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Feeding and Other Responses of Tsetse Flies to Man and Ox and their Epidemiological Significance

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This paper describes some responses of male *Glossina morsitans submorsitans* Newstead and *G. tachinoides* Westwood to men or to an ox led by men at Ilorin (8° 30′ N. and 4° 30′ E.) and at Yankari (9° 30′ N. and 10° 30′ E.) in Northern Nigeria. Collections were made in the wet season (June–July) of 1966 and in the dry season (February–March) of 1967. Laboratory work was done at the Nigerian Institute for Trypanosomiasis Research at Kaduna [1].

Ilorin lies near the boundary between the derived savanna and Southern Guinea ecological zones and Yankari is situated in the Sudan zone. For general description of these zones reference may be made to KEAY (1953) or GLOVER (1965). Analysis of the vegetation characteristic of these zones in no way illuminates the results reported. Ilorin is the centre of a densely populated area which, in the absence of man, would lie at the northern limit of the Nigerian closed forest. Yankari supports a savanna vegetation with an abundant population of wild life. Climatically the most conspicuous difference between the two areas appears to be that Ilorin has about 3 dry months a year (i.e. months with less than 1 inch of rain) whereas Yankari usually has 6 dry months (PULLAN, 1962).

At Ilorin *G. m. submorsitans* probably feeds almost entirely on the domestic cattle passing along a trade route about 5 miles from the town, but at Yankari JORDAN (1964) states that 33% feed on warthogs, 17% on buffaloes, another 36% on a variety of Bovidae and the remainder on other animals of which porcupines were the most frequent. This is a normal spectrum of *G. morsitans* diet (WEITZ, 1963).

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Methods

Tsetse were caught by parties moving along a chosen path and stopping at marked stations at 100-yard intervals. Each fly was killed with ethyl acetate, placed in a separate tube and stored in a desiccator. The following information was recorded: (1) species; (2) sex; (3) if teneral or not; (4) bait used (men alone or ox with men); (5) position in which caught: (a) – on ground or low herbage; (b) on bait – ox or man; (c) with proboscis lowered to probe or not; (d) if not, when on man, whether head-up or head-down (JACKSON, 1933); (e) in flight or not. Tsetse are rarely taken in flight unless they are males performing a violent 'dance' around a single female (LAMBORN, 1916). 11 males and 1 female were so caught on one occasion. In addition to the above the time and duration of each catching period was noted and readings, usually at half-hourly intervals, were taken from a whirling psychrometer. Catching parties of men alone usually consisted of a recorder and three catchers. When the ox was in use it and its leader were additional to this party. Different animals (both young bulls) were used in the two seasons but in each season the same animal was used at Ilorin and at Yankari.

In the laboratory, one wing was removed from each fly and measurements were made of wing fray and of the length of the middle section of the fourth longitudinal vein (JACKSON, 1946). This was only done with the dry season collection. The flies were then dried at 100°C and weighed, after which they were immersed in three successive changes of chloroform, together lasting at least 36 hours, and again dried and weighed. This gave the residual dry weight (RDW) and, by subtraction, the weight of chloroform extract, mostly lipids, referred to henceforth as 'fat'. This technique was first used on tsetse by BUXTON & LEWIS (1934). BURSELL (1966), who has greatly refined methods of estimating nutrition reserves in these insects, believes that the fat content of flies sampled by fly-round, i.e. the method used by us, constitutes the most satisfactory single criterion of nutritional state.

Biting rates of G. m. submorsitans

When the ox was in use it was seldom that a tsetse approached one of the men accompanying it. Responses to the party of men alone differed in the two areas. At Ilorin, although tsetse were numerous, very few perched on a man either to probe or to rest. At Yankari flies readily probed man or alighted and remained

inactive on him. The mean intervals between recorded probes, i.e. total catching time divided by number of probes observed, are given in Table 1.

TABLE 1

Intervals between observed probes: *G. m. submorsitans*

Season	Locality	On man	On ox
Dry	Ilorin	105 minutes	12 minutes
	Yankari	12 minutes	11 minutes
Wet	Ilorin	89 minutes	7 minutes
	Yankari	42 minutes	35 minutes

The flies that attempted to feed on man at Ilorin obviously depart from expectation. At Yankari the biting intervals on man and ox are the same (although, as noted above, if the ox was present man was not bitten).

Size of the following swarm

The above distinctions are reflected in the size of the following swarms as compared with the numbers of flies that alight on the bait to feed. This comparison can only be made in the dry season data, since not all following flies were collected in the wet season catches. In Table 2 the contrast between males probing and following men alone or with the ox at Ilorin is very evident. It is less striking at Yankari, but is nevertheless significant, with a chi^2 value of 11.5374.

TABLE 2

G. m. submorsitans. Size of following swarms compared with numbers of male flies probing: Dry season only

Locality	Bait	Numbers of male flies caught	
		In feeding position	In following swarm
Ilorin	Men only	0	162
	Ox and men	33	79
Yankari	Men only	50	83
	Ox and men	42	25

An experiment was carried out at Ilorin during the wet season observations. Three men traversed a route on which they caught, marked and released 53 male and 1 female *G. m. submorsitans* in the following swarm. 3 males and 1 female caught while probing were preserved. 15 minutes later a second party followed with the ox. This party caught only 7 following flies, one of which had been marked. In addition, 21 males and 5 females were taken probing the bull. Of these 5 of the males and 1 female had received a mark from the first party. Subsequent analysis showed that these 5 males had a mean RDW of 7.04 mg and fat amounting to 24.15% of the RDW (cf. Table 3). This experiment supported, if it did not prove, the view that when the bait included the preferred ox host, participation in the following swarm was relatively brief and that some of the flies, on ceasing to follow, alighted on the ox to feed.

Nutrition states of male G. morsitans submorsitans

The mean residual dry weights and the means of fat weights expressed as percentages of their RDW are sorted according to observed behaviour in Table 3. As already noted, in the wet season categories other than probing flies are represented by sample catches only. In the dry season all flies were caught.

It is convenient to simplify the groupings of Table 3 and this is done in Table 4. Three principal types of behaviour are seen in the field. The first includes flies at rest on trees and shrubs. They do not respond to a bait and therefore do not appear in the present study. The second group comprises following males of the sexually appetitive swarms (FISKE, 1920; BURSELL, 1961a). In Table 3 they are divided into flies following the bait in flight near the ground on which they alight when the bait halts; and flies perched on the bait, but not probing, unless they are perched on a man in the 'head-up' position (see below). Flies taken in the nuptial 'dance' are also included with the following swarm. Table 4 shows that the following swarm flies have significantly more fat than the probing flies. The latter illustrate the third behaviour type and Table 4 shows that male *G. m. submorsitans* probing the ox have a mean fat content significantly smaller than that of swarming flies but significantly larger than that of flies probing man. This again supports the suggestion made above that the ox, a preferred host, attracts flies from the following swarm to feed, whereas man either does not do this at all (at Ilorin) or takes longer to do so (at Yankari).

TABLE 3

Mean residual dry weights in mg (RDW) of male *G. m. submorsitans* and means of chloroform extract weights expressed as percentages of RDW, with standard errors, sorted according to observed behaviour

Season, bait and behaviour	Ilorin			Yankari		
	N	RDW ± S.E.	%Fat ± S.E.	N	RDW ± S.E.	%Fat ± S.E.
Wet season 1966						
Men only						
Following on ground	33	7.26 ± 0.117	26.79 ± 2.044	13	7.27 ± 0.176	37.18 ± 3.586
Head down on bait	0	—	—	10	7.45 ± 0.215	34.63 ± 3.634
Head up on bait	4	6.52 ± 0.688	9.17 ± 3.699	11	6.98 ± 0.145	16.94 ± 3.442
Probing bait	5	5.12 ± 0.479	11.22 ± 5.211	13	7.31 ± 0.277	19.29 ± 4.671
Ox (plus men)						
Following on ground	17	7.17 ± 0.188	31.62 ± 3.947	20	7.52 ± 0.124	33.98 ± 2.601
Probing bait	67	6.72 ± 0.148	21.47 ± 1.163	48	7.29 ± 0.106	26.18 ± 1.846
Dry season 1967						
Men only						
Following on ground	151	7.11 ± 0.485	41.15 ± 0.745	39	6.86 ± 0.236	34.79 ± 4.741
Nuptial flight	0	—	—	11	6.83 ± 0.271	30.32 ± 1.716
Head down on bait	11	6.88 ± 0.119	40.38 ± 4.395	31	6.74 ± 0.062	28.12 ± 2.014
Head up on bait	0	—	—	26	6.22 ± 0.189	19.58 ± 2.043
Probing bait	0	—	—	31	6.38 ± 0.182	18.03 ± 1.596
Ox (plus men)						
Following on ground	59	7.04 ± 0.064	42.25 ± 1.109	11	6.36 ± 0.291	38.82 ± 2.738
Perched on bait	20	6.84 ± 0.104	35.89 ± 1.791	11	6.58 ± 0.269	30.29 ± 3.118
Probing bait	33	6.98 ± 0.170	31.19 ± 1.826	38	6.55 ± 0.263	23.99 ± 2.447

Flies perching on bait

JACKSON (1933) showed that *Glossina morsitans* that perched on a man walking through the bush behaved in two ways. Those that rested with the head pointing upwards were 'hungry' and usually proceeded to feed. Those that settled with the head pointing downwards were 'replete' and did not feed. In the present work it was shown that the fat content of 'head-up' flies that did not proceed to feed (while watched for periods of about 15 seconds up to 2 minutes) did not differ from that of those that did (Table 3). The two catgories are combined under the heading of 'feeding posture' in Tables 4 and 5. It was not possible to distinguish these between 'head-up' and 'head-down' flies on the ox and the fat content of those perching on it but not probing tended to have intermediate values. They were included as following swarm flies in Table 4.

The age of probing and following flies

In Table 3 the ranking order of RDW tends to follow that of the percentage fat weights. Full development of tsetse musculature does not occur till after the second meal (BURSELL, 1961b). The smaller RDW of probing flies could therefore be due to a preponderance among them of young flies. Also, as BURSELL (1961a) has shown, tsetse do not digest a complete blood meal at once and the residue of undigested blood in the gut therefore augments the RDW. Mature flies that have used up all the blood meal will give the true and smaller RDW.

G. m. submorsitans males seen to probe man in the dry season at Yankari included 21.7% tenerals; those probing ox 11.6%. The corresponding following swarms included 1.1 and 8.0% tenerals. At Ilorin 50% probing man were teneral and 9.1% probing ox; but no tenerals were taken in the following swarms. The lower RDW of probing flies is, at least in part, due to the presence among them of a high proportion of tenerals. This would be expected if the following swarms are, indeed, sexually appetitive. However, analysis of physiological ageing by the wing fray method gave a different picture. In Table 5 the six wing fray categories of JACKSON (1946) are grouped in pairs excluding tenerals which are shown separately. The 1 + 2 wing fray group is now seen to be less frequent among the flies adopting feeding postures than among the following swarms. This is most marked at Ilorin where there are over four times more of the youngest group among the following

TABLE 4

Chloroform extracted fats of male *G. m. submorsitans* expressed as percentages of residual dry weight

Locality		Wet season			Dry season		
		Feeding posture on man[1]	Probing ox	Following swarm[2]	Feeding posture on man[1]	Probing ox	Following swarm[2]
Ilorin	N	9	67	50	2[3]	33	241
	$\bar{x}$	10.31	21.47	28.43	6.50	31.19	40.95
		± 3.155	± 1.163	± 1.908	± 4.700	± 1.826	± 0.613
	t	3.727	3.272		3.262	5.457	
	P	< 0.001	< 0.01		< 0.01	< 0.001	
Yankari	N	24	48	43	57	38	103
	$\bar{x}$	18.21	26.18	32.51	18.74	23.99	32.25
		± 2.602	± 1.846	± 1.831	± 1.266	± 2.447	± 0.842
	t	2.485	2.122		2.078	4.073	
	P	< 0.02	< 0.05		< 0.05	< 0.001	

[1] 'Feeding posture' includes flies observed probing and also flies perched 'head-up' but not probing.

[2] Flies following both kinds of bait are included.

[3] No males were taken during routine sampling at Ilorin in the dry season. These two, included here to show their very low fat content, had travelled 5 miles with the writer's vehicle from the sampling area to his hotel, where they attempted to feed from him.

TABLE 5

Comparison of wing fray groups of following and feeding *Glossina m. submorsitans*

Place	Behaviour	Tenerals	1+2 (%)	3+4 (%)	5+6 (%)	Totals (%)
Ilorin	Following	0	194 (80.5)	46 (19.1)	1 (0.4)	241 (100.0)
	Feeding posture	4	14 (45.2)	15 (48.4)	2 (6.4)	31 (100.0)
Yankari	Following	2	69 (66.3)	31 (29.8)	4 (3.8)	104 (99.9)
	Feeding posture	12	48 (60.7)	28 (35.4)	3 (3.8)	79 (99.9)
		14	117 (63.9)	59 (32.2)	7 (3.8)	183 (99.9)

flies than of the two older groups; but among the probing flies, the older flies are more numerous than the younger. The chi^2 value of 24.1517 gives a probability less than 0.001 that the distributions are the same. At Yankari no significant difference in the distribution of the three age categories is detectable, although again, the proportion of older to younger flies is greater among those that probed (39.2%) than among those that followed (33.6%).

The obvious explanation is that at Ilorin and perhaps also at Yankari the older males lose their faculty for participation in the sexually appetitive following swarms and, in this respect, behave like the tenerals which have not yet acquired it. Inability with increasing age to participate in sexually appetitive following swarms must influence estimates of population based upon recapture data obtained from tsetse attracted to moving baits. Any errors due to this would, presumably, be eliminated by using stationary baits (see LEGGATE & PILSON, 1961).

It is also evident from Table 5 that the mean physiological age of male *G. m. submorsitans* at Yankari is greater than at Ilorin. This might be expected since at the former place the environment is a natural one, with an abundance of natural hosts, while at Ilorin the tsetse population is supported almost entirely by passing herds of trade cattle.

Glossina tachinoides

A few *G. tachinoides* were captured near streams. Following swarms were not observed and the sex ratio approached equality. Again, behaviour at Ilorin was different from that seen at Yankari. Table 6 combines data from both seasons. At Ilorin the RDW of males feeding on man is very significantly less than that of flies

TABLE 6

Glossina tachinoides males. RDW and percentage fat content, combining data from both seasons

Bait	Ilorin			Yankari		
	N	RDW ± S.E.	%Fat ± S.E.	N	RDW ± S.E.	%Fat ± S.E.
Men only	10	3.21 ± 0.219	13.33 ± 3.266	8	3.40 ± 0.212	27.16 ± 2.723
Ox (and men)	57	3.87 ± 0.120	20.26 ± 1.236	18	3.60 ± 0.168	24.93 ± 2.193

feeding on the ox (t = 6.401) as is the percentage fat content (t = 8.953). At Yankari, however, neither RDW nor fat shows any significant difference between the two baits. BALDRY (1964) has shown that while *G. tachinoides* in the more arid northern savanna may be fairly described as an opportunist feeder, in some southern areas it is highly selective. At Ilorin 99.0% of *G. tachinoides* feed on cattle (LEACH, 1965). The lower RDW of flies feeding on man at that place suggests that this selectivity is not exercised by immature flies. Including figures for both sexes we find that of those attacking the ox only 4.7% were tenerals, but of those attacking man there were 40.0%. The corresponding figures for Yankari, where selection was not apparent, were 21.4 and 19.0%.

Experiments with G. palpalis on host preference

84 *Glossina palpalis* Rob.-Desv. emerged at the N.I.T.R. Laboratory at Kaduna on 27/28 March 1967. Each was placed in a 3×1 inch glass tube closed with gauze and kept without feeding for 24 hours. 55 of them were then given the opportunity, for 2 minutes each, to probe either a man or a goat. All 84 were then fed on the goat. On the next day (when 4 flies had died) 40 were offered the goat and 40 a man, but were not allowed to draw blood. The next day and on subsequent days the trials were repeated until day 6 when 69% of the flies were dead of starvation. Results are given in Table 7.

TABLE 7

Probing trial with *Glossina palpalis* Rob.-Desv. of known age on man and goat

Day	Per cent mortality	Man			Goat		
		Offers	Probes	Per cent probing	Offers	Probes	Per cent probing
0	Emergence						
1	0.0	29	16	55.2	26	20	76.9
	Flies fed after trial on Day 1						
2	4.8	40	16	40.0	40	13	32.5
3	9.5	38	11	28.9	38	21	55.3
4	13.1	36	18	50.0	37	29	78.4
5	No trial						
6	69.0	12	10	83.3	14	14	100.0

Comparing numbers of attempts to probe man or goat on each day in 2 by 2 tables, we get significant chi² values on days 3 and 4 (4.372 and 5.234) but not on other days. These are the days (the 2nd and 3rd after the only feed) when feeding might be expected to occur in nature. At these times host discrimination is marked, but teneral flies and flies near to death by starvation did not exercise selection. No difference was detected in the behaviour of males and females.

An earlier but less complete experiment used 50 *G. palpalis* mature females from laboratory stock which had received a routine feed from goat on the day before the experiment began. Otherwise the procedure followed was the same as that already described from day 2 onwards. The mean number of probes on the goat as compared with 1 probe on the man were, on successive days, from day 2 to day 5: 1.67, 2.75, 2.17, 1.57, 1.14. Again, it is evident that discrimination between man and goat is greatest on days 3 and 4 after the meal on day 1 and that on days 4 and 5, when surviving flies are very 'hungry' this discrimination is not exercised so fully.

A small experiment was carried out at Yankari during the wet season. 60 male *G. m. submorsitans* were collected from a following swarm behind a party of men between 1700 and 1800 hours. Each fly was tubed separately on collection and on the next morning 45 were still vigorously alive. 22 were offered a feed on a man and 7 probed in the two minutes allowed. The remaining 23 were offered a feed on the bait ox and 15 probed within 2 minutes. They were not allowed to ingest any blood. 24 hours later only 12 were alive. Of the 6 offered man, 3 probed and of the 6 offered the ox, 4. Again it appeared that the preference shown for the ox was diminished when the flies were starved.

The teneral catch among probing tsetse

The conclusions from these experiments are supported by analysis of catches of teneral flies in the dry season. (No age criteria were recorded in the 1966 wet season survey.) If man is less acceptable as food than the ox or cannot so easily provoke a feeding response unless flies are immature or starving, the teneral percentage among flies feeding on man ought to be highest in places where discrimination against man is most marked. In Table 8 both male and female catches are combined, principally to augment the numbers of flies actually seen to probe man at Ilorin. The very high teneral percentage of both *G. m. submorsi-*

TABLE 8

Teneral percentages of tsetse (both sexes) feeding from man and ox

		G. m. submorsitans		*G. tachinoides*	
		No. caught	% teneral	No. caught	% teneral
Ilorin	Probing man	5	40.0	6	66.7
	Probing ox	36	8.3	105	4.8
Yankari	Probing man	48	22.9	16	18.8
	Probing ox	61	14.8	21	19.0

tans and *G. tachinoides* feeding on man as compared with that observed among flies feeding from the ox at Ilorin is a strong indication that mature tsetse very rarely attack man at that place. On the other hand, at Yankari there is no difference in the proportion of teneral *G. tachinoides* feeding on man and on ox and the discrimination between the two hosts by *G. m. submorsitans* would not be noticed if not expected. (The smaller proportion of tenerals among ox-feeding flies at Ilorin as compared with Yankari is, perhaps, another indication of a somewhat unfavourable environment at the former place.)

Discussion

The explanation for the small proportion of females caught by a moving party of men and for the formation of the following male swarm was given long ago (LLOYD, 1912; LAMBORN, 1916; FISKE, 1920). NASH (1933) suggested that female *G. morsitans* found man distasteful in comparison with the ox. JACKSON (1933) observed posture differences among flies perched on men and correlated them with hunger. LEGGATE & PILSON (1961) stressed the need to take account of behaviour in density sampling. BURSELL (1961a) distinguished between attraction of males to moving objects and to food hosts. The former led to formation of the sexually appetitive swarm of males with high fat content. Males ceased to participate in these swarms after food reserves had fallen below a certain level. They then moved only in response to the attraction of a food host. The present study is based upon the idea that measurement of responses of tsetse to two different hosts (man and ox) in different environments may lead to understanding of the different responses to man exhibited by the same species of tsetse in different areas.

That this is a question of epidemiological importance was first realized by FISKE (1920), but little was done until NASH (1948) distinguished between different types of man/fly contact on *G. palpalis* infested rivers in Nigeria. PAGE & MACDONALD (1959) measured the recapture rate of the latter species at water holes in Northern and Southern Nigeria and showed that in the north it was significantly greater than in the south. JOHNS (1958) demonstrated that *G. pallidipes* that had been marked and released became increasingly recapturable with advancing age (or, perhaps, with each successive recapture). The observation suggested that some individuals in the population might be regarded as anthropophilic and so have a greater availability (GLASGOW, 1963) towards catchers than the average for the whole population. *G. pallidipes* is notably a tsetse that exhibits a great variety of behaviour totowards man. In spite of continuous entomological observation from 1916 onwards, it escaped detection in the Zambezi valley until 1942 (CHORLEY, 1943), yet APTED, ORMEROD, SMYLY, STRONACH & SZLAMP (1963) suggest that it may have an important role in maintaining endemic sleeping sickness in that area. It was a principal vector of the same disease in Uganda in 1940 (MACKICHAN, 1944). In the moister forests of that country it will feed from man in the wet season, but is much less ready to do so in the dry.

The present paper brings further evidence that tsetse may show quite different patterns of feeding behaviour in different areas. At Yankari, in the north of Nigeria, a man walking through the bush is bitten as frequently by *G. m. submorsitans* as is an ox, provided he is not in the presence of the latter. At Ilorin, south of the Niger River, although *G. m. submorsitans* is very abundant on the cattle, route, it so rarely attacks man that the infection risk must be very small. Moreover, of those flies that do feed on man a high proportion are tenerals and therefore are free of trypanosomes.

It is evident that we are dealing with the same phenomena as have already been demonstrated by another technique by BALDRY (1964) in respect of *G. tachinoides* and probably by PAGE & MACDONALD (1959) in respect of *G. palpalis*. The most remarkable feature of BALDRY's work is not that the peridomestic tsetse in derived savanna villages have become habituated to feeding on domestic animals, but that in doing so they have, to a great degree, lost the readiness to feed on man which, in northern areas, makes them so important as vectors of epidemic sleeping sickness. *Glossina morsitans submorsitans* behaves in a similar way. Where it has adapted itself to dependence upon domestic cattle it has, at the same time, lost is propensity to feed on man, except when it is immature and taking its first meal or, if older, has failed to obtain

a meal within the normal period and is approaching death by starvation. BALDRY (l. c.) has drawn attention to the epidemiological significance of his results, especially in the light of the demonstration by WATSON (1962) that domestic pigs are able to support infections of *gambiense*-type strains of *T. brucei*. The contrast between the endemic *gambiense*-type infections in the Niger-Benue trough and the epidemic foci further north in Nigeria, which are especially associated with the Chad basin, has been described by DUGGAN (1962). That author's suggestion that *rhodesiense*-like strains which have occurred from time to time in these northern foci might have been derived from the wild game by transmission through *G. m. submorsitans* receives support from the work here described, which also shows why such infections could not easily appear on the southern borders of the *G. m. submorsitans* fly-belts.

One purpose of this paper is to suggest that a new approach to the epidemiological role of tsetse can be made by careful observation and recording of the behaviour exhibited by each fly caught and the subsequent use of simple nutrition analysis in the laboratory. The use of a favoured animal host in all experiments will provide the standard against which differing responses to man may be measured. An extension of the method of simultaneous comparisons of responses to two hosts might also lead to elucidation of the causes of some animals being favoured hosts of tsetse while others are neglected (WEITZ, 1963).

Conclusions

1. *Glossina morsitans submorsitans* Newstead rarely approach to man to feed at Ilorin in the derived savanna zone of Nigeria, though they readily feed from an ox. At Yankari in the more arid Sudan zone, biting rates on man and ox are the same. Man is not bitten when accompanied by the ox.

2. During the dry season in Ilorin the whole male catch, when man alone provided the bait, was taken from the following swarm: but with the ox in use only 70.5% of males were followers. At Yankari the difference was less marked, but still significant.

3. Nutrition state was measured by fat content (chloroform extracted lipids) expressed as a percentage of the residual dry weight. In both places following swarm flies had significantly higher fat contents than those that probed the ox and the latter, in turn, had a higher fat content than those that probed man.

4. The two probing postures on man, described by JACKSON (1933), were observed at Yankari and it was confirmed that flies

that adopted the 'head-up' position, but did not attempt to probe, were as deficient in fat reserves as those that began to feed.

5. Residual dry weights (RDW) tended to be smallest among flies that attacked man to feed or perch 'head-up'. In part this was attributable to the high proportion of tenerals among those flies that fed on man.

6. Wing fray analysis, however, showed that younger individuals were few in number among flies that probed as compared with flies in the following swarm. This, though apparent at both places, was only significantly so at Ilorin. It is supposed that flies in the older age groups either do not participate in the following swarm, or do so for a shorter time than younger flies. Tenerals do not join in the following swarm.

7. At Ilorin *Glossina tachinoides* feeding on man included more tenerals than those feeding on ox and were significantly less well supplied with fat. At Yankari no differences were detectable in catches on the two baits.

8. An experiment with laboratory reared *G. palpalis* showed that on the second and third day after a feed on goat, this animal was more attractive as a food host than man, but that this discrimination was not shown by teneral flies nor by flies that were approaching death by starvation.

9. The epidemiological significance of different feeding patterns exhibited by the same species of *Glossina* in different places is discussed and it is suggested that the method used of precise recording of behaviour of each fly caught and its subsequent nutrition analysis in the laboratory, opens up a new field for epidemiological investigation.

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Zusammenfassung

Die vorliegende Arbeit geht von dem Gedanken aus, daß das Studium des Verhaltens von Tsetse-Fliegen gegenüber verschiedenen Wirten (Mensch und Rind) in verschiedener Umgebung zu einem besseren Verständnis des unterschiedlichen Verhaltens einer gegebenen Tsetse-Art gegenüber dem Menschen in verschiedenen geographischen Regionen führen könnte. Bei Yankari, in Nord-Nigeria, wird der Mensch von *Glossina morsitans submorsitans* so häufig ange-

gangen wie das Rind, vorausgesetzt, daß er sich nicht in dessen Gegenwart befindet. Bei Ilorin, südlich vom Niger, greifen *G. m. submorsitans,* obwohl sie an der Viehstraße sehr häufig sind, den Menschen so selten an, daß die Gefahr der Schlafkrankheitsübertragung sehr gering sein muß. Dazu kommt, daß ein hoher Prozentsatz der Fliegen, welche Menschenblut aufnehmen, jung und infolgedessen von Trypanosomen frei sind.

Beobachtungen des individuellen Verhaltens, verglichen mit Messungen des Fettgehaltes der Fliegen sowie mit dem Abnützungszustand ihrer Flügel, führen zur Ansicht, daß *G. m. submorsitans,* wo diese Art für die Nahrungsaufnahme vom Rind abhängig wurde, die Gewohnheit den Menschen zu stechen, verlor. Eine Ausnahme bilden einerseits junge Männchen, die ihre erste Blutmahlzeit aufnehmen, andrerseits ältere Fliegen, welche dem Hungertod nahe sind. Beobachtungen und Versuche an *G. tachinoides* und *G. palpalis* führen zu ähnlichen Folgerungen wie mit *G. m. submorsitans.*

Um die epidemiologische Bedeutung von Tsetse-Fliegen zu ermessen, dürften sorgfältige Beobachtungen des individuellen Verhaltens in Verbindung mit einfachen Untersuchungen über den Ernährungszustand von großem praktischem Nutzen sein.

Résumé

Le présent travail part de l'idée qu'une étude du comportement de la mouche tsétsé vis-à-vis de deux hôtes différents, l'homme et le bœuf, rencontré simultanément dans des alentours différents, peut mener à une meilleure compréhension des attitudes divergentes d'une même espèce de tsétsé confrontée à l'homme dans deux régions différentes. Sur le territoire de Yankari, dans le nord du Nigeria, *Glossina morsitans submorsitans* s'attaque aussi souvent à l'homme qu'au bœuf, à moins que les deux ne soient en présence l'un de l'autre. Dans la région d'Ilorin, au sud du Niger, l'homme est rarement piqué, bien que *G. m. submorsitans* soit très abondante dans les parages de la route de bétail. Il en résulte que le risque d'infection y est extrêmement faible, d'autant plus que bon nombre de mouches qui se nourrissent de sang humain sont des mâles nouvellement éclos et par conséquent non vecteurs de trypanosomes.

L'observation minutieuse du comportement de chaque mouche capturée, l'évalution de sa teneur en lipides et le test de l'usure des ailes mènent à la conclusions que là où *G. m. submorsitans* s'est habituée au sang des animaux domestiques, elle a perdu en même temps la tendance de s'attaquer à l'homme. Exception font les mâles jeunes qui prennent leur premier repas sanguin et les mâles plus âgés qui sont près de mourir par inanition.

Des expériences avec *G. tachinoides* et avec *G. palpalis* tendent à appuyer les conclusions tirées pour *G. m. submorsitans.*

Nous voyons donc la possibilité d'une nouvelle précision du rôle épidemiologique de la mouche tsétsé, d'un côté par une observation méticuleuse du comportement individuel et de l'autre par une simple analyse du stade de nutrition.