Diurnal and seasonal flight activity cycles of *Glossina palpalis gambiensis* Vanderplank and *Glossina morsitans submorsitans* Newstead in Mali

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Abstract

Diurnal and seasonal flight activity cycles of Glossina palpalis gambiensis *Vanderplank and* Glossina morsitans submorsitans *Newstead were studied in the Northern Guinea Savanna of Central Mali, between June, 1979 and May, 1980, with the aid of the Challier-Laveissière trap.* G. p. gambiensis *were observed exclusively in the gallery forest, while* G. m. submorsitans *were studied both in the gallery forest and savanna woodland.*

There was uniform distribution of activity by G. p. gambiensis *during the day, in the rainy season. In the mid dry season, distribution of active flies during the day was significantly heterogenous, although no peak was discernible. In the late dry season, a peak was observed at 09.00-12.00 hr. Nocturnal activity was reduced or absent in all seasons.*

In the rainy season, G. m. submorsitans *exhibited uniform activity during the day in savanna woodland. Two peaks (06.00-09.00 and 15.00-18.00 hr) of activity were observed in the mid dry season. One peak of activity (09.00-12.00 hr) was recorded in the late dry season. In the gallery forest,* G. m. submorsitans *exhibited uniform activity during the day, in the late rainy and mid dry seasons. A single peak (09.00-12.00 hr) of activity was observed in the late dry season. Nocturnal activity was reduced or absent in both plant communities.*

The separate activity patterns of males and females of each species were similar to those of the combined sexes. Significant activity was also noted for pregnant females. Possible reasons for the patterns of activity cycles observed are discussed.

Key words : Flight — Activity cycle — Tsetseflies — Trapping — Mali.

Résumé

LES CYCLES DIURNES ET SAISONNIERS D'ACTIVITÉ EN VOL DE *Glossina palpalis gambiensis* V. ET DE *Glossina morsitans submorsitans* N. AU MALI

Les cycles diurnes et saisonniers d'activité en vol de Glossina palpalis gambiensis *Vanderplank et* Glossina morsitans submorsitans *Newstead ont été étudiés en savane guinéenne du nord au centre du Mali, entre juin 1979 et mai 1980 avec l'aide du piège Challier-Laveissière.* Glossina palpalis gambiensis *a été observé uniquement dans la forêt galerie tandis que* Glossina morsitans submorsitans *a été étudié aussi bien dans la forêt galerie qu'en savane boisée.*

Pendant la saison des pluies les activités de Glossina palpalis gambiensis *sont distribuées uniformément*

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au cours de la journée. En pleine saison sèche la distribution diurne des mouches actives est remarquablement hétérogène même si aucune période de pointe n'est perceptible (9 h-12 h). En toutes saisons les activités nocturnes sont réduites ou absentes.

Quant à Glossina morsitans submorsitans, *pendant la saison des pluies ses activités diurnes en savane boisée sont uniformes. En pleine saison sèche deux périodes de pointe sont observées (6 h-9 h et 15 h-18 h). Une seule période de pointe (9 h-12 h) est enregistrée vers la fin de la saison sèche. Dans la forêt galerie* Glossina morsitans submorsitans *est observé en activité uniforme pendant la journée vers la fin de la saison des pluies et en pleine saison sèche. Une seule période de pointe (9 h-12 h) est enregistrée vers la fin de la saison sèche. Les activités nocturnes sont réduites ou mêmes absentes dans les deux cas étudiés.*

L'aspect des activités séparées des mâles et des femelles de chaque espèce est identique à celui des deux sexes réunis. Cependant, une activité particulière a été observée en ce qui concerne les femelles gravides. Des explications sont proposées à propos des différents cycles d'activités observés.

Mots-clés : Vol — Cycle d'activité — Glossines — Piégeage — Mali.

INTRODUCTION

An accurate knowledge of the diurnal and seasonal flight activity cycles of *Glossina* is a prerequisite to a tsetse control programme. This information is useful in the determination of the appropriate period for pre post-control sampling of populations. It also aids in the development of accurate timing of insecticide applications during control operations.

Numerous studies on the flight activity patterns of many species of *Glossina* in various parts of Africa have been documented : *Glossina longipalpis* (Morris, 1934) ; *Glossina morsitans submorsitans* (Nash, 1939) ; *Glossina pallidipes* (Vanderplank, 1941), *Glossina longipennis* (Lewis, 1950), *Glossina morsitans orientalis* (Welch, 1958), *Glossina brevipalpis* (Harley, 1965), *Glossina palpalis gambiensis* (Challier, 1973) and *Glossina tachinoides* (Gruvel, 1974). None of these studies was conducted in Mali. Consequently, a study of the diurnal and seasonal flight activity patterns of the two main species (*G. p. gambiensis* and *G. m. submorsitans*) in Central Mali was considered vital. The results reported here, were based on investigations conducted between June, 1979 and May, 1980, prior to the initiation of a tsetse control programme in the zone.

DESCRIPTION OF STUDY AREA

The area is located approximately 12°30′ N and 8°12′ W in the forest reserve Monts Mandingues in the northern Guinea Savanna, about 20 km west of Bamako (fig. 1). It is a threestoried savanna woodland. The dominant is mostly made up of *Isoberlinia doka*, *Burkea africana*, *Monotes kerstingii*, *Khaya senegalensis* and *Afzelia africana*, The lower layer is composed mainly of *Terminalia* sp., *Lanaea* sp. and *Combretum* sp. The grass cover is composed of *Andropogonaceae*, *Vitivera* and *Imperata cylindrica* in periodically inundated areas. The above-mentioned plants are grouped into well-defined communities : gallery forests along rivers and depressions, savanna woodland on plateau and hillsides, and shrub savanna on hills and lateritic outcrops.

Climatically, the seasons can be divided into three overlapping ones : warm and rainy (June-October) 27°C and 71 % RH ; warm and dry (November-January) 26°C and 37 % RH ; hot and dry (February-May) 31°C and 34 % RH.

MATERIALS AND METHODS

Harley (1965) expressed the activity cycle of testse as relative numbers collected at different times of day ; these numbers are indices of flight activity. Several methods have been used in activity cycle studies ; Harley (1965) collected *G. pallidipes*, *G. palpalis fuscipes* and *G. brevipalpis* off bait oxen, while Challier (1973) caught *G. p. gambiensis* attracted to humans. Traps have been used extensively as both survey and research tools for *G. palpalis* (Morris, 1961 ; Challier & Laveissière, 1973) and *G. morsitans* (Vale, 1974 ; Roger et Smith, 1977). They are advantageous in that once in position, they work throughout the day and usually catch a high proportion of females. Traps were therefore considered appropriate, because flight activity over 24 hr periods was to be determined. The bi-conical Challier-

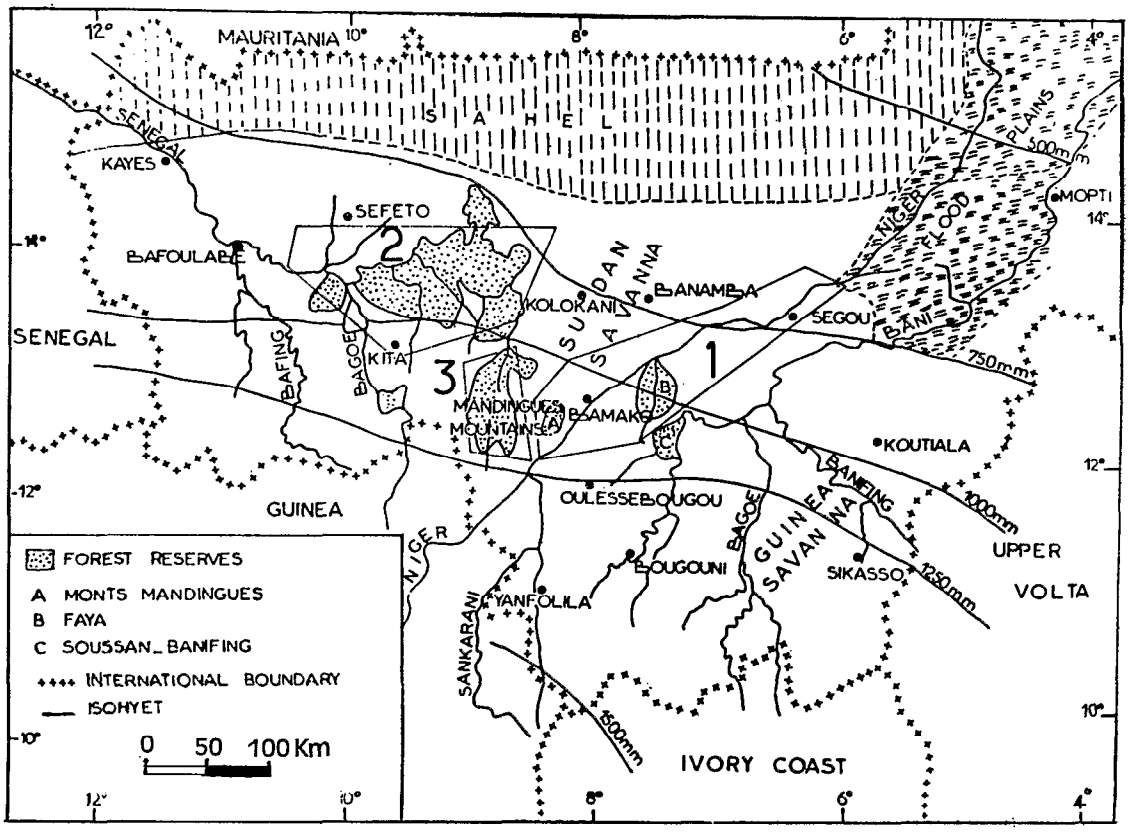

FIG. 1. — Mali : Study area

Laveissière trap which has been shown to be very efficient in trapping a representative cross-section of *Glossina* populations (Challier & Laveissière, 1973) was considered suitable. The model with a lower blue portion, which had been shown to be the most efficient, was used (Challier *et al.*, 1977).

Studies were conducted in September (late rainy), January (mid dry) and April (late dry). Investigations were made both in the gallery forest and savanna woodland. Ten traps were randomly placed in the gallery forest ; a similar number were also placed in the savanna woodland. Collections of *G. p. gambiensis* were made exclusively in the gallery forest, while *G. m. submorsitans* were collected from both the gallery forest and savanna woodland. Collections were made at 06.00, 09.00, 12.00, 15.00 and 18.00 hr. The 06.00 and 18.00 collections coincided with sunrise and sunset to enable the determination of nocturnal activity. Numbers collected were used as indices of flight activity for the period between two collections ; collected specimens were grouped into species, sexed and differented into pregnant and non-pregnant females.

Owing to heterogeneity of data, these were transformed into the logarithmic scale prior to statistical analyses.

RESULTS

G. p. gambiensis (gallery forest)

RAINY SEASON

Distribution of flies among periods was homogenous : 06.00-09.00 hr (24.74 %), 09.00-12.00 (25.53 %), 12.00-15.00 (23.40 %), 15.00-18.00

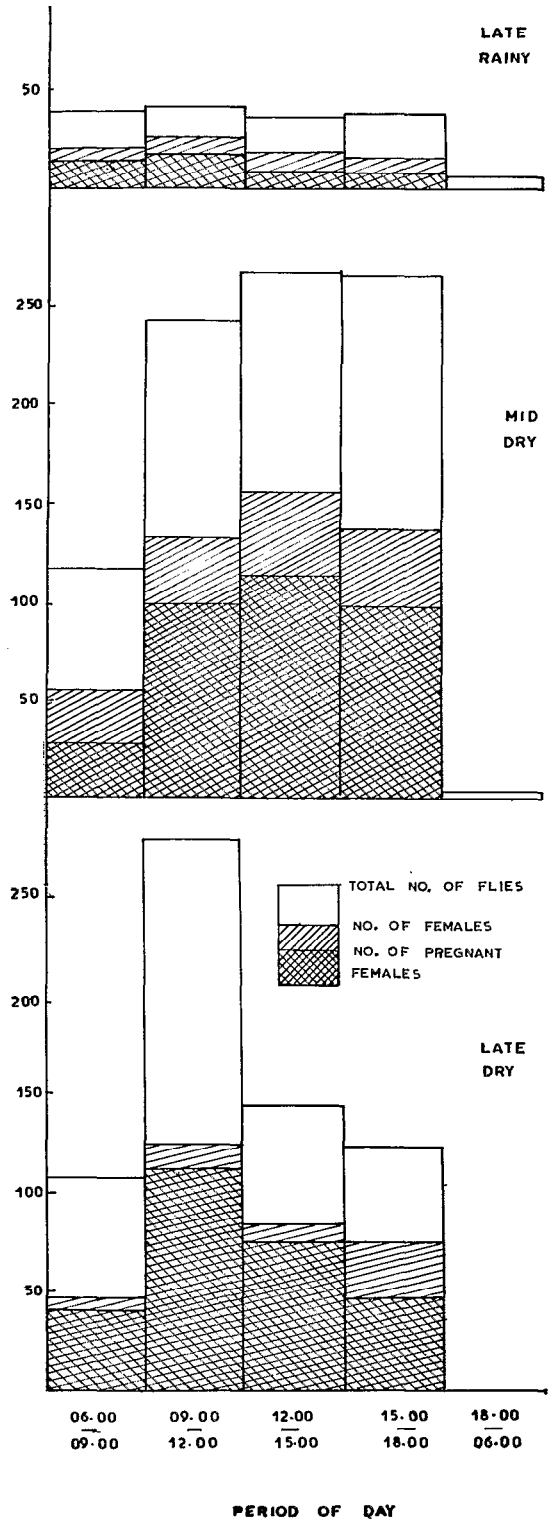

FIG. 2. — *Glossina p. gambiensis.* Gallery forest

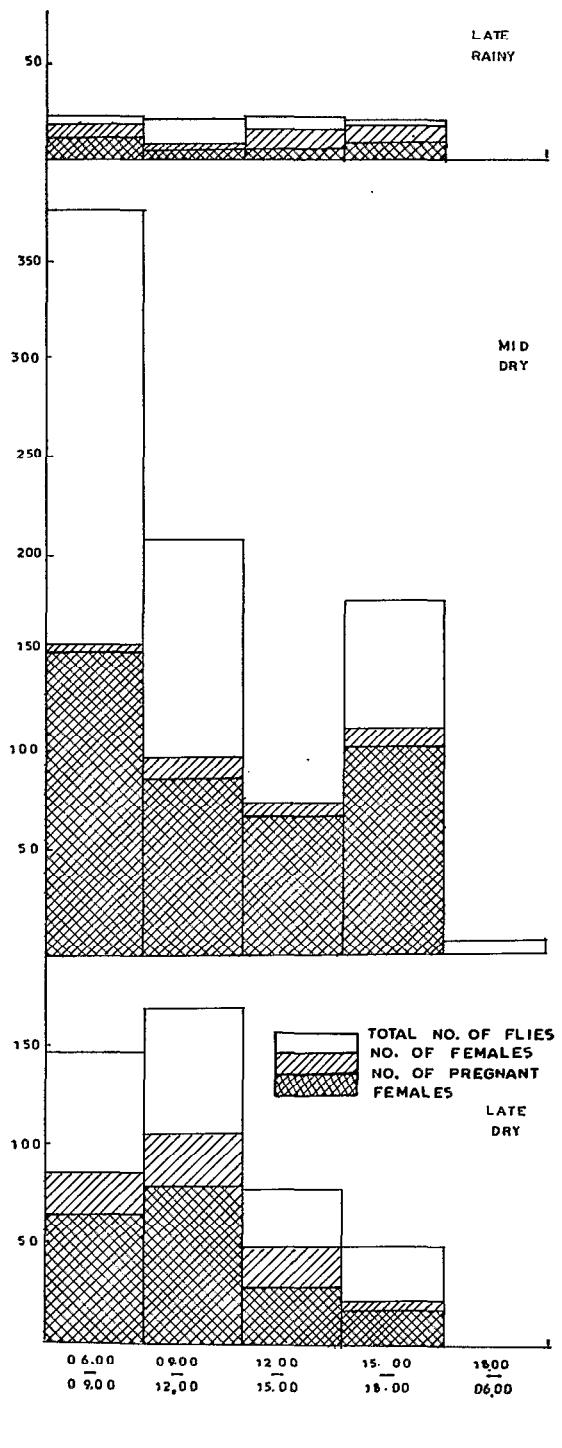

FIG. 3. — *G. m. submorsitans.* Savanna woodland

(24.47 %) and 18.00-06.00 (2.13 %) (fig. 2). Females accounted for 55.55 % of all flies ; 58.33 % of females were pregnant. Nocturnal activity was very reduced.

MID DRY SEASON

Differences in numbers of flies collected at various periods of the day were significantly heterogenous ($P < 0.001$, d.f. = 4, $F = 7.535$) ; the distribution was as follows : 06.00-09.00 (13.89 %), 09.00-12.00 (27.22 %), 12.00-15.00 (29.44 %), 15.00-18.00 (28.89 %) and 18.00-06.00 (0.56 %) (fig. 2). Although the highest number was recorded at 12.00-15.00, the geometric means for numbers collected at 09.00-12.00, 12.00-15.00 and 15.00-18.00 were not significantly different from one another. Consequently, there was a single, extended peak period of flight activity between 09.00 and 18.00. Females represented 54.12 % of the population, 67.31 % of females were pregnant (fig. 2). Nocturnal flight activity was very reduced. The activity cycles for males or females were similar to those of the combined sexes, except that the peak for females was more pronounced.

LATE DRY SEASON

Distribution of flies was as follows : 06.00-09.00 (17.95 %), 09.00-12.00 (38.34 %), 12.00-15.00 (23.81 %), 15.00-18.00 (19.90 %), 18.00-06.00 (0.00 %) (fig. 2) ; there was a discernible peak at 09.00-12.00. Females were 50.62 % of all flies ; 83.33 % of them were pregnant (fig. 2). Nocturnal activity was not recorded. Activity cycles for males and females were similar.

G. m. submorsitans **(savanna woodland)**

LATE RAINY SEASON

Distribution of flies among periods was homogenous : 06.00-09.00 (25.51 %), 09.00-12.00 (24.49 %), 12.00-15.00 (25.51 %), 15.00-18.00 (24.49 %) and 18.00-06.00 (0.00 %) (fig. 3) ; nocturnal activity was not observed. No peak was discernible. Pregnant females were active throughout the day.

MID DRY SEASON

Distribution of flies among periods was significantly heterogenous ($P < 0,01$, d. f = 4, M. S. = 500.94) : 06.00-09.00 (45,73 %), 09.00-12.00 (25.00 %), 12.00-15.00 (7.93 %), 15.00-1800 (20.73 %) and 18.00-06.00 (0.61 %) (fig. 3). Two peaks were therefore discernible ; the higher peak was at 06.00-09.00 and the lower at 15.00-18.00. Males or females exhibited similar cycles. Nocturnal activity was very reduced. Pregnant females were collected throughout the daytime periods. The proportions of pregnant females collected in savanna woodland in the mid dry and late rainy seasons were significantly different ($P < 0.01$, X^2 (1 d. f.) = 9.7667) ; 93.98 % and 53.33 % of females in the mid dry and late rainy seasons respectively were pregnant (fig. 3).

The correlation coefficients between patterns in diurnal activity cycles in savanna woodland during the mid dry and late rainy seasons were not significant for males ($r = 0.6649$) but for females ($P < 0,05$, $r = 0.8675$) and combined sexes ($P < 0.05$, $r = 0.8934$).

LATE DRY SEASON

Distribution of flies was as follows : 06.00-09.00 (33.72 %), 09.00-12.00 (37,91 %), 12.00-15.00 (17.44 %), 15.00-18.00 (10.93 %), and 18.00-06.00 (0.00 %) (fig. 2). Although the early morning (06.00-09.00) flight activity was relatively high, a single peak was recorded at 09.00-12.00 ; this was followed by a steep decline in activity. There was no nocturnal activity. Females were active throughout the day ; 76.73 % were pregnant (fig. 3).

G. m. submorsitans **(Gallery forest)**

LATE RAINY SEASON

Distribution of flies during different periods of day was homogenous : 06.00-09.00 (20.69 %), 09.00-12.00 (24.14 %), 12.00-15.00 (24.14 %), 15.00-18.00 (27.59 %), 18.00-06.00 (3.44 %) (fig. 4). No peak was discernible and nocturnal activity was extremely low.

The diurnal flight activity trends of *G. m. submorsitans* do not differ significantly in the gallery forest and savanna woodland during the late rainy season. The proportions of pregnant females as a segment of females in the two vegetation types during the late rainy season do not differ significantly.

MID DRY SEASON

Distribution of flies among periods was significantly heterogenous ($P < 0.05$, d. f. = 4, M. S. = 31.06) : 06.00-09.00 (25.46 %), 09.00-12.00 (26.85 % (26.85 %), 12.00-15.00 (25.00 %), 15.00-18.00

(22.69 %), 18.00-06.00 (0.00 %) (fig. 4). Although the highest number was collected at 09.00-12.00, the peak was not pronounced ; geometric means for the four daytime periods were not significantly different from one another. No nocturnal activity was observed.

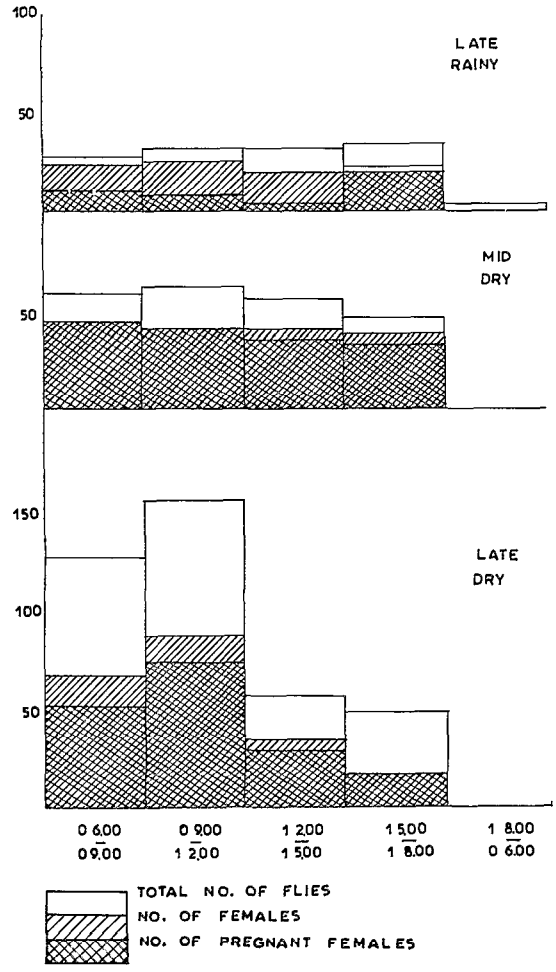

FIG. 4. — *G. m. submorsitans.* Gallery forest

The correlation coefficients between trends in diurnal activity cycles of *G. m. submorsitans* in gallery forest during the mid dry and late rainy seasons were not significant for males, but were significant for females ($P < 0.01$, $r = 0.9696$) and all flies ($P < 0.05$, $r = 0.9289$). The proportions of pregnant females collected in the gallery forest were significantly different between late rainy and mid dry seasons ($P < 0.001$, X^2 (1 d. f.) = 16.6674) ; 91.36 % and 44.19 % of females in the mid dry and late rainy seasons respectively were pregnant (fig. 4).

LATE DRY SEASON

Distribution of flies among periods was heterogenous : 06.00-09.00 (33.51 %), 09.00-12.00 (39.95 %), 12.00-15.00 (14.17 %), 15.00-18.00 (12.37 %) and 18.00-06.00 (0.00 %) (fig. 3). A single peak was recorded at 09.00-12.00. Nocturnal activity was not detected. Females were collected throughout the day ; 83.54 % were pregnant (fig. 4).

DISCUSSION

Different sampling methods of *Glossina* often capture different sections of the population. Glasgow (1961) noted that the composition of *Glossina* from the man-flyrounds, devised by Potts in 1930, was highly variable and contained only a small proportion of females. Bursell (1961) found that males from flyroungs were in sexually appetitive state and not ready to feed. Many of the earlier studies on diurnal and seasonal activity cycles of *Glossina* involved collections by handnets of flies attracted to walking parties of capturers (Nash, 1948, Foster, 1963, 1964, Challier, 1973, Gruvel, 1975) and cattle (Dean *et al.*, 1969). Although proportions of females were higher in numbers attracted to cattle, they were still lower than 50 %, and the percentage of pregnant females were insignificant. In contrast, the present results show approximately a 1 : 1 ration for numbers of males and females, irrespective of species or season. This ration is closer to the sex ratio for *Glossina* under natural conditions, determined by collecting wild pupae and rearing out adults (Dean *et al.*, 1968). These results show that females, including pregnant ones are also active. The preponderance of males in flyrounds catches had always given the erroneous impressions that females are very inactive. Factors influencing activity of *Glossina* include search for food, female partners by males, larviposition sites by females and resting sites by both sexes. Pregnant females feed more frequently and ingest larger meals than males (Finlayson and Langley, 1977) ; consequently, it is not surprising that they were frequently collected. It is likely that most of the pregnant females were in the early periods of their pregnancy, since

Boyle (1971) showed that feeding by pregnant females was restricted to the early part (first half) of pregnancy. It is therefore likely that the lower percentages of pregant females of both species recorded in the late rainy season may not be due to any depression in breeding as has been suggested by earlier workers (Johnson & Lloyd, 1923; Gordon & Davey, 1930; Taylor, 1932). It may be related to a probable increase in percentages of females in late pregnancy during that season, as a result of more suitable climatic conditions and increased food availability; these females are not active, and were therefore not found in substantial numbers. The reduction in flight activity of pregnant females during the rainy season, may also be a factor.

It should be stressed that not all types of tsetse traps yield high proportions of females; Saunders (1964) collected mainly males from brown and black Morris traps, while Vale (1974) recorded significant percentages of females in his electric traps.

G. p. gambiensis (gallery forest)

Challier (1973) recorded six main phases in diurnal activity of members of the subgenus Nemorhina (includes *G. p. gambiensis*); appearance of tsetse at sunrise, progressive increase of attacks to a morning maximum, slackening of biting activity in the middle of the day, vespertine maximum of activity, rather sharp decline in the evening and cessation of activity at dusk. Challier related these variations to fluctuations in temperature and saturation deficit. The patterns of activity recorded in the present study do not synchronize completely with Challier's phases. In each of the three seasons, flight activity of *G. p. gambiensis* started at sunrise (06.00-09.00). Challier postulated that above the threshold of 16°C, *G. p. gambiensis* became active. Light may also be important, since Lewis and Taylor (1965) showed that light was important in the flight of many insects. Brady (1972) also noted very negligible flight activity in the dark during laboratory studies on spontaneous activity in *Glossina*. Eouzan (1977) theorized that *G. p. gambiensis* becomes active when two conditions are realized simultaneously : temperatures above 16°C and light intensity close to that observed at sunrise. The mid dry season yielded the lowest percentage of active flies at 06.00-09.00; this suggests a delayed start of activity during this season. In the mid dry season, morning temperatures rise more slowly, as a result of the cold northeast winds. The progressive increase in activity to a morning maximum noted by Challier, was observed in all seasons. Excluding the morning maximum, differences in patterns of activity were discovered among seasons. In the late rainy season, flight activity was uniformly distributed during the day. This pattern was probably due to the uniform moderate temperatures at that period of the year. Page (1959) found a similar pattern for *G. p. palpalis* during the rainy season in Nigeria. The maintenance of relatively high numbers of active flies during the periods 12.00-15.00 and 15.00-18.00 in the mid dry season, was probably because, although temperatures were higher than those prevailing during the rainy season, they were not excessive. The gallery forest canopy still provided sufficient cover. However, in the late dry season, when gallery forest canopy was minimal and afternoon temperatures in the shade often reached 40-41°C, the steep decline in numbers of actives flies is not surprising. The virtual absence of night flight activity confirms Brady's (1972) laboratory observation that the endogenous flight rhythm in *Glossina* is negligible in darkness. However, the recording of very low nocturnal activity during the late rainy and mid dry seasons implies some activity, as has been demonstrated for other *Glossina* spp. : *G. longipennis* (Lewis, 1950), *G. pallidipes* (Moggridge, 1948), *G. brevipalpis* (Harley, 1965).

The differences between the patterns noted in the present results and Challier's (1973) classification could be attributed to several factors. These include differences in sample compositions; the present results show a high proportion of females, particularly pregnant females. Probable differences in nutritionnal states could also contribute to differences in flight activity; Brady (1971) showed higher activity among hungry flies. Bursell (1961) discussed the physiological aspects of *Glossina* activity and recognized four stages, related to stages of digestion and reconstitution of fat reserves. Since an endogenous rhythm for *Glossina* flight activity has been established, other differences in physiological states of flies may also cause differences in flight activity patterns among populations.

G. m. submorsitans (Savanna woodland)

The start of activity at sunrise, recorded for *G. p. gambiensis* was also observed for *G. m. sub-*

morsitans. Dean *et al.* (1969) establied field threshold temperature of 13-14°C, for the initiation of flight activity by *G. morsitans* ; this is slightly lower than Challier's 16°C for *G. p. gambiensis*. Jack (1939, 1941) determined a higher threshold of 18°C for *G. morsitans*. Nash (1937) was able to demonstrate an activity cycle closely related to temperature for *G. m. submorsitans*. The progressive increase in activity leading to a morning maximum, was noted in all seasons. However, this maximum was most easily reached in the mid dry season, when temperatures at sunrise are lowest. Welch (1958) also found *G. m. orientalis* very active between 06.00 and 08.00 hr. It is therefore likely that temperature fluctuations do not explain all *Glossina* flight activity variations ; furthermore, thresholds for activity vary from one worker to another.

The homogeneity in flight activity during the day, in the rainy season was probably related to moderate uniform climatic conditions. The depression in activity shortly after midday for *G. m. submorsitans*, noted by Nash (1937) was also observed in the mid and late dry seasons, when afternoon temperatures in the woodland were high. The late afternoon peak of activity observed by Nash was recorded only in the mid dry season ; temperatures in the late dry season were probably very high, causing a decline in activity. Jack & Williams (1937) found changes in *G. morsitans* behaviour close to 32°C ; this temperature is usually surpassed in the late dry season. The mid dry season flight activity pattern for *G. m. submorsitans* in the savanna woodland is the closest to Brady's (1972) V-shaped spontaneous circadian flight activity rhythm for *G. morsitans*. Nocturnal activity was virtually absent ; however, the low activity noted in the mid dry season confirms Nash's (1933) observation that *G. morsitans* occasionally bites at night.

G. m. submorsitans **(Gallery forest)**

The lack of any significant difference in the flight activity cycle patterns of *G. m. submorsitans* in the gallery forest and savanna woodland shows that uniform moderate climatic conditions were also prevailing in the gallery forest. Dean *et al.* (1969) noted a similar pattern for *G. morsitans* during the rainy season in Rhodesia (Zimbabwe). The significant difference in patterns of activity of this species in the gallery forest and savanna woodland in the mid dry season probably indicates differences in climatics conditions. The homogeneity in flight activity among periods in the gallery forest during the mid dry season suggests that climatic conditions were uniform in the gallery forest. The gallery forest canopy was probably still providing enough shade. The similarities in flight activity cycle patterns for *G. m. submorsitans* in the gallery forest and savanna woodland during the late dry season is surprising, since conditions were generally more moderate in the gallery forest at that time of the year, hence the concentrations of woodland species (*G. morsitans*) in the gallery forest during the late dry season. It is therefore obvious that changes in climatic conditions can not wholly explain variations in *Glossina* flight activity cycles.

These results also show that within the same vegetational zone, differences in flight activity cycles of *Glossina* may occur between plant communities.

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