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Effect of the life-span of female *Glossina palpalis gambiensis* on the weight and size of its progeny

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Abstract. Pupae and teneral flies of *Glossina palpalis gambiensis* originating from three successive reproductive cycles were compared for their size and weight. In general, pupal weight and fly weight increased, whereas fly size, measured as wing vein length, decreased with the number of reproductive cycles. The linear regression observed between weight and wing vein length of the fly demonstrated that, particularly for flies originating from the first and second larvipositions, small changes in wing vein length reflected substantial differences in weight.

The results of these laboratory experiments were compared with some field data on *Glossina morsitans* from Zambia and related literature. The life span of the female tsetse, affecting the size of her progeny, could clarify partially some of the field observed seasonal changes in size, whereas the correlation between fly size and weight could eventually explain the differential mortality of some size classes of tsetse flies. However, whether these laboratory observations can be extrapolated to the field has still to be confirmed.

Key words. *Glossina*, tsetse fly, pupa, size, weight, life-span, Zambia.

Introduction

Seasonal variation in size, weight and size-dependent mortality of tsetse flies in the field are frequently reported (Jackson 1948, 1952; Glasgow & Bursell, 1960; Bursell & Glasgow, 1960; Glasgow, 1961; Phelps & Clarke, 1974; Dransfield *et al.*, 1989; Rogers & Randolph, 1991). In most of these papers, tsetse fly size is expressed as a measure of linear dimension (viz the wing vein length of the fly). Several authors observed that this wing vein length was positively correlated with density-independent mortality acting on the parent population (Dransfield *et al.*, 1989; Rogers & Randolph, 1991). Flies having a shorter life-span will produce fewer offspring (less larvipositions). As they get older, in the laboratory female tsetse produce heavier pupae which give rise, in turn, to heavier teneral adults (Jordan *et al.*, 1967). If pupal or adult weight and wing vein length are correlated, then observed seasonal changes in wing vein length could be explained partially by changes in the age structure of the adult female population. Experiments were accordingly conducted to examine, under stable laboratory conditions, the relation between the weight of pupae emanating from successive larvipositions and the size and weight of the ensuing adults of *Glossina palpalis gambiensis*.

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Results of the experiments were examined for compatibility with field data (wing vein length of male and female flies, corrected residual dry weight of adult males, ovarian age category of females and mean wing fray values of males) on *G.m.morsitans* collected during a 4-year study in the Katete District (Eastern Province of Zambia). The study site was situated at an altitude between 900 and 1000 m.

Materials and Methods

Glossina palpalis gambiensis Vanderplank (Diptera: Glossinidae) was maintained at 25°C (±1°C) and 80% (±5%) humidity and fed five times a week on guinea-pigs. Breeding conditions for the different *Glossina* spp. kept at the Institute of Tropical Medicine of Antwerp were fully described (Elsen *et al.*, 1993).

In the first experiment the descendants of three batches of ninety female tsetse (groups A, B and C) were examined. Each batch had an age difference of 1 week. The flies were mated when 3 days old and the first and second larvae of each female was weighed when it became immobile and was darkening. Larvae deposited on the ninth up to the eleventh day after the first larviposition were discarded to minimize errors due to overlap of successive larvipositions. Pupae were kept in the breeding rooms at constant temperature (25°C) and humidity (80%).

Teneral females hatching from either the first or the second pupa of batch A females were killed and their wet weight, dry weight, residual dry weight (after fat extraction) and size (wing vein length) determined according to the technique described by Jackson (1946). Teneral males of group C were treated likewise. The remaining flies were used for breeding, in order to enable comparison of the progeny of flies originating from either a first or a second larviposition.

Female *G.p.gambiensis* are sexually mature 2–3 days after eclosion, whereas males are not fully fertile until 7 days old. Therefore, at least 8-day-old males of groups A and B were mated with at least 2-day-old females of groups B and C respectively (see Table 1). The first pupa resulting from these matings was weighed and pupal weights were compared according to the origin of the parents: first (F2L1) or second larviposition (F2L2).

During the first experiment, only small numbers of teneral flies originating from a first or a second reproductive cycle could be compared, and no distinction was made between pupae producing either female or male flies. Also, teneral flies were produced at different weeks by different groups of parent flies, which were therefor not entirely comparable. Consequently a second experiment was carried out.

In the second experiment, the progeny of a single batch of 300 female *G.p.gambiensis* was followed and individual pupae and teneral flies, originating from three successive reproductive cycles were compared. Each pupa was weighed, identified, and placed in a separate tube. Each teneral fly was killed within 2–14 hours after eclosion and its weight and size (wing vein length) was determined.

In this second experiment, larvae deposited on the ninth and tenth day and those of the eighteenth and nineteenth day were discarded, in order to minimize errors due to overlap of successive larvipositions.

The data on weight and size of flies originating from different larvipositions did not show a normal distribution, therefore the nonparametric Mann Whitney U test was used to compare these data. The Student's *t*-test and analysis of variance was used to compare data between sexes.

Results

First experiment

A significant weight difference ($P < 0.05$) was noticed between pupae from either a first or a second larviposition for flies from group A, group B and all groups together, but not for those from group C (Table 2). The pupae of the last group were significantly lighter than the pupae deposited by the other two groups. Poor nutrition might be an acceptable explanation for this anomaly, since high mortality occurred among the parent females of group C simultaneously with an unexplained mortality among the guinea-pigs used as host.

Table 1. Copulation procedure for flies originating from a first or second larviposition.

Origin of parent flies				First pupa of the second generation
Male		Female	Larviposition	
Group A	×	Group B	1	F2L1 ($n = 23$)
Group B	×	Group C	1	F2L1 ($n = 15$)
Group A	×	Group B	2	F2L2 ($n = 24$)
Group B	×	Group C	2	F2L2 ($n = 13$)

Table 2. Mean weight (mg) of pupae originating from a first or a second larviposition.

Pupae	Larviposition 1	Larviposition 2
Group A	25.3 ± 3.7 ($n = 72$)	27.4 ± 3.3 ($n = 66$)
Group B	27.3 ± 2.8 ($n = 79$)	29.2 ± 2.8 ($n = 59$)
Group C	23.5 ± 3.7 ($n = 45$)	23.7 ± 3.8 ($n = 32$)
Total	25.7 ± 3.7 ($n = 196$)	27.3 ± 3.8 ($n = 157$)

Pupal weight also differed significantly ($P < 0.001$) between groups indicating that these were not entirely comparable.

The weight and wing vein length of teneral males and females originating from both larvipositions are shown in Table 3.

The Mann-Whitney U test did not indicate any significant difference between the two successive larvipositions, either for weight or for wing vein length of female or male flies. As expected, there were significant differences ($P < 0.05$) between the sexes for both variables. A positive and significant ($P < 0.001$) correlation was observed between wing vein length and wet weight of female flies ($r = 0.51$, $n = 62$) and male flies ($r = 0.62$, $n = 35$). The correlation between wing vein length and weight did not improve if, instead of wet weight, dry weight ($r = 0.50$ and $r = 0.53$ for females and males respectively) or residual dry weight ($r = 0.50$ and $r = 0.54$ for females and males respectively) was used.

Strong correlations were observed between the wet weight of these laboratory-bred teneral flies and their dry weight ($r = 0.97$ and $r = 0.96$ for females and males respectively) or residual dry weight ($r = 0.91$ and $r = 0.92$ for females and males respectively).

Male (group A or B) and female (group B or C) flies originating from either the first or the second reproductive cycle were mated and the first pupae produced by these two groups were compared (see Table 1). The mean weight of the first pupa produced by parent flies, emanating from a first larviposition (F2L1), was significantly ($P = 0.018$) less than that of parent flies emanating from a second larviposition (F2L2) (Table 4). In other words, the longer the parent population lives the heavier the pupae that will be produced.

We note, however, that the weight difference between pupae produced by parent flies originating from a first or a second reproductive cycle was not statistically significant, when only

Table 3. Mean weight and wing vein length of teneral flies produced during a first or a second reproductive cycle.

	Larviposition	Weight (mg)	WVL (μm)
Female (group A)	1 ($n = 30$)	19.9 (±2.5)	1629.5 (±51.3)
	2 ($n = 32$)	20.5 (±3.0)	1635.7 (±64.1)
Male (group C)	1 ($n = 16$)	17.8 (±2.9)	1430.2 (±70.7)
	2 ($n = 19$)	17.0 (±2.9)	1393.4 (±57.6)

Table 4. Mean pupal weight of the first pupa produced by parent flies originating from a first or a second larviposition.

Origin of parent flies	Larviposition 1	Larviposition 2
Mean pupal weight	26.30 mg (F2L1)	28.03 mg (F2L2)
No. of pupae	38	37

the pupae from group B males mated with group C females were considered. This may be related to the breeding problems encountered in group C, resulting in poor pupal and fly weight and no weight difference between the pupae originating from the two larvipositions (see Tables 2 and 3).

Second experiment

A total of 670 pupae produced by 300 female *G.p.gambiensis* during three consecutive reproductive cycles were retained for this experiment. The number of pupae, their eclosion percentage, and the sex of the teneral flies for the consecutive larvipositions are shown in Table 5.

Table 5. Pupae and teneral *G.p.gambiensis* originating from the first three reproductive cycles.

	Pupae		Teneral flies	
Larviposition	Total	Eclosion (%)	Males	Females
1	210	92.9	91	104
2	216	93.1	105	96
3	244	95.9	123	111
Total	670	94.0	319	311

Table 6 gives the average weight of the pupae and the average weight and wing vein length of emerging teneral flies according to reproductive cycle of the parent fly and sex of the descendant fly.

Significant differences between pupal weight, fly weight and wing vein length were observed for the successive reproductive cycles. Pupal and teneral weight had a tendency to increase, whereas wing vein length had a tendency to decrease. The onset of these changes, however, differed between sexes. Pupal and fly weight of males emerging from a third reproductive cycle were significantly higher than those emanating from earlier cycles. In females a significant weight difference already occurred between flies from the first two cycles.

Males produced during a first reproductive cycle had longer wing veins than those produced in subsequent cycles, whereas females showed significantly decreased wing vein length only at the third cycle.

Student's *t*-test and analysis of variance showed significant differences for all variables between sexes: pupal weight ($P = 0.014$), weight of teneral fly ($P < 0.001$) and wing vein length ($P < 0.001$). Differences in pupal weight, however, were not significant for all reproductive cycles and sex could only explain 1% of the variation in pupal weight. Fly weight and size, on the other hand, differed significantly between sexes independent of the reproductive cycle. From the differences between pupal and teneral fly weight it appears that males lose relatively more weight during puparial stage and eclosion (27.1% of pupal weight) than females (25.6% of pupal weight).

A highly significant regression ($P < 0.001$) and positive correlation ($r = 0.93$ and 0.92 for males and females respectively) was observed between pupal weight and teneral fly weight. The correlation between pupal weight and the wing vein length of the ensuing fly ($r = 0.36$ and 0.30 for males and females respectively) or between the weight of the teneral fly and its wing vein length ($r = 0.41$ and 0.33 for males and females respectively) was less pronounced, but the regression still significant ($P < 0.001$). Both correlations showed a tendency to decrease for flies originating from the third larviposition (Table 7). In flies originating from the third cycle, wing vein length

Table 6. Mean pupal weight, teneral fly weight and wing vein length for male and female descendants of *Glossina p.gambiensis* during three consecutive reproductive cycles.

Variable	Larviposition	Males	Females
Pupal weight (mg)	1	25.7 ± 2.9 aa*	26.3 ± 2.9 aa
	2	26.3 ± 3.3 aa	27.5 ± 3.4 bb
	3	27.5 ± 2.8 ba	27.8 ± 3.0 ba
	Total	26.6 ± 3.1	27.3 ± 3.2
Fly weight (mg)	1	19.0 ± 2.3 aa	19.7 ± 2.6 ab
	2	19.1 ± 2.4 aa	20.6 ± 3.1 bb
	3	19.9 ± 2.4 ba	20.5 ± 2.3 bb
	Total	19.4 ± 2.9	20.3 ± 2.7
Wing vein length (μm)	1	1441.7 ± 61.4 aa	1625.9 ± 66.5 ab
	2	1407.0 ± 61.2 ba	1612.3 ± 75.6 ab
	3	1401.3 ± 44.5 ba	1578.2 ± 61.3 bb
	Total	1413.5 ± 57.5	1610.6 ± 65.3

* Significant difference between larvipositions when the first character varies between rows and significant difference between sexes when the second character varies between columns.

Table 7. Correlation coefficients between pupal weight and weight or size of teneral flies.

	Fly size (WVL)	Pupal weight
Fly weight of males	Larviposition 1: 0.58 2: 0.56 3: 0.33	0.93
Fly weight of females	Larviposition 1: 0.38 2: 0.49 3: 0.26	0.92
Pupal weight of males	Larviposition 1: 0.52 2: 0.51 3: 0.34	1
Pupal weight of females	Larviposition 1: 0.38 2: 0.52 3: 0.22	1

becomes more stable and is less influenced by the weight of the fly than in flies from previous cycles (Table 8).

Field observations on age of G.m.morsitans in Zambia

The mean monthly ovarian age distribution of female *G.m.morsitans*, captured in 1992 and 1993 (n = between 173 and 620 females/month), and the mean monthly wing fray value of male *G.m.morsitans*, captured from 1990 until 1993 (n = between 789 and 995 flies/month) are represented in Fig. 1.

Table 8. Regression between wing vein length y (μm) and fly weight x (mg) for teneral males and females from three successive larvipositions.

Larviposition	Males	Females
1	$y = 1142 + 15.8x$	$y = 1452 + 9.7x$
2	$y = 1129 + 14.4x$	$y = 1400 + 10.7x$
3	$y = 1278 + 6.1x$	$y = 1467 + 5.9x$

Field observations on size of G.m.morsitans in Zambia

The mean monthly wing vein length of female and male *G.m.morsitans*, captured from April 1990 until September 1992 (n = a mean of 437 males and 135 females/month), and the corrected residual dry weight (= residual dry weight corrected to its value at zero haematin by subtracting the weight of the residual blood meal (Rogers & Randolph, 1986)) of adult male *G.m.morsitans*, captured from January 1991 until September 1992 (n = a mean of 202 males/month) are represented in Fig. 2. From the data of this figure it is clear that wing vein lengths of female and male flies follow a similar course over time. Long wing vein lengths are observed at the end of the humid seasons, particularly when the rains are prolonged (Fig. 2: 1990, prolonged period of abundant rains until April; 1991, normal rainy season; 1992, lack of rain in February). Corrected residual dry weight (CRDW) of male *G.morsitans* follows the same trend as wing vein length and seems even more sensitive to changing environmental conditions as demonstrated by the rapid fall in CRDW 2 months after, following the severe drought of February 1992.

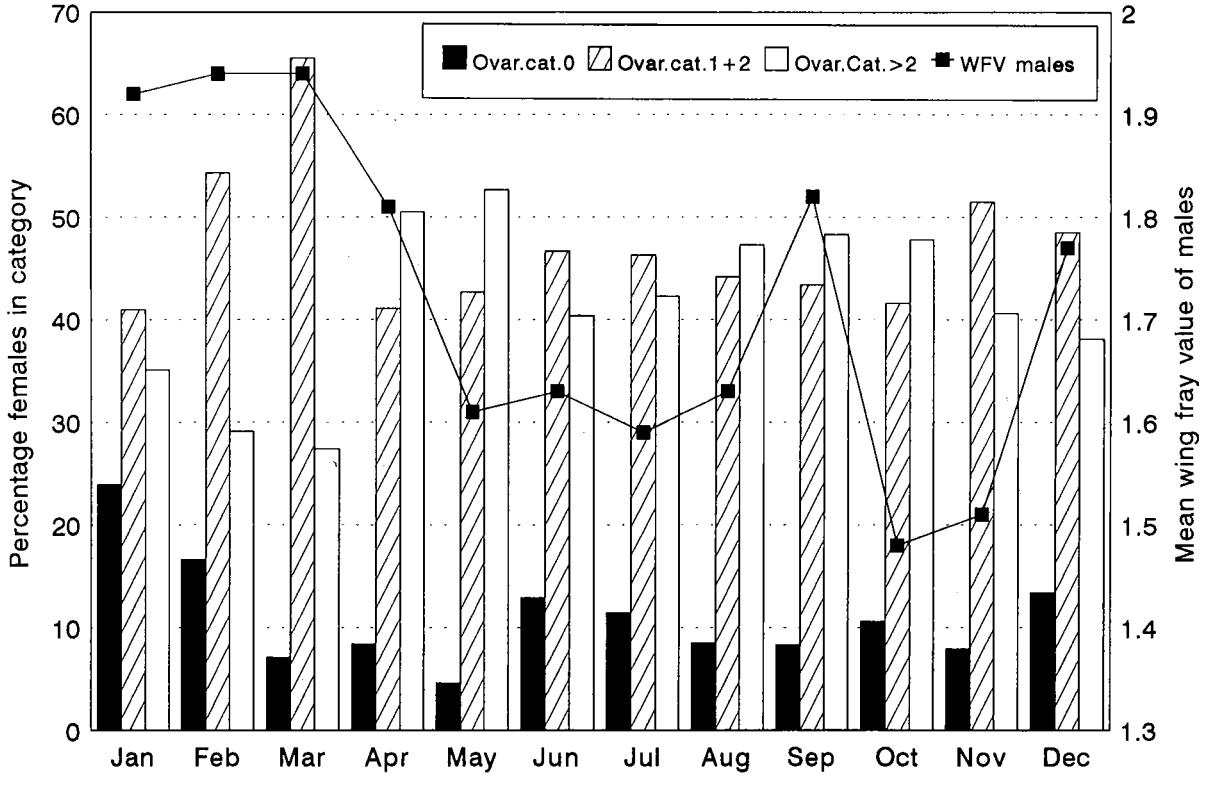

Fig. 1. Monthly distribution of ovarian age categories and monthly mean wing fray value of field collected *Glossina m.morsitans*.

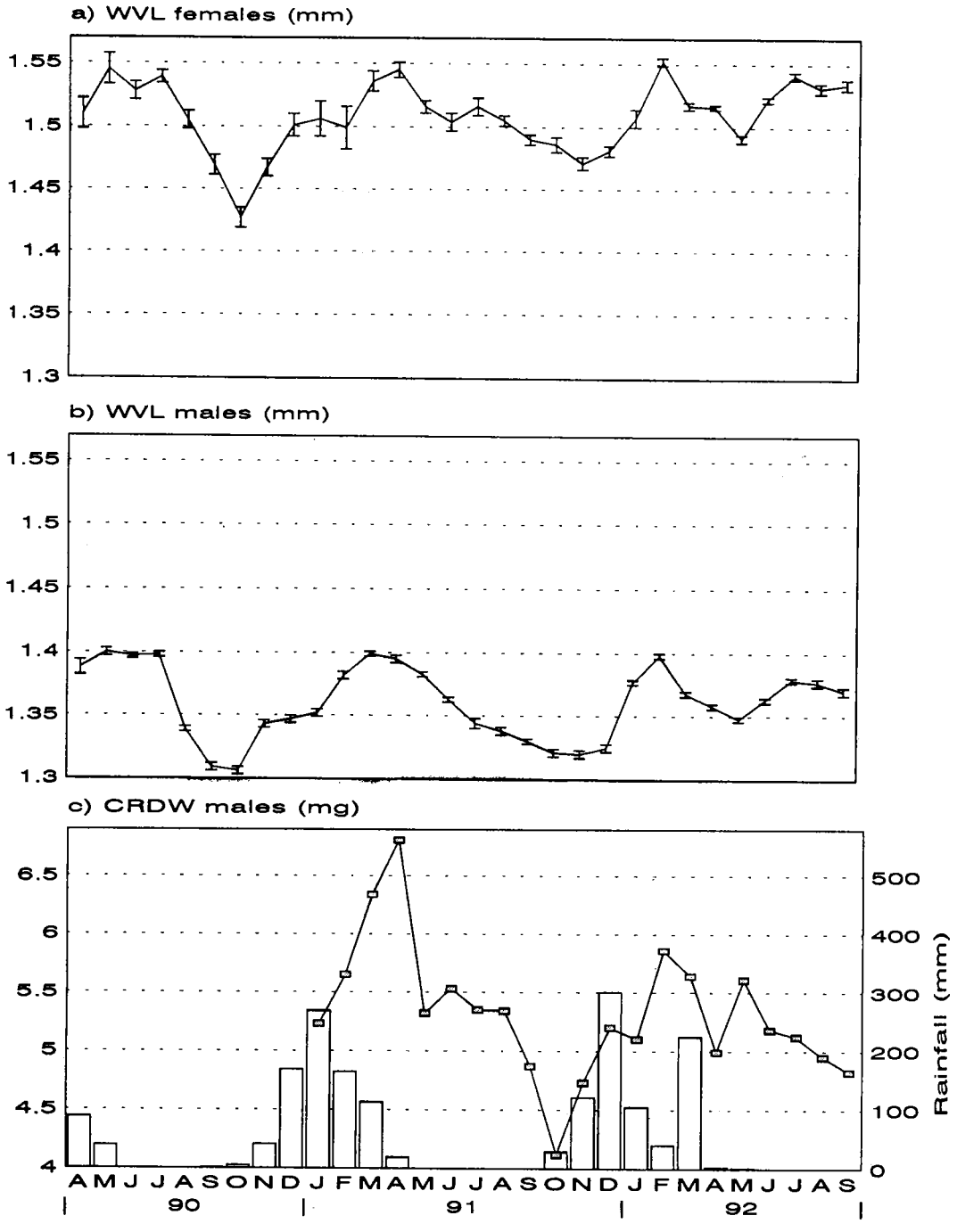

Fig. 2. Monthly mean wing vein length (WVL) and corrected residual dry weight (CRDW) of field collected *Glossina m.morsitans.*

Discussion

Pupal weight

From the results of these experiments it can be concluded that in the laboratory pupal weight of *G.p.gambiensis* increases until at least the third reproductive cycle of the parent fly. For *G.austeni*, a similar increase until the fifth cycle was observed by Jordan *et al.* (1967).

Under the favourable conditions maintained during this experiment pupal weight and fly weight were highly correlated ($r = 0.93$ and 0.92 for males and females respectively). Sex of the fly could only explain 1% of the variation in pupal weight.

The first experiment established also that parent flies emanating from a second larviposition produce generally a heavier pupa than those originating from a first larviposition, i.e. when under laboratory conditions females live long enough to produce a

second pupa a gradual increase of pupal weight can be expected in the next generations. However, the second experiment demonstrated that females originating from a second larviposition were significantly heavier than those originating from a first larviposition. According to Boyle (1971), pupal weight in laboratory-bred *G.austeni* is a function of the mother's weight and the amount of blood she imbibed throughout the interlarval period. Therefore the heavier pupae produced by the parent flies emanating from a second larviposition may be a consequence of the heavier weight of these mothers.

If these experimental observations on pupal weight could be applied directly to the field, a positive correlation between pupal weight and the longevity of the female parent fly would be expected, although the age of the mother is certainly not the only factor controlling pupal weight. Pupal weight was found to depend also on the temperature experienced by the parental population (Harley, 1968), the weight of the mother, and the amount and quality of blood she imbibed throughout the interlarval period (Boyle, 1971; Langley *et al.*, 1978; Davies-Cole *et al.*, 1992).

Fly weight and size: laboratory observations

In this study, fly weight was estimated on the basis of the wet weight, whereas for these laboratory-bred flies dry or residual dry weight were not better correlated to wing vein length as wet weight.

Fly size was measured on the length of the cutting edge of the hatchet cell of the wing. Bursell (1960a) found this method unreliable, while this measurement was poorly correlated with the residual dry weight of unfed flies. However, the practice of estimating the size of a fly on the basis of its residual dry weight was questioned by Langley & Stafford (1990), whereas residual dry weight of the tsetse thorax seemed to fluctuate with respect to nutritional state in both sexes and in relation to the reproductive cycle in females.

In the present study a linear relationship was found to exist between fly weight and wing vein length. Although regressions were highly significant ($P < 0.001$) correlation coefficients were not very high (first experiment: $r = 0.62$ and 0.51 for males and females respectively; second experiment: $r = 0.41$ and 0.33). In this last experiment it was observed that these correlation coefficients showed a tendency to decrease for flies originating from the third larviposition (Table 7), which suggests that, from the third cycle onwards, wing vein length becomes more stable and is less influenced by the weight of the fly than in flies from previous cycles. Dransfield *et al.* (1989) found similar highly significant linear regressions and similar low correlation coefficients ($r = 0.31$ and 0.32 for males and females respectively) between wing vein length and dry weight of teneral *G.pallidipes* emerging from field collected pupae. These results do suggest, however, that on average small differences in wing vein length reflect substantial differences in weight, particularly so for flies originating from the two first larvipositions.

Flies emerging from the lighter pupae produced during the first reproductive cycle had on average a low weight, but no small wing vein lengths. To the contrary, male flies from the first cycle had significantly longer mean wing vein lengths than those from the second or third cycle. Similarly, wing lengths of females from the first two cycles were on average longer than those from the third cycle.

Although in the first experiment male and female flies from the second reproductive cycle also had respectively shorter wing vein lengths and larger fly weights than those from the first cycle, these differences were not significant, probably because the number of flies was too low.

Fly weight and size: compatibility of laboratory observations on size with field data

Based on the results of this laboratory study, one would expect an increase in wing vein length at those times of the year when longevity of the female fly is low or recruitment high and consequently the proportion of first larvipositions will be important. According to the age estimation study of *G.m.morsitans* in Zambia (Fig. 1) and assuming that the sampling bias for the different age classes was independent of the season, the percentage females belonging to the lower and higher ovarian age categories reached a climax during respectively the hot-wet (December–February) and the warm-dry season (April–May). Therefore the age structure of the fly population might be partially responsible for the presence of long wing vein lengths during the rainy season and the fall in tsetse fly size observed at the start of the cold dry season (Fig 2). Nevertheless, the age of the parent fly is not the only factor regulating offspring size, for example fly size was seen to decrease quite sharply when pupal development occurred above a temperature of 25°C (Bursell, 1960b).

Size-dependent mortality

Should the results of this laboratory study on *G.p.gambiensis* apply equally to the field situation and other *Glossina* species, they might explain partially seasonal size-dependent mortality. This mortality is believed to be related principally to young flies unable to find a suitable host before depletion of their energy reserves (Phelps & Clarke, 1974; Bursell & Glasgow, 1960). Therefore the lightest teneral flies are at a disadvantage, particularly as the rate of energy expenditure per unit mass declines with increasing body mass (Peters, 1983) and while fat reserve in teneral flies seems to rise concomitantly with residual dry weight (Bursell, 1960b; Phelps, 1973). From the results of this laboratory study, the lightest flies in the population are expected to be those originating from early larvipositions (Table 6) and among those predominately the ones with short wing vein length (Tables 7 and 8). Such a selection could explain why Glasgow (1961) in Tanzania and Phelps & Clarke (1974) in Zimbabwe remarked that during the coldest and hottest months male *G.morsitans* were losing their smallest individuals. The selection against the smaller members of the *G.morsitans* population disappeared towards September in Tanzania (Glasgow, 1961) and Zimbabwe (Phelps & Clarke, 1974). As a sudden increase in food availability at this time is not very likely, the disappearance of the selection might be due to a decrease in energy consumption enabling the lighter teneral flies to survive. At that time of the

year mean temperatures are in the region of 24°C, which is close to the optimum temperature in terms of fat reserves in emerging flies (Phelps, 1973). During that period, environmental conditions are also favourable in Zambia, which can be responsible for the increasing mean wing fray value of *G.m.morsitans* males at that time (Fig. 1). The further decrease in fly size and weight observed during this period (Fig. 2) can be explained by the smallest tenerals no longer being selected against.

Although this study can contribute to the understanding of the factors, governing seasonal variations of tsetse fly weight and size in the field, the applicability of the results to the field situation needs to be confirmed.

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