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The nutritional state of male tsetse flies, *Glossina pallidipes*, at the time of feeding

MATTHEW BAYLIS* and CHARLES O. NAMBIRO Kenya Trypanosomiasis Research Institute, Kikuyu, Kenya, and *Tsetse Research Laboratory, University of Bristol, U.K.

Abstract. The feeding intervals of tsetse flies have been estimated from the nutritional state of flies caught in traps. However, such estimates have been disputed on the grounds that traps catch a biased, hungry sample of the flies which are seeking hosts and will feed. In this paper we present data on the nutritional state of tsetse flies caught approaching and feeding on oxen. Individual oxen were surrounded with an incomplete ring of electric nets which caught *Glossina pallidipes* Austen that were approaching, departing unfed and departing fed from an ox. Non-teneral males caught in this way were analysed for their fat and haematin contents. The feeding interval was estimated from a comparison of the frequency distributions of the pre- and post-feed haematin contents of the flies which fed. The former was not measured directly, and was deduced from the frequency distributions of the haematin contents of the male flies caught approaching and departing unfed from the oxen, since it is assumed that the departing unfed and fed flies together form a sample of the approaching flies. There was no difference between the frequency distributions of haematin contents of flies caught approaching and departing unfed, and therefore the pre-feed haematin contents of the males which fed should have the same frequency distribution. Comparison of this distribution with that of the post-feed haematin contents of the males which fed indicated that the majority of male *G. pallidipes* were returning to feed after digesting on average 1.4 log haematin units of the previous bloodmeal. From data published elsewhere, this corresponds to a mean feeding interval of 42–60 h. There was a strong, linear, negative relationship between the fat contents of males and their probability of taking a bloodmeal, suggesting that fat content is important in determining the feeding behaviour of tsetse flies.

Key words. Tsetse, *Glossina pallidipes*, nutritional state, haematin, fat.

Introduction

Recent mathematical models have demonstrated that the feeding interval of tsetse flies (*Glossina* spp.) is one of the most important parameters in the epidemiology of African trypanosomiasis (Milligan & Baker, 1988; Rogers, 1988). Accurate measurement of the feeding interval is vital, therefore, if the epidemiology of trypanosomiasis under natural conditions is to be understood. Estimates of the feeding interval have been based on measurements of the nutritional state of field-caught flies but such estimates have been disputed on the grounds that the methods used to catch the tsetse flies give biased samples.

Changes in the fat and haematin contents of tsetse flies after feeding have been studied under laboratory conditions (Bursell, 1963; Langley, 1966; Brady, 1975). After ingestion of a bloodmeal, the haematin content of the tsetse flies is high. As the bloodmeal is converted to fat and haematin is excreted, the haematin content falls and the fat content rises. Later, the rate of fat usage exceeds the rate of fat synthesis and both haematin and fat levels fall. The rate of decline in haematin content after a bloodmeal is linear when expressed logarithmically (Randolph & Rogers, 1978). Therefore, assuming that tsetse flies have low fat and haematin contents immediately prior to feeding, the nutritional state of tsetse flies caught

Correspondence: Dr M. Baylis, Tsetse Research Laboratory, University of Bristol, Langford, Bristol BS18 7DU, U.K.

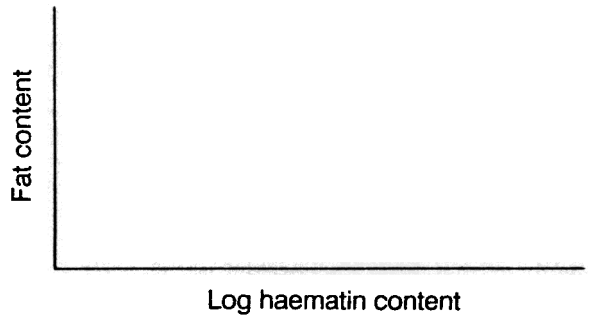

Fig. 1. The relationship between fat and haematin levels of male tsetse flies caught in the field (from Randolph & Rogers, 1978).

in the field should fall somewhere on the graph shown in Fig. 1, the position determined by the time since feeding. Such an effect has been reported for several species of tsetse (Randolph & Rogers, 1978, 1981; Randolph *et al.*, 1991a, b) sampled in the field using traps; from the frequency distributions of haematin content, a feeding interval of approximately 3–4 days has been estimated for several species of tsetse (Randolph & Rogers, 1978; Randolph *et al.*, 1991a, b).

This interpretation of fat/haematin curves has been challenged by Langley & Stafford (1990) and Langley & Wall (1990), who demonstrated that the tsetse flies caught in traps have lower fat contents on average than those which approach such traps but do not enter. They argue that many flies which approach but do not enter traps would feed if given an opportunity to do so, and therefore the flies caught in traps are, with respect to fat content, a biased sample of those that would feed on a host. If this is correct, and fat content is related to haematin content, it follows that a feeding interval calculated from trap catches is an over-estimate.

A better approach to estimating feeding intervals is to examine the fat and haematin contents of tsetse flies at the time of feeding on a host. In this paper we present data from Galana Ranch, south-eastern Kenya, on the nutritional state of male *G.pallidipes* Austen which were caught either approaching an ox before having an opportunity to feed, departing from an ox after feeding, or departing from an ox without having fed.

Materials and Methods

Galana Ranch is a 6000 km^2 cattle ranch in south-eastern Kenya (39–40°E, 3–4°S), bordered to the west by Tsavo East National Park, and to the south by the Sabaki River. The ranch is semi-arid with abundant *G.pallidipes* in the wetter eastern zone. The experimental site was on the eastern edge of the ranch which is covered with dense coastal vegetation.

A female ox, from a breeding herd of Orma Boran cattle, was placed in a crush built in a clearing in the scrub. Six electric nets (Vale, 1974) were placed around the crush in such a way that one third of the circumference of a ring was covered. Each electric net comprised a 1.5 × 1.5 m square of fine black netting, covered on both sides with a grid of electrocuting wires. *G.pallidipes* which collided with the nets were killed or stunned (although some may have escaped: Packer & Brady, 1990) and fell into 2 × 1 m trays containing water and detergent, two of which were placed at the base of each net. Tsetse flies caught on the outside of each net (i.e. away from the crush) were assumed to have been caught approaching the ox. Those caught on the inside of each net were assumed to have been caught departing from the ox. The validity of these assumptions is considered later in the Discussion. The *G.pallidipes* were classified as fed if red blood was clearly visible through the wall of the abdomen. Some fed flies were caught on the outside of the electric nets. These are assumed to have circled the devices before colliding, and have therefore been lumped with the fed flies caught on the inside of the nets.

Where more than five unfed, non-teneral male *G.pallidipes* were caught on one side of an electric net on one day, five were randomly selected for nutritional analysis. All fed male *G.pallidipes* were analysed except for a small number that were trapped in the electric wires and destroyed. Flies selected for nutritional analysis were dried at 55°C and sent to the Tsetse Research Laboratory, U.K., where their fat and haematin contents were measured using the methods described by Ford *et al.* (1972) and Langley *et al.* (1990). Teneral males were not analysed because they contain no haematin. Female *G.pallidipes* were not analysed because fat contents of females are of little value without knowledge of their stage in the pregnancy cycle (Randolph & Rogers, 1978).

The experiment was run on 35 days, with different oxen each day, between July 1991 and March 1992. Thirty of the 35 days were during the months of August, December and February. On each day the experiment was run from 16.00 to 18.00 hours. Temperature (mean of daily maximum and daily minimum), humidity (at 15.00 hours) and rainfall were measured with an Automatic Weather Station (E.L.E., Hemel Hempstead, U.K.), stationed 30 km from the experimental site.

Results

A total of 806 male *G.pallidipes* were caught on the 35 days of the experiment, including 160 fed individuals (Table 1). Of the fed flies, twenty-five (15.6%) were

Table 1. The catches of male *G.pallidipes* on the inside and outside of the electric nets during the experiment, and the numbers of non-teneral males analysed for nutritional state.

	Unfed		Fed	
	Inside	Outside	Inside	Outside
No. caught	265	381	135	25
No. analysed	222	290	153	

caught on the outside of the electric nets. Lumping these with the fed flies caught on the inside of the nets gives catches of approaching and departing flies of 381 and 425 flies respectively. These numbers differ significantly from those expected if the electric nets randomly sample one third of approaching and departing flies (expected outside catch = 484; expected inside catch = 322; Chi-square = 54.4, df = 1, $P < 0.001$).

Of the 806 flies caught, a total of 665 were analysed for their nutritional state (Table 1). There was no difference in the mean log haematin content of male *G.pallidipes* caught approaching an ox, and that of flies caught departing unfed (Table 2). Inevitably, flies which fed had a significantly higher mean log haematin content than that of flies which had not fed because of the bloodmeal just taken. It is not possible to ascertain directly the pre-feed haematin content of the flies which fed. However, since the fed and departing unfed flies together comprise a sample of the approaching flies, an indication of the pre-feed haematin content of the flies which fed is obtained by comparing the frequency distributions of the log haematin contents of the approaching and departing unfed flies. There was no difference between these distributions (Fig. 2; Kolmogorov-Smirnov test for goodness of fit, $D = 0.02$, ns), suggesting that the pre-feed log haematin content of the flies which fed had a similar frequency distribution.

75% of approaching and departing unfed flies had a log haematin content between 0.2 and 1.0 µg (Fig. 2). If the frequency distribution of pre-feed log haematin content of the flies which fed was similar to that of the approaching and departing unfed flies, it follows that a similar percentage of the flies which fed had a pre-feed log haematin content within this range. Immediately after feeding, a similar proportion (82%) of the fed flies had a log haematin content between 1.6 and 2.4 µg. Assuming that this bloodmeal size is representative of those obtained from the previous host, it appears that the majority of non-teneral male *G.pallidipes* returned for a bloodmeal after digesting on average 1.4 µg of log haematin units from the previous bloodmeal. This corresponds to the digestion of 96% of the haematin in the previous bloodmeal.

The mean fat content of non-teneral male *G.pallidipes* which fed on oxen was significantly lower than that of flies approaching the oxen (Table 2). Consequently, since the fed and departing unfed flies comprise a sample of the

Table 2. The mean and standard deviations of the fat and haematin contents of male *G.pallidipes* caught approaching an ox, departing unfed from an ox, or departing after having fed. Means were compared with unpaired *t*-tests. Means with the same letter are not significantly different at $P < 0.05$.

	Approaching ($N = 290$)		Departing ($N = 222$)		Fed ($N = 153$)	
	Mean	SD	Mean	SD	Mean	SD
Fat (mg)	3.37[a]	1.71	3.63[a]	1.70	2.53[b]	1.50
$\log_{10}$ Haematin	0.69[c]	0.43	0.70[c]	0.44	1.86[d]	0.39

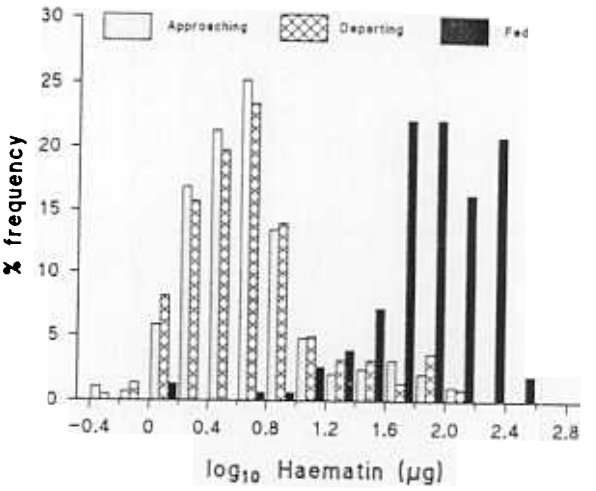

Fig. 2. Frequency distribution of the haematin content of male *G.pallidipes* caught approaching an ox, departing unfed from an ox and departing fed from an ox. Tick marks on the *x* axis delimit a range of haematin contents, from −0.4 to −0.2, −0.2 to 0, etc.

approaching flies, the mean fat content of departing unfed flies was expected to be greater than that of approaching flies. This was, indeed, the case, although the difference was not quite significant ($t = 1.69$, df = 476, $0.05 < P < 0.1$).

To allow a more precise comparison of the fat contents of the approaching and departing unfed flies, fat content was plotted against log haematin content (Fig. 3). For presentation, means ± standard errors of fat were plotted against ranges of haematin content, which revealed curves similar to those found by Randolph & Rogers (1978). These authors found significant regressions between fat and log haematin content for low to medium levels of log haematin. Considering our data for individual flies, there were significant regressions between 0.2 and 1.0 µg log haematin units for both approaching and departing unfed flies (approaching flies: $y = 2.32 + 1.72x$, $F_{1,222} = 9.6$, $P < 0.005$; departing unfed flies: $y = 2.95 + 1.34x$, $F_{1,161} = 4.4$, $P < 0.05$). It should be noted that although these regressions were significant, over the range given above only a very small percentage of the variance in fat content was accounted for by variation in log haematin content (approaching flies, $r^2 = 4.2\%$; departing flies, $r^2 = 2.7\%$).

The two regression lines did not differ significantly in slope ($F_{1,381} = 0.207$, ns) and therefore ANCOVA was used to test for difference in intercept. The intercept for departing flies was significantly greater than that of approaching flies ($F_{1,382} = 5.74$, $P < 0.02$), demonstrating that over a wide range of haematin contents departing unfed flies had greater fat contents than approaching flies.

The percentage of fed flies, out of all those caught departing from the ox, was calculated for different levels of fat content. Flies with fat contents above 7 mg were excluded because there were too few (< 10) to give reliable estimates. There was an approximately linear decline in the probability of a fly feeding with increase in its fat content (Fig. 4; correlation coefficient = −0.96, $P < 0.01$).

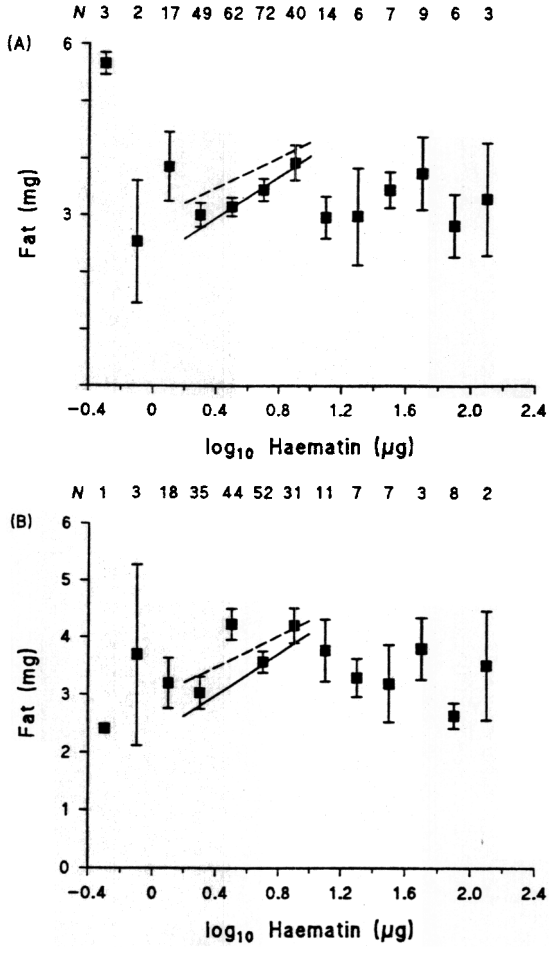

Fig. 3. Fat content plotted against haematin content of male *G.pallidipes* caught (A) approaching an ox and (B) departing unfed from an ox. Vertical lines are standard errors of the mean fat contents. Diagonal lines are the regression lines of fat content on log haematin content for log haematin contents between 0.2 and 1.0 (solid line = approaching flies; broken line = departing flies). *N* is the number of flies in each category. Tick marks on the *x* axis delimit a range of haematin contents, from −0.4 to −0.2, −0.2 to 0, etc.

Of the 665 male *G.pallidipes* analysed for nutritional state, 96% were caught in the months of August, December and February. August was cool, with some rain and high humidity. December was hotter with less rainfall, but with high humidity. February was hotter still, with no rainfall at all and low humidity (Fig. 5).

In order to ascertain whether the fat contents of the approaching and fed flies differed among these months, the fat contents of flies caught during August, December and February were analysed by ANOVA with 'month' and 'approaching/fed' as factors. The fat contents of approaching and fed flies differed significantly among

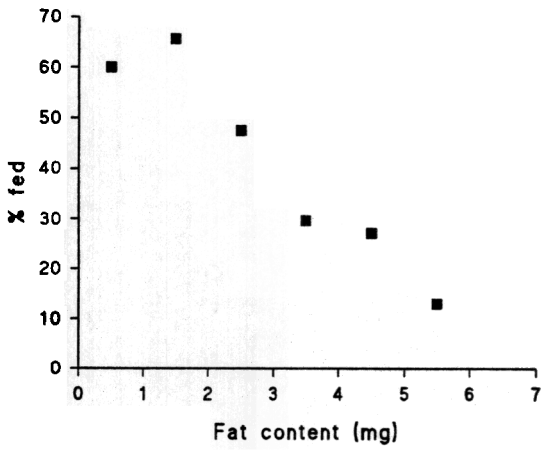

Fig. 4. The percentage of male *G.pallidipes* which had fed out of all those caught departing from an ox, for different levels of fat content. Tick marks on the *x* axis delimit a range of fat contents, from 0 to 1, 1 to 2, etc.

months, with lower fat contents in August than in December or February (Table 3). In all three months the fat content of approaching flies was greater than that of fed flies. There was no interaction between month and whether flies were approaching or fed on fat content.

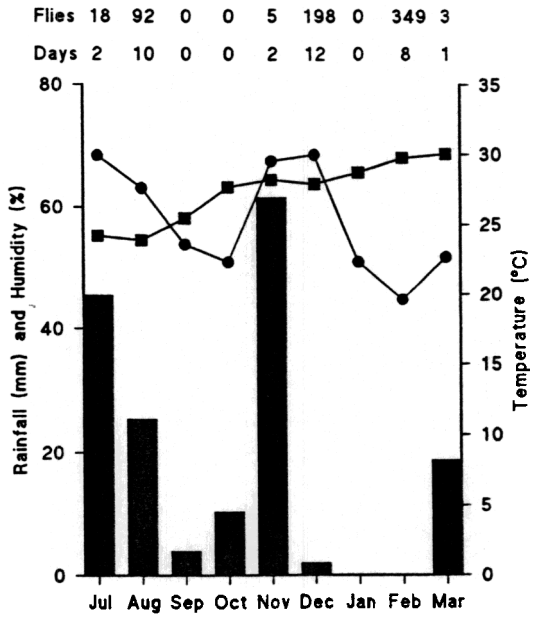

Fig. 5. The rainfall (histogram), humidity (circles) and temperature (squares) at Galana Ranch during the course of the experiment. 'Days' refers to the number of days in each month on which the experiment was performed. 'Flies' refers to the number of male *G.pallidipes* caught each month which were analysed for their fat and haematin contents.

Table 3. The fat contents of non-teneral, male *G.pallidipes* caught approaching oxen or having fed on an ox, at different times of year.

	Fat (mg)					
	Approaching			Fed		
Month			*N*	Mean	SD	*N*
Aug 1991	2.81	1.61	46	1.99	1.17	15
Dec 1992	3.45	1.6	92	2.33	1.44	41
Feb 1992	3.46	1.75	135	2.73	1.53	94

ANOVA
Effect of approaching/fed: df = 1, F = 19.32, $P < 0.001$
Effect of month: df = 2, F = 3.59, $P < 0.05$
Effect of interaction: df = 2, F = 0.57, ns

A cursory inspection of Table 3 suggests that the percentage of flies which fed increased substantially from August to February. This effect is largely attributable to the greater amount of sub-sampling of unfed flies for nutritional analysis as the total catch increased towards February. Considering data of the total number of flies caught in the different months, the proportion of fed flies out of all those assumed to have been departing (inside catch + fed individuals in outside catch), was 15/52 = 0.29 in August, 41/112 = 0.37 in December and 100/251 = 0.40 in February (Chi-square = 2.28, df = 2, ns).

The haematin contents of approaching and fed flies caught in August, December and February were also analysed by ANOVA with 'month' and 'approaching/fed' as factors. The haematin contents of approaching and fed flies differed significantly among months, with the highest haematin contents in December (Table 4). From August to February there was a small, but not significant, decline in the difference between the haematin contents of the approaching and fed flies (Table 4).

Table 4. The log haematin contents of non-teneral, male *G.pallidipes* caught approaching an ox or having fed on an ox, at different times of year.

	Log haematin (μg)						
	Approaching			Fed			Difference
Month	Mean	SD	*N*	Mean	SD	*N*	between means
Aug 1991	0.622	0.310	46	1.911	0.345	15	1.289
Dec 1992	0.762	0.490	92	1.988	0.364	41	1.226
Feb 1992	0.644	0.423	135	1.840	0.317	94	1.196

ANOVA
Effect of approaching/fed: df = 2, F = 610, $P < 0.001$
Effect of month: df = 1, F = 4.21, $P < 0.02$
Effect of interaction: df = 2, F = 0.27, ns

Discussion

Clear interpretation of the data presented here relies on the assumption that flies caught on the outside of the electric nets were approaching the oxen and flies caught on the inside of the electric nets were departing from the oxen; yet in this experiment 15.6% of fed flies were caught on the outside of the electric nets. While these fed flies were easily lumped with those caught on the inside of the electric nets, it is likely that unfed flies also circled the nets to some extent and thus that approaching and departing unfed flies were partially mixed. Such mixing would lessen the probability of detecting differences between approaching and departing unfed flies where such differences exist. A predicted difference between the fat contents of approaching and departing unfed flies was statistically significant when analysed by ANCOVA, and it approached significance when analysed by *t*-test, which suggests that the effect of mixing of unfed flies was small. Because of mixing, any difference between approaching and departing unfed flies should be considered to be a minimum.

The total numbers of flies caught on the inside and outside of the electric nets differed considerably from the expected numbers. If the effect of circling of electric nets was small, and since there is no *a priori* reason to expect approaching flies to circle more or less than departing unfed flies, a likely explanation is that some flies circled the ox and thereby increased the probability of being caught on the inside of an electric net.

The only available data on bloodmeal excretion rates in tsetse in the field come from *G.m.morsitans* caught in the field and kept in the laboratory (Langley, 1966, 1967). The decline in the amount of remaining bloodmeal of *G.m.morsitans* with time has been presented graphically by Randolph & Rogers (1978: Fig. 1b). Since the average meal size of male *G.m.morsitans* is approximately 100 μg haematin, the relationship between haematin content and time since feeding can be expressed as the percentage of remaining bloodmeal with time since feeding (Langley & Wall, 1990; Fig. 5). Assuming that the rate of decline in percentage of remaining bloodmeal is the same for male *G.pallidipes* and male *G.m.morsitans*, the feeding interval of male *G.pallidipes* caught in the experiments presented here can be estimated from Fig. 5 in Langley & Wall (1990).

Our data suggest that the majority of male *G.pallidipes* fed on oxen after digesting on average 96% of the haematin from their previous bloodmeal. This corresponds to a feeding interval of 42–60 h (Langley & Wall, 1990: Fig. 5). This estimate must, however, be treated with caution. First, the rate of decline of decline of percentage of remaining bloodmeal may not be the same for male *G.pallidipes* and male *G.m.morsitans*. The mean wing vein length of male *G.pallidipes* is >10% larger than that of male *G.m.morsitans* (Randolph *et al.*, 1991a), and larger animals are expected to digest a smaller proportion of ingested food per unit time (Sibly & Calow, 1986: p. 36). Second, the rate of digestion of field-caught, laboratory-held flies may be different from that of wild flies. Third, the estimate is a mean, but it is not possible to

calculate its variance, because the observed variation in haematin content may have arisen from variation in time since feeding, or from variation in the size of the previous bloodmeal. Other workers have assumed a constant bloodmeal size for tsetse flies of a given sex and species, based on the estimates of Taylor (1976), and variation in the haematin content of such flies has been taken to represent variation in time since feeding (Langley & Wall, 1990; Randolph & Rogers, 1978, 1981; Randolph *et al.*, 1991a, b). Here, we found large variation in the bloodmeal size that the male *G.pallidipes* took on oxen, such that the variance of log haematin content of approaching and fed flies were almost identical (Table 1). If it is assumed that approaching flies which had higher levels of haematin took larger previous bloodmeals, while approaching flies with lower levels of haematin took smaller previous bloodmeals, then the majority of flies may have returned after digesting 96% of the previous bloodmeal and the estimate of a feeding interval of 42–60 h may apply to the majority of flies. However, the assumption may not be valid. Considering that the majority of approaching flies had log haematin contents between 0.2 and 1.0 μg, and the majority of fed flies had log haematin contents between 1.6 and 2.4 μg, if the assumption is not valid the majority of flies may only be said to have returned after digesting between 0.6 (1.6 minus 1.0) and 2.2 (2.4 minus 0.2) μg of log haematin, corresponding to 75–99.4% of the previous bloodmeal. This allows feeding intervals within a range from 18–36 to 60–78 h, but, as before, with a mean of 42–60 h (Langley & Wall, 1990: Fig. 5). It is not possible to test the validity of the assumption from the data presented here. Large variation in feeding interval may account for the small percentage of variance in fat content explained by log haematin content in the fat/haematin curves of the approaching and departing unfed flies (Fig. 3). However, this could also result from variation in other factors, such as bloodmeal size and rate of digestion, or from the accumulation and depletion of fat over several feeding cycles (Bursell, 1966).

The results presented above suggest that the tsetse flies approaching an ox had digested on average 1.4 μg log haematin units of the previous bloodmeal. There is no evidence for an effect of haematin content on whether or not flies that arrive at an ox take a bloodmeal. However, this possibility cannot be discounted because there was probably some degree of mixing of the approaching and departing unfed flies. Flies with lower fat contents, however, were more likely to feed than those with higher fat contents. This conclusion has also been reached from examination of fat/haematin curves (Randolph & Rogers, 1981). Similarly, *G.pallidipes* with lower fat contents are more likely to enter traps than those with higher fat contents (Langley & Stafford, 1990; Langley & Wall, 1990). These authors argue that many of the higher-fat content flies which approach traps but do not enter would feed if given an opportunity to do so, and therefore trap catches do not fully represent the sub-population of field flies which seek bloodmeals. Since many of the higher-fat content flies which approached an ox did not feed, this argument does not appear to be valid. The question of whether trap catches represent the feeding sub-population of field flies can only be resolved by comparison of flies caught in traps and feeding on hosts.

The approximately linear decline in the proportion of flies which fed as their fat content increased suggests that there is not a threshold fat content at which tsetse flies feed. Instead, a lower fat content may increase the probability of feeding, perhaps by increasing the persistence with which a bloodmeal is sought at a host.

There was an increase in the mean fat content of the approaching tsetse flies from August 1991 to February 1992. This increase could have resulted from seasonal changes in the nutritional state of the flies in the field, perhaps as a result of changes in the ages of the flies and hence the amount of fat accumulated over feeding cycles (Bursell, 1966), the size of the flies (Bursell, 1966), the activity levels of the flies, or the success with which they obtained bloodmeals. Alternatively, flies with higher fat content might have been more available to capture in February than in August. It is possible that tsetse flies with greater nutritional reserves, which would remain inactive in August, will seek food in the hotter, drier month of February. This suggestion is supported by the observation that the mean fat content of the fed flies was greater in February than in August. It is also supported, to a lesser extent, by the observations (which were not significant) that from August to February there was an increase in the proportion of flies which fed, and a slight decrease in the difference between the haematin contents of the approaching and fed flies, which would be expected if the feeding interval decreased.

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References

Brady, J. (1975) 'Hunger' in the tsetse fly: the nutritional correlates of behaviour. *Journal of Insect Physiology*, **21**, 807–829.

Bursell, E. (1963) Aspects of the metabolism of amino acids in the tsetse fly, *Glossina* (Diptera). *Journal of Insect Physiology*, **9**, 439–452.

Bursell, E. (1966) The nutritional state of tsetse flies from different

vegetation types in Rhodesia. *Bulletin of Entomological Research*, **57**, 171–180.

Ford, J., Maudlin, I. & Humphryes, K.C. (1972) Comparisons between three small collections of *Glossina morsitans morsitans* (Machado) (Diptera: Glossinidae) from the Kilombero River Valley, Tanzania. Part 1. Characteristics of flies exhibiting different patterns of behaviour. *Acta Tropica*, **29**, 231–249.

Langley, P.A. (1966) The effect of environment and host type on the rate of digestion in the tsetse fly *Glossina morsitans* Westw. *Bulletin of Entomological Research*, **57**, 39–48.

Langley, P.A. (1967) The control of digestion in the tsetse fly, *Glossina morsitans*: a comparison between field flies and flies reared in captivity. *Journal of Insect Physiology*, **13**, 477–486.

Langley, P.A., Hargrove, J.W. & Wall, R.L. (1990) Maturation of the tsetse fly *Glossina pallidipes* (Diptera: Glossinidae) in relation to trap-oriented behaviour. *Physiological Entomology*, **15**, 179–186.

Langley, P.A. & Stafford, K. (1990) Feeding frequency in relation to reproduction in *Glossina morsitans morsitans* and *G.pallidipes*. *Physiological Entomology*, **15**, 415–421.

Langley, P.A. & Wall, R. (1990) The implications of hunger in the tsetse fly, *Glossina pallidipes*, in relation to its availability to trapping techniques. *Journal of Insect Physiology*, **36**, 903–908.

Milligan, P.J. & Baker, R.D. (1988) A model of tsetse-transmitted animal trypanosomiasis. *Parasitology*, **96**, 211–239.

Packer, M.J. & Brady, J. (1990) Efficiency of electric nets as sampling devices for tsetse flies (Diptera: Glossinidae). *Bulletin of Entomological Research*, **80**, 43–47.

Randolph, S.E., Dransfield, R.D. & Rogers, D.J. (1989) Effect of host odours on trap composition of *Glossina pallidipes* in Kenya. *Medical and Veterinary Entomology*, **3**, 297–306.

Randolph, S.E. & Rogers, D.J. (1978) Feeding cycles and flight activity in field populations of tsetse (Diptera: Glossinidae). *Bulletin of Entomological Research*, **68**, 655–671.

Randolph, S.E. & Rogers, D.J. (1981) Physiological correlates of the availability of *Glossina morsitans centralis* Machado to different sampling methods. *Ecological Entomology*, **6**, 63–77.

Randolph, S.E., Rogers, D.J., Dransfield, R.D. & Brightwell, R. (1991a) Trap-catches, nutritional condition and the timing of activity of the tsetse fly *Glossina longipennis* (Diptera: Glossinidae). *Bulletin of Entomological Research*, **81**, 455–464.

Randolph, S.E., Rogers, D.J. & Kiilu, J. (1991b) The feeding behaviour, activity and trappability of wild female *Glossina pallidipes* in relation to their pregnancy cycle. *Medical and Veterinary Entomology*, **5**, 335–350.

Rogers, D.J. (1988) A general model for the African trypanosomiases. *Parasitology*, **97**, 193–212.

Sibly, R.M. & Calow, P. (1986) *Physiological Ecology of Animals – an evolutionary approach*. Blackwell Scientific Publications, Oxford.

Taylor, P. (1976) Blood-meal size of *Glossina morsitans* Westw. and *G.pallidipes* Austen (Diptera: Glossinidae) under field conditions. *Transactions of the Rhodesian Scientific Association*, **57**, 29–34.

Vale, G.A. (1974) New field methods for studying the responses of tsetse flies (Diptera: Glossinidae) to hosts. *Bulletin of Entomological Research*, **64**, 199–208.

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