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<b>Autor:</b>	Etten, J. van
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International Centre of Insect Physiology and Ecology (ICIPE), P.O. Box 30772, Nairobi, Kenya

## Comparative studies on fat reserves, feeding and metabolic strategies of flies from two allopatric populations of *Glossina pallidipes* Austen in Kenya

J. VAN ETTE

### Summary

Flies from two allopatric populations of *Glossina pallidipes* in Kenya, from the Rift Valley (Nkruman) and the coastal area (Mwalewa), collected with traps, stationary car, moving car, and by hand nets, show differences in fat reserves, residual dry weight (RDW) and age structure of the males, but not in size and age structure of the females. The results indicate that flies from Mwalewa have a better physiological condition than flies from Nkruman. In Nkruman, fat reserves of flies collected in stationary collecting systems (car and traps) are lower than those of flies collected in moving systems (car), while in Mwalewa, the car, irrespective of whether stationary or moving, collected flies with higher fat reserves than traps did. *Males* from the two areas have a different metabolic strategy. After a period of flight muscle maturation, males from Nkruman show a variable fat level around a certain RDW range, suggesting that they use their meals almost entirely for energy utilization. Males from Mwalewa show a significant correlation between RDW and fat, suggesting that they use their meals partly for an increase in RDW and fat storage. Under laboratory conditions, males from the areas do not show any differences in feeding or in fat reserves. *Females* from both the areas show after flight muscle maturation a significant correlation between RDW and fat. The regression coefficients of this relationship in samples from Nkruman are similar, independent of the average fat level of the sample, and are lower than the regression coefficient of such a relationship in a sample of females from Mwalewa. When the regression coefficients of the relation between RDW and fat of females from the two areas are compared with those of their freshly deposited larvae, the increase in fat in the females is higher than expected. The fat excess of females from both areas is calculated, and is found to be three times higher for Mwale-

Correspondence: Dr. Jaap van Etten, Department of Zoological Ecology and Taxonomy, University of Utrecht, Plompelorengracht 9, 3512 CA Utrecht, The Netherlands

wa females than for females from Nkruman. The implication of this observation is discussed. The field results suggest that females from Mwalewa feed at a higher frequency than females from Nkruman, and this was confirmed in laboratory experiments.

**Key words:** *Glossina pallidipes* Austen; allopatric populations; fat reserves; residual dry weight; haematin; feeding; metabolic strategies; genetic differences.

## Introduction

The nutritional state of tsetse flies has a clear influence on behaviour. Bursell (1961, 1966) suggested four phases in the behaviour of males during a hunger cycle. Brady (1972b) demonstrated that the spontaneous activity of *Glossina morsitans* increased with increasing hunger. Van Etten (1982) showed a similar phenomenon for *G. pallidipes*, while he also demonstrated that in certain populations the shape of the diurnal activity pattern changed with increasing hunger. Also the visual responsiveness of *G. morsitans* changes during a hunger cycle (Brady, 1972a).

In initial studies (van Etten, 1977) it was shown that two allopatric populations of *G. pallidipes* in Kenya, collected either from traps or from a stationary car, showed significant difference in fat reserves. Laboratory experiments suggested that, in females, these differences resulted from differences in feeding frequency. The difference in fat reserves of males could not be explained by results of laboratory experiments and was thought to be due to so far unknown exogenous factors. Rogers and Randolph (1978) investigated the cycles of change in three physiological characteristics of field collected flies: residual dry weight (RDW), chloroform extractable fat, and residual blood meal (RBM). Using these three parameters they predicted "priority pathways for nutrient utilization". They developed the following model. For tenerals of both sexes the priority is to increase thoracic musculature (RDW) without excessive production of fat. Subsequently, non-teneral males devote each blood meal exclusively to the production of fat as an energy storage used mainly for flight activity. Females show a gradual increase in both fat and RDW levels, which probably correspond to the development of the larva. Wing fray measurements supported this interpretation.

Because fat reserves are important in relation to behaviour, additional studies in the field and in the laboratory were carried out to further investigate the observed differences in fat reserves in the two populations of *G. pallidipes* in Kenya, and the factors responsible for these. The model developed by Rogers and Randolph is used for the interpretation of the observed data, including those of an earlier paper (van Etten, 1977).

## Materials and Methods

The field studies were carried out in the Nkruman area (Rift Valley, 1° 50' S, 36° 05' E) and Mwalewa forest (coastal area, 4° 34' S, 39° 08' E) (see van Etten, 1981, for a detailed description of these areas). Flies were collected from 2 types of traps: the Langridge Box Screen and the Awning Screen Skirt (cf. van Etten, 1981), from a stationary car (a white Jeep Wagoneer, with sides and rear end draped with dark blue blankets), from a moving car (a white Jeep Wagoneer), or by a person with handnets from vegetation and ground, while walking randomly around. Flies were killed immediately in ethyl acetate vapour, stored individually in numbered glass jars in a dessicator, and brought to the laboratory for analysis. The levels of fat and haematin were estimated using the techniques described by Ford et al. (1972) (cf. Randolph and Rogers, 1978). Fat was expressed either in mg or as a percentage of the corrected residual dry weight, to allow for differences in body size and to correct for the residual blood meal (RBM) (Bursell, 1959). The correction for the RBM was made as follows: the residual dry weight in mg of Nkruman males collected in a stationary car was plotted on the y-axis against the haematin values, expressed as absorbance read at 558 nm on a spectrophotometer. The calculated regression ( $Y = 3.475X + 10.435$ ) was used to correct the RDW in all samples, independent of method of fly capture.

From each fly, a wing was removed and assessed for wing fray and length of the cutting edge of the hachet cell (Ford et al., 1972).

The statistical analysis of the comparison of the tested parameters of flies from the two areas was based on mean values of samples. In the model of "priority pathways for nutrient utilization", however, data of individual flies were used. Laboratory experiments were carried out to determine the feeding frequency, the size of blood meals and the amount of fat built up as a reserve under constant laboratory conditions, and to compare the data obtained with flies from the two study areas. Flies used for the experiments were obtained from laboratory colonies, which were kept at conditions of about 24°C and a relative humidity of 75% (van Etten, 1980). Only flies of the second or later laboratory generation were used. During the experiments, flies were kept in the breeding room, individually in plastic tubes with netting at both ends. They were allowed to feed daily on rabbits for 10 min. The females used in the experiments were mated, but the males were not used for mating. The fly in its tube was weighed, before and after feeding on a Mettler balance, to determine the amount of blood intake. Differences were tested by Student's t-test, unless otherwise indicated.

## Results

### *Field studies*

Table 1 summarizes the mean values of the residual dry weight (RDW), fat weight, residual blood meal (RBM = pyridin-haematin-complex [PHC] of Ford et al., 1972), wing fray, and size of samples collected with four different catching systems, from Nkruman and Mwalewa, between July 1975 and August 1977. RDW was expressed as mg, fat as mg and as percentage of the corrected RDW, RBM as absorbance read from a spectrophotometer at 558 nm, wing fray in numbers according to Jackson's (1946) system, and size in micrometer units (10 units = 2.0 mm). The results show for each sex that the RDW and the fat weight of flies from Mwalewa are significantly higher than those from Nkruman. Flies from Mwalewa also show significantly higher fat reserves when fat is expressed as percentage of the corrected RDW. Flies from Nkruman are slightly larger than flies from Mwalewa.

In Nkruman, flies collected by the two stationary catching methods (traps

Table 1. The averages of the residual dry weight (RDW), fat, residual blood meal (PHC), length of vein, wing fray (wf), fat as % of corr(ected) RDW, maximum fat observed and number of flies in samples of *Glossina pallidipes* collected with 4 different catching systems in Nkruman and Mwalewa. The results of the t-test comparing all samples of Mwalewa with those of Nkruman are also given

Nkruman		Mwalewa							
		car	traps	moving car	vegetation	car	traps	moving car	vegetation
n (samples)	♀ 9 ♂ 9	4 4	4 10	3 1	0 7	7 7	2 3	1 2	0 2
RDW (mg) ± S.D.	♀ 12.00 ± 1.10 ♂ 9.33 ± 0.51	11.45 ± 0.83 9.24 ± 0.54	10.94 ± 2.39 8.86 ± 0.64	— 9.80	— 10.10 ± 0.54	12.95 ± 0.47 9.88 ± 0.42	12.86 ± 0.91 9.98 ± 0.64	11.52 9.98 ± 0.64	— 11.18 ± 0.98
Fat (mg) ± S.D.	♀ 3.54 ± 1.29 ♂ 1.52 ± 0.55	2.90 ± 0.33 1.34 ± 0.49	3.98 ± 1.47 1.96 ± 0.57	— 2.25	— 3.21 ± 0.53	5.94 ± 1.19 2.27 ± 0.15	4.68 ± 1.37 2.88 ± 0.21	4.00 4.48 ± 0.78	— 4.48 ± 0.78
PHC (O.D.) ± S.D.	♀ 0.105 ± 0.041 ♂ 0.045 ± 0.018	0.86 ± 0.006 0.053 ± 0.037	0.136 ± 0.045 0.061 ± 0.026	— 0.022	— 0.048 ± 0.019	0.111 ± 0.058 0.023 ± 0.007	0.105 ± 0.002 0.037 ± 0.026	0.082 0.060 ± 0.019	— 0.060 ± 0.019
Length vein (units ± S.D.)	♀ 11.20 ± 0.22 ♂ 10.27 ± 0.20	11.12 ± 0.22 10.26 ± 0.21	11.12 ± 0.28 10.25 ± 0.10	— 0.037	— 10.21 ± 0.19	11.06 ± 0.17 10.11 ± 0.19	11.03 ± 0.08 10.04 ± 0.08	10.90 10.12 ± 0.04	— 10.12 ± 0.04
wf ± S.D.	♀ 1.98 ± 0.38 ♂ 2.01 ± 0.28	2.02 ± 0.23 1.78 ± 0.20	1.99 ± 0.73 1.71 ± 0.40	— 2.40	— 2.20 ± 0.51	2.26 ± 0.63 2.58 ± 0.54	2.38 ± 0.74 2.05 ± 0.01	1.85 2.39 ± 0.13	— 2.39 ± 0.13
Fat (% of corr. RDW) ± S.D.	♀ 30.30 ± 10.68 ♂ 16.61 ± 6.21	26.23 ± 4.20 14.85 ± 5.97	37.90 ± 11.02 22.75 ± 6.80	— 23.1	— 32.19 ± 4.87	47.19 ± 8.68 32.40 ± 14.99	35.6 29.35 ± 3.75	— 41.25 ± 10.54	— 41.25 ± 10.54
Max. observed fat (% of corr. RDW)	♀ 50.7 ♂ 24.9	31.2 23.4	49.3 34.9	— 23.1	— 39.7	55.5 43.0	35.6 32.0	— 48.7	— 48.7
n (flies)	♀ 546 ♂ 502	238 323	173 358	— 15	— 158	228 287	329 144	42 87	— 87

Comparison of the total number of samples from Nkruman with the total number of samples from Mwalewa:

RDW of	♀♀: p < 0.02 ♂♂: p < 0.001	fat (mg) of	♀♀: p < 0.001 ♂♂: p < 0.001
length vein of	♀♀: n.s. ♂♂: n.s.	fat (% of corr. RDW)	♀♀: p < 0.001 ♂♂: p < 0.001
wing fray of	♀♀: n.s. ♂♂: p < 0.01		

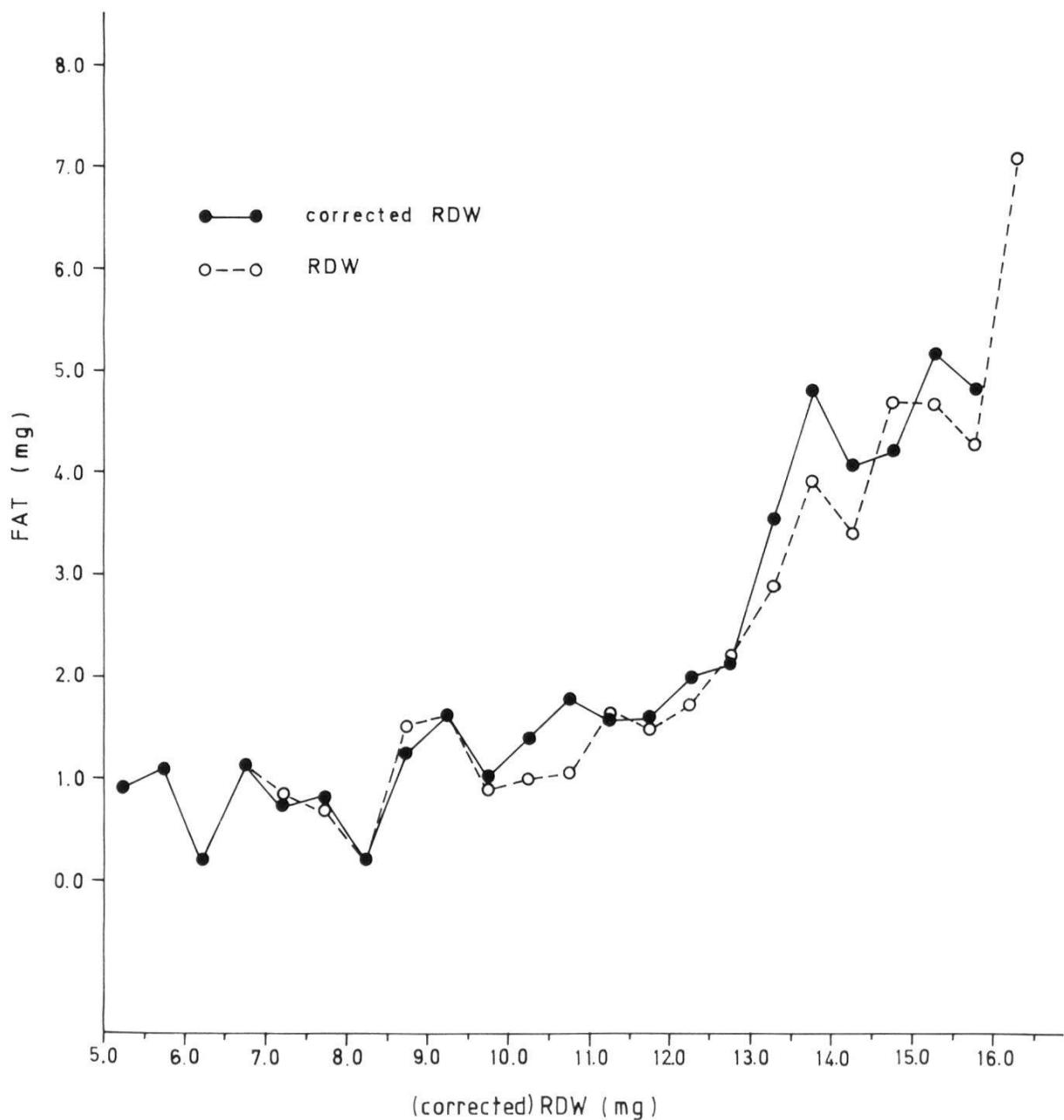


Fig. 1. Comparison between the changes in mean fat with increasing residual dry weight (RDW) (○), and with increasing corrected RDW (●) for female *Glossina pallidipes* from Nkruman. The mean fat is calculated and indicated per 0.5 mg RDW categories. Number of flies for both observations is 163.

and stationary car), do not differ in fat reserves. In Mwalewa, however, males collected in a stationary car have significantly more fat than males collected in traps ( $p < 0.02$ ); for females the difference was not significant. Males from Nkruman collected from a moving car have significantly more fat than stationary captures ( $p < 0.05$ ). In Mwalewa, however, no difference was found between stationary and moving captures. Here a significant difference was found between the car (either standing or moving) and traps ( $p < 0.02$ ).

In Mwalewa, male flies followed a person walking, especially on tracks

Table 2. Characteristics of scattergrams of fat and RDW for males from Nkruman (3 samples) and Mwalewa

	Nkruman			Mwalewa
	LF	IF	HF	
<i>Horizontal part of the scattergram</i>				
N	58	22	22	22
range of RDW (mg)	5.00–7.99	5.40–7.99	5.10–7.99	5.70–7.99
mean fat $\pm$ S.E. (mg)	0.83 $\pm$ 0.08	2.05 $\pm$ 0.14	2.14 $\pm$ 0.22	2.00 $\pm$ 0.23
<i>"Vertical" part of the scattergram</i>				
RDW:				
N	154	51	24	139
mean RDW $\pm$ 1 S.E. (mg)	10.37 $\pm$ 0.09	9.95 $\pm$ 0.14	9.73 $\pm$ 0.21	10.57 $\pm$ 0.10
range	8.00–13.57	8.00–12.40	8.00–13.00	8.00–14.40
Fat:				
mean $\pm$ 1 S.E.	0.98 $\pm$ 0.07	2.06 $\pm$ 0.14	3.32 $\pm$ 0.29	3.35 $\pm$ 0.14
range	0.00–4.6	0.00–4.4	0.00–6.5	0.00–7.5
r	0.208*	0.060	0.105	0.320***

LF, IF, HF = low, intermediate and high fat level; \* p < 0.05, \*\*\* p < 0.001

inside thickets, and along the thicket edge. As soon as movement ceased they settled on the ground, on vegetation, or on dead wood. These flies, which were collected with a handnet, had the highest fat reserves of all samples. The RBM was the same, however, as in samples collected with other catching systems (Table 1). In Nkruman, although the population density was higher (van Etten, 1981), males showing this behaviour were observed less frequently, and only one small sample was collected (n = 15). These males did not show a particularly high fat reserve.

The highest fat reserve found in females from Mwalewa was only about 10% more than the highest value in females from Nkruman. For males this difference was much larger, being 40% higher for males from Mwalewa. This was due to the high fat reserve found in the males from Mwalewa collected by handnets. For the car and the traps alone this difference was also about 10% (Table 1). To explain the differences in fat reserves found between the two populations, the results were compared, using the model of "priority pathways" for nutrient utilization (Rogers and Randolph, 1978). In our studies only a limited number of flies were analysed for haematin content; in most cases the RBM was determined per sample, thus not allowing the calculation of the RBM corrected RDW for all flies individually. The haematin content was, on average, low and the difference between the RDW and the corrected RDW generally less than 0.35 mg. A few flies with higher haematin content were possibly put in the wrong RDW group (groups of 0.5 mg), but this did not influence the basic pattern, as demonstrated in Fig 1. The regressions of the ascending parts of the corrected and uncorrected RDW versus fat were very similar ( $Y = 0.741X - 6.683$  and  $Y = 0.753X - 7.088$ ). Because the average haematin content in flies of

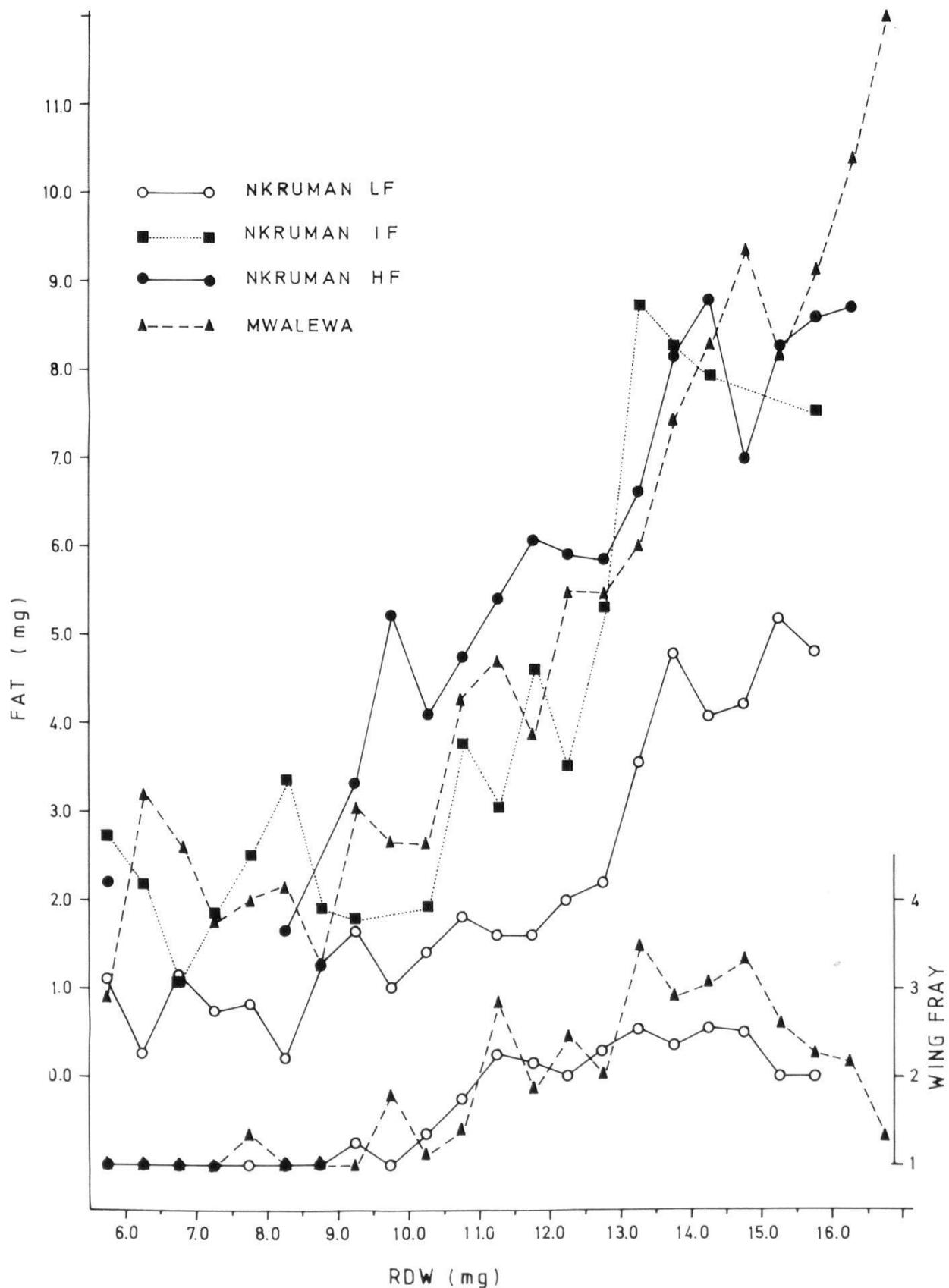


Fig. 2. Changes in mean fat and mean wing fray with increasing residual dry weight (RDW) for *Glossina pallidipes* females from Nkruman in samples with low (○—○), high (●—●) and intermediate (■—■) average fat levels, and from Mwalewa (▲—▲). The mean fat and wing fray are calculated and indicated per 0.5 mg RDW categories. Number of flies per sample: see Table 3.

the two populations was about the same (Table 1), the comparison between them would not be affected by the use of uncorrected RDW values.

Fat and RDW of three samples of males from Nkruman (with low, high and intermediate fat levels) were plotted as scattergrams. After emergence, with increasing RDW a more or less constant fat level was maintained, which was related to flight muscle maturation, while after a certain increase, they showed very variable fat levels around a more or less constant RDW ("vertical part" of the scattergram), although in the sample with low fat reserves, in this part of the scattergram a significant correlation ( $p < 0.05$ ) was found between fat and RDW (Table 2). Males from Mwalewa showed a highly significant ( $p < 0.001$ ) correlation between the RDW and fat in the "vertical part" of the scattergram in a pooled sample (5 observations) with the equation  $Y = 0.405X - 0.933$ . Details of the scattergrams of the three samples from Nkruman and the pooled sample from Mwalewa are shown in Table 2.

When fat levels falling in a 0.5 mg band on the RDW axis are presented graphically for females from both areas, figures similar to those found by Rogers and Randolph (1978) for other tsetse fly species, were obtained (Fig. 2). Like teneral males, teneral females show, after emergence, first an increase in RDW without much increase in fat, which is the period of flight muscle maturation. Later, the females show a strong increase in both RDW and fat. This increase starts at a RDW of about 10 mg, and is probably related to larval development. After producing the larva, the RDW and the fat return to the levels obtained before larval development.

As with other tsetse species, with increasing RDW, increasing fat levels alternate with approximately constant or decreasing fat levels (Fig. 2). This is related to the intake of blood meals, since a rise in fat levels can be expected after a blood meal (cf. Rogers and Randolph, 1978). Before the breaking point (the point where the ascending part of the scattergram starts, i.e. around a RDW of 10 mg) females from Mwalewa take at least 3 meals, and females from Nkruman 2 to 3 meals. After the breaking point, females from Mwalewa take 3 to 4 meals during each pregnancy cycle, while females from Nkruman take 2 to 3 meals each cycle. This suggests a difference in feeding frequency.

In Table 3 the characteristics of the scattergrams of fat and RDW for females from the two areas are summarized. As with males, the results of three samples from Nkruman with resp. low, high and intermediate fat levels, and a pooled sample from Mwalewa, are shown. The regression coefficients of the ascending part of the scattergrams of females from Mwalewa was higher than of any of the three groups of females from Nkruman, while the regression coefficients of these three groups of females were similar. The differences in fat levels in these three groups is mainly due to the differences in fat levels in the horizontal part of the scattergram (Table 3).

Table 3. Characteristics of scattergrams of females from Nkruman (3 samples) and Mwalewa

Locality	Horizontal part of the scattergram			"Vertical" part of the scattergram			
	N	range of RDW (mg)	mean fat $\pm$ 1 S.E. (mg)	N	range of RDW (mg)	regression coefficient	r
Nkruman LF	34	5.0–9.9	0.96 $\pm$ 0.12	129	10.0–20.3	0.753	0.568***
Nkruman IF	44	5.0–9.9	2.04 $\pm$ 0.17	53	10.0–26.0	0.873	0.598***
Nkruman HF	10	5.8–9.9	2.95 $\pm$ 0.42	108	10.0–22.1	0.707	0.600***
Mwalewa	27	5.8–9.9	1.91 $\pm$ 0.23	142	10.0–20.9	1.184	0.628***

LF, IF, HF = low, intermediate and high fat levels; \*\*\* p < 0.001

Table 4. Mealsize, number of meals, residual dry weight (RDW) and fat reserves of both sexes of *Glossina pallidipes*, maintained at least two generations under laboratory conditions, originating from two allopatric populations in Kenya. Data are determined after 30 days for females and 20 days for males, and are given as averages  $\pm$  S.D.

Locality	N	Average size meals in mg	Number of meals	RDW in mg	Fat weight in mg	Fat as % of corr. RDW
Nkruman ♀♀	30	50.4 $\pm$ 14.0	13.8 $\pm$ 3.3	17.9 $\pm$ 6.6	6.2 $\pm$ 2.9	37.5 $\pm$ 15.9
Mwalewa ♀♀	24	43.3 $\pm$ 9.7	16.1 $\pm$ 3.9	17.5 $\pm$ 6.7	6.5 $\pm$ 3.6	42.7 $\pm$ 24.9
Nkruman ♂♂	30	30.9 $\pm$ 6.3	12.3 $\pm$ 2.4	10.3 $\pm$ 1.2	4.2 $\pm$ 1.6	40.7 $\pm$ 13.6
Mwalewa ♂♂	41	25.5 $\pm$ 6.7	12.6 $\pm$ 2.7	10.6 $\pm$ 1.3	4.3 $\pm$ 2.0	41.7 $\pm$ 18.9

### Laboratory studies

A laboratory experiment was carried out to obtain additional information, hopefully to help interpret the field results (Table 4). Females from Mwalewa fed significantly more frequently than females from Nkruman. The total blood intake by females from the two areas was, however, the same, because females from Nkruman took a larger meal than females from Mwalewa. Although the blood intake of the females from the two areas was similar, females from Mwalewa had higher fat reserves (after 30 days) than females from Nkruman, although the difference was not statistically significant.

Males from the two areas did not show any difference in feeding frequency, or in the average size of the meals (Table 4), and consequently no difference in fat reserves was found.

### Discussion

The presented data confirm earlier findings, based on a relatively small number of samples (van Etten, 1977). Flies from Mwalewa collected in the field have, on the average, a higher fat reserve than flies from Nkruman. In addition it was shown that flies from Mwalewa had a significantly higher RDW than flies from Nkruman, despite the fact that the sizes of flies from the two areas were

about the same. The females in the studied samples did not differ in age structure, but males from the two areas did, males from Mwalewa being on the average older than males from Nkruman. These data indicate that flies from Mwalewa are in a better physiological condition than flies from Nkruman: they have more energy reserves (fat). Also the RDW of flies from Mwalewa was higher, while size was about the same, suggesting that they may have better developed flight muscles.

The observation that the fat reserves of flies collected in traps and stationary car are similar (van Etten, 1977), is true for flies from Nkruman only. In Mwalewa, however, the fat reserves of flies collected in traps was lower than of flies collected in a stationary car.

Some further conclusions can be drawn from this. In Nkruman, no differences were found between the fat reserves of flies from the two stationary catching systems, while the moving car collected flies with higher fat reserves. Following Bursell's (1961, 1966) suggestion of four phases in the behaviour of males during a hunger cycle, flies collected in a stationary system (independent of the type of system) are hungry flies seeking to feed, while the flies from the moving car are mainly flies seeking to mate. In Mwalewa, however, the situation is different. The flies with the lowest fat reserves are found in the traps only, while the car, whether moving or stationary, collected flies with higher fat reserves. Vale (1974) also reported no difference in fat reserves of male *G. morsitans* and *pallidipes* attracted to a stationary and moving object of the same size, being in this case, an ox. The results suggest that in Mwalewa it is not movement, but size and perhaps shape, which determines the type of behaviour flies exhibit.

Males collected from the ground or from vegetation showed high fat reserves, especially males from Mwalewa, which had the highest fat reserves of all samples collected. This was also found by Ford et al. (1972) for *G. morsitans*. The flies are obviously following-swarm males seeking to mate, since they have nearly completely digested their blood meal, but have hardly utilized any fat reserves (Table 1).

The use of the model of metabolic strategies of males and females as described by Rogers and Randolph (1978), allow a better understanding of the field results and lead to some important conclusions. Mwalewa males show a significant correlation between RDW and fat after flight muscle maturation, while males from Nkruman show basically a variable fat level around a certain RDW range (Table 2). This indicates that males from Mwalewa are able to increase fat levels with increasing RDW, while males from Nkruman have variable fat levels with increasing RDW. If a sample of males from Nkruman has a high fat level, it is connected with high fat levels in males falling in the horizontal part of the scattergram (Table 2). Obviously, the metabolic strategies of males from the areas are different. Mwalewa males, after the flight muscle maturation, use their meals partly for increase in RDW and fat storage, while

Table 5. Details of the relationship between RDW and fat of newly produced pupae under laboratory conditions of females from Nkruman and Mwalewa

Locality	N	Wet weight mean $\pm$ 1 S.E. (mg)	RDW mean $\pm$ 1 S.E. (mg)	Correlation RDW (X)/fat (Y)	r
Nkruman .....	31	37.7 $\pm$ 1.0	8.95 $\pm$ 0.25	$Y = 0.589X - 0.813$	0.821***
Mwalewa .....	29	39.3 $\pm$ 0.9	9.44 $\pm$ 0.22	$Y = 0.641X - 1.321$	0.658***

\*\*\* p < 0.001

males from Nkruman seem to use their meals almost entirely for energy utilization. The difference in age between the males from the two areas (Table 1) alone cannot explain the field data. Laboratory results indicate that males from the two areas neither show differences in feeding and fat reserves (van Etten, 1977, and Table 4), nor differences in total daily activity, providing temperatures are not higher than 30°C and flies are not too hungry (van Etten, 1982). It seems unlikely that the availability of hosts is the limiting factor for feeding, because hosts are more abundant in Nkruman than in Mwalewa (van Etten, 1981). Factors inducing these differences remain to be investigated.

Presenting the scattergrams of RDW versus fat as average of fat per 0.5 mg units of RDW (Fig. 2), females from the two areas show a similar relationship to that observed in females of 5 other tsetse species (Rogers and Randolph, 1978), although a few differences can be observed between the patterns of the females from the two areas. The regression coefficients of the ascending part of the scattergrams of females of the three samples from Nkruman are similar, and are lower than the regression coefficient of the ascending part of the scattergram of females from Mwalewa (Table 3). This means that over the same range of RDW, females from Mwalewa have a higher fat increase than females from Nkruman. A higher average fat level in a sample from Nkruman is connected with a high initial fat level, i.e. a high fat level in flies with a RDW falling in the horizontal part of the scattergram, and not to a higher regression coefficient.

Freshly deposited larvae of flies from the two areas show a significant correlation between RDW and fat (Table 5). From the RDW of the freshly deposited larvae (Table 5), the estimated point on the RDW axis of the scattergrams the RDW falls back to after the depositing of a larva (10 mg) (Table 3), and the range of RDW observed (Table 3), can be concluded that the whole expected range of RDW can be observed, i.e., the RDW reached after flight muscle maturation plus the RDW of the completely developed larva. This is different from other tsetse species, when only a part of the total range is covered (Rogers and Randolph, 1978).

If the regression coefficients of the relationship between RDW and fat of the ascending part of the scattergrams are compared with those of the freshly deposited pupae, the increase in fat for the females is higher than expected. Rogers and Randolph reported this for other tsetse species as well.

The fat excess in a pregnancy cycle of females from the two areas can be estimated. For Nkruman females, the average of the three regression coefficients of the ascending part of the scattergrams is 0.778 (Table 3) and the larval contribution to this slope is 0.589 (Table 5). Over a RDW increase of 8.95 mg (Table 5) the net fat excess will be  $(0.778 - 0.589) \times 8.95 = 1.69$  mg. For females from Mwalewa this will be  $(1.184 - 0.641) \times 9.44 = 5.13$  mg. This means that females from Mwalewa have a much higher fat excess during a pregnancy cycle. The fat excess will supply the energy for the flight while seeking a breeding site, the parturition, the flight while seeking a host, and the basal metabolism when a fly rests in between. Females from Nkruman have a much smaller safety factor to complete these actions than females from Mwalewa.

Data on the energy spent in metabolic processes during different aspects of activity of female *G. pallidipes* are not available. If we assume, however, that a higher rate of oxygen use of 60% for wild caught male *G. pallidipes* compared with laboratory male *G. morsitans* (Taylor, 1977), is representative for all metabolic processes, we can estimate, by using the data of Bursell and Taylor (1980) for *G. morsitans* at 25°C, that females from Nkruman can fly about 40 min, during which they have to seek a breeding site, and a host to feed on. If a fly is successful in feeding 24 h after it starts seeking a breeding place, the time it can spend in flight is only about 20 min. This seems a rather small safety factor, especially because flies are found to be active at temperatures higher than 25°C (van Etten, 1982). Females from Mwalewa, however, have, even after two days of rest, enough excess fat for a flight period of about 90 min.

Important in relation to the differences in net fat excess between females from the two areas, is the observation that females from the two areas feed at different frequencies. The number of peaks in the vertical part of the scattergrams (Fig. 2) suggest that females from Mwalewa take a meal more frequently than females from Nkruman. This is confirmed in laboratory experiments, where females from Mwalewa take a meal significantly more often than females from Nkruman (van Etten, 1977, and Table 4). Because females used in the experiments are from the 2nd or later laboratory generations, the differences seem to be under genetic control. The higher frequency of feeding in females from Mwalewa also result in a higher fat reserve than in females from Nkruman (Table 4), although the difference is not significant. The metabolism under laboratory conditions, however, is slower than in the field (cf. Randolph and Rogers, 1978) and the total period of 30 days might be rather short. It can be concluded that flies from Mwalewa have developed a better strategy for optimal survival and thus reproduction than females from Nkruman. Much research, however, especially on the energy budget of this species remains to be done to understand fully the importance of the differences in feeding and metabolic strategies of flies from these two areas.

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