientalis. The feeding pattern of this subspecies is very much the same as that of *G. morsitans morsitans*, but a greater proportion of kudu feeds (64% of bovid feeds, 25% of all identified feeds) is largely due to the high preponderance of kudu in Southern Rhodesia, where large numbers of flies were collected. There were less human feeds and more elephant feeds (13%), resulting from differences in availability.

G. morsitans submorsitans. The pattern in this subspecies, although very similar to that of the other two, is characterized by a relatively high proportion of feeds on hartebeest. This host is not used by any other species of *Glossina* except *G. swynnertoni*, of which in Kenya 0.2% were found to have fed on this animal. The importance of hartebeest to *G. morsitans submorsitans* is evident in the collections made from North Karamoja, Uganda, which is the only area sampled for this fly containing hartebeest, there being none in West Africa. The over-all proportion of hartebeest feeds is 2% (10% of all bovid feeds), but in the Uganda specimens it is 5% of all feeds in that area—a very high proportion, since other subspecies, given similar opportunities, failed to feed on this host at all. In other respects, apart from a higher percentage of avian feeds (5% of all feeds) the feeding habits are indistinguishable from the other *morsitans* subspecies.

The characteristic feature of *morsitans* species is the absence of feeding on some species of animals which are present in collecting areas. Hartebeest (apart from *G. morsitans submorsitans)*, impala, gazelles, zebra and wildebeest are conspicuous by their absence from the list of animals fed on, in spite of their high incidence in all areas. The preference of this fly for suid blood is more evident in some areas than in others.

Group 3 : Flies feeding mainly on bovids (Fig. 3 and Table 4)

G. pallidipes. The results in Table 4 and Fig. 3 suggest that the feeding pattern of *G. pallidipes* resembles that of *G. morsitans*; both use bovids (63% of all feeds) and suids (30% of all feeds) as their main source of food. Of the 2687 feeds from this fly, 490 were obtained from Block 9 in Shinyanga, Tanganyika (Glasgow et al., 1958), of which 462 (94%) were from suids, mainly warthog. In this area there were no bushbuck and very few buffalo. In south-eastern Uganda there were 117 bushpig feeds out of a total of 451 (26%). Only in these two areas were pigs an important source of food. In all other areas the main hosts were bovids, which provided about 80% of the 1747 remaining feeds, and they appear to be the more usual hosts of *G. pallidipes*. Bushbuck, which was the host from which *Trypanosoma rhodesiense* was isolated by Heisch et al. (1958) in an area where *G. pallidipes* was present, was the principal bovid host (49% of all feeds and 75% of all bovid feeds).

G. longipalpis. It is of interest that this West African species, ecologically similar to *G. pallidipes* in the East, has similar feeding habits. Bovids provided 91% of all feeds, mainly bushbuck (80% of bovid feeds). Only 4% were suid feeds, mostly from red river hog.

G. fusca. Bushbuck was again the main host of this species (73% of all feeds). The suids in the collecting areas were represented by the red river hog, on which 14% of the flies had fed.

Tsetse fly feeding patterns in this division are fairly constant except that the behaviour of *G. pallidipes* in Shinyanga may be the result of an adaptation from the more usual choice of bushbuck to suids in the absence of the main bovid host.

Group 4 : Flies feeding mainly on mammals other than pigs and bovids (Fig. 4 and Table 5)

G. longipennis. This fly has not yet been found in a habitat where rhinoceros is absent, a host forming the staple diet of this species (60% of all feeds). Monthly records indicate that the fly is diverted from rhinoceros to other large animals like elephant and buffalo when these are available (12% and 14% of all feeds respectively). Other hosts of appreciable importance are the ostrich and the giraffe (7% and 3% respectively of all feeds). It is curious and perhaps significant that *G. longipennis* confines its feeding to very large animals.

G. brevipalpis. The habitat of this species—occurring mainly near watercourses—accounts for the high proportion of feeds on hippopotamus (31% of all feeds). Otherwise the fly mainly lives on bushpig (40% of feeds). Buffalo (11%), bushbuck (8%), elephant (4%) and rhinoceros (2%) account for most of the other main hosts of this fly, which also seems to feed on the larger hosts available. Apart from the large proportion of hippopotamus feeds, the feeding habits of this species are those of *G. morsitans* type.

Group 5 : Flies feeding on most available hosts and man (Fig. 5 and Table 6)

G. palpalis fuscipes and G. palpalis palpalis. The main hosts of these species are primates (mainly human) (18% and 38%), bovids (38% and 22%) and reptiles (34% and 28%), The human feeds depend on the availability of man, but there is a distinct attraction to man not so consistently displayed by other species of *Glossina*, a character consistent with

this fly's ability to transmit gambian sleeping sickness. The high proportion of feeds on aquatic reptiles is consistent with the riverine habitat of the fly. Bushbuck is another important host in some areas (20% and 10% of all feeds identified), particularly where reptiles (e.g., crocodiles) have been eliminated by hunting.

G. tachinoides. This West African species, also responsible for the transmission of sleeping-sickness to man, has similar feeding habits to *G. palpalis*. The high proportion of human feeds (54% of species-identified feeds) and of cattle feeds (15% of all feeds), indicates the domestic habits of this fly. The high incidence of porcupine feeds (7.3% of feeds identified as species) may be due to the greater availability of porcupines than of aquatic reptiles in West Africa.

The feeding patterns of the *palpalis* group are consistent with its habitat. Hosts (including man) frequenting the water's edge are attacked. In areas with no domesticated animals, the majority of feeds are from crocodiles or monitor lizards. Very few baboon and monkey feeds were found.

CONCLUSIONS

The behaviour of each species of fly is characteristic and is clearly not entirely dependent on the availability of different hosts, suggesting that the feeding habits are genetically determined. Thus, the subspecies, *G. morsitans submorsitans*, feeds on hartebeest whereas other flies of the same species and of similar habitat do not. In addition, the hosts of different species of flies living in the same area, although perhaps in a different habitat but in contact with the same fauna, have distinctive feeding habits, as *G. brevipalpis* and *G. pallidipes* (Isherwood et al., 1961). A preference of *G. swynnertoni* and *G. pallidipes* for Suidae was shown by Glasgow et al. (1958) in Block 9 at Shinyanga. More recently, Langridge (1960) showed that *G. longipennis* preferred rhinoceros over other available animals.

This view is supported by the fact that commonly available animals are not fed on by *Glossina*. The notable example is zebra (*Equus burchelli*), an animal which frequents the feeding grounds of *G. morsitans* in very large numbers and whose blood has never been found in any species of fly. Other animals which are definitely ignored by all tsetse flies as a source of food, except on isolated occasions, include impala, wildebeest (*Gorgon taurinus*), and waterbuck, all occurring in large numbers in many areas from which collections were made.

Nothing is yet known about the adaptability of the fly to a varying host fauna except that *G. pallidipes* survives on warthog in the absence of its more usual host, the bushbuck. In the absence of pigs, *G. morsitans* uses kudu instead of warthog in several areas and hippopotamus in one area in Ankole. It is likely that flies such as *G. morsitans*, the *palpalis* group and possibly *G. swynnertoni* and *G. pallidipes* would quickly adapt to changes in fauna, so that the control of the fly by starvation would entail the elimination of a fairly large number of animal species. These flies seem unlikely to maintain themselves on such species as zebra, wildebeest, topi, waterbuck, impala, gazelles, dikdik, monkeys and baboons, carnivores, birds and reptiles, all of which could remain, provided that no domestic cattle, sheep or goats are available before the fly population is sufficiently reduced. The *palpalis* group, however, could not, it seems, be reasonably controlled in this way without also removing reptiles and the human population. Other species of fly, like those with Group 1 and Group 3 feeding patterns, may be very rapidly affected by the removal of only a few species. Thus *G. fuscipleuris*, *G. austeni* and *G. tabaniformis* may suffer considerably from the disappearance of the suids, and *G. longipalpis* and *G. fusca* by the elimination of bushbuck and buffalo. The elimination of rhinoceros, elephant and buffalo might be sufficient to starve *G. longipennis* and, similarly, the removal of hippopotamus, suids and possibly buffalo and bushbuck, would probably adversely affect *G. brevipalpis* populations.

The extent to which such procedures would succeed in reducing fly population is a matter of speculation, but more experimental work in the field is needed before the validity of these conclusions can be checked.

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RÉSUMÉ

Une enquête portant sur les sources d'alimentation des mouches tsé-tsé a comporté l'analyse de 22 640 repas de sang prélevés sur 15 espèces de glossines. Les mouches ont été capturées en période post-prandiale en différents points de l'Afrique orientale (Kenya, Ouganda, Tanganyika), de la Rhodésie du Nord et du Sud, et de l'Afrique occidentale (notamment du Nigeria).

Afin de déterminer le groupe principal auquel appartenaient les animaux qui avaient servi aux repas sanguins, ces derniers ont été soumis au test de séro-précipitation; ultérieurement, l'épreuve d'inhibition de l'agglutination des érythrocytes traités à l'acide tannique et sensibilisés a permis d'identifier l'espèce.

Les données recueillies font apparaître que chaque espèce de glossines se caractérise par un mode d'alimentation qui lui est propre; réserve faite de quelques variations locales d'importance mineure, cette conclusion s'est avérée exacte dans l'ensemble. Le mode d'alimentation a permis de répartir les glossines en 5 catégories, à savoir celles qui se nourrissent: 1) principalement sur les suidés (*Glossina swynnertoni*, *G. austeni* et *G. fuscipleuris*); 2) sur les suidés et les bovidés (*G. morsitans morsitans*, *G. morsitans submorsitans* et *G. morsitans orientalis*); 3) essentiellement sur les bovidés (*G. pallidipes*, *G. longipalpis* et *G. fusca*); 4) essentiellement sur les mammifères autres que les suidés et les bovidés (*G. longipennis* et *G. brevipalpis*); 5) sur l'homme et la plupart des animaux de la région considérée (*G. palpalis palpalis*, *G. palpalis fuscipes* et *G. tachinoides*).

Le choix d'un hôte donné, quelle que soit la composition de la faune locale, caractérise chaque espèce de glossines. Un certain nombre d'animaux ne servent d'hôtes aux mouches tsé-tsé qu'à titre occasionnel: il en est ainsi du zèbre, du gnou, du kob, et du bubale (*G. morsitans submorsitans* est seule à se nourrir sur cet animal).

L'auteur discute le principe et évalue les chances de succès d'une éventuelle méthode de lutte contre certaines espèces de glossines par l'élimination de leurs hôtes principaux.

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