Acta Oecologica 19 (5) (1998) 453-471 / © Elsevier, Paris

# Tsetse flies, biodiversity and the control of sleeping sickness. Structure of a *Glossina* guild in southwest Côte d'Ivoire

Jean-Paul Gouteux \*, Marc Jarry

Laboratoire d'écologie moléculaire, Orstom, UPRES-A CNRS 5053, IBEAS-UPPA, avenue de l'Université, 64000 Pau, France. \* Corresponding author

Received November 14, 1996; revised English translation April 15, 1998; accepted September 29, 1998

Abstract - Tsetse fly guilds usually comprise two or three species. However, the presence of only one species often indicates that anthropic modifications have occurred in the habitat. On the other hand, more than three species are seldom observed in the same zone and the presence of five is extremely rare. Previous detailed studies have always focused on a single species, without taking into account interactions between species. The authors present the results of observations carried out in Côte d'Ivoire on a guild consisting of Glossina palpalis, G. pallicera, G. nigrofusca, G. longipalpis and G. fusca. Glossina have unusual physiological characteristics: both sexes feed exclusively on blood, they have a highly developed larviparity associated with a slow rhythm of reproduction (one larva about every ten days) and a long life expectancy (up to nine months). The authors report on the size of the flies, the hosts, feeding habits, ecodistribution, resting-places, flying heights, circadian activity and seasonal dynamics of tsetse fly populations in order to understand the organization of this guild. Each species feeds indiscriminately on a wide spectrum of hosts without a particular preference. Different species shared habitat (ecodistribution) and time (circadian and annual cycles). Thus, during an annual cycle, there is always a slight time-lag between the density peaks of G. palpalis and G. pallicera, the peak of the dominant species immediately preceding that of the dominated species. In a village area, 77 % of the variations in density of G. pallicera were accounted for by the previous variations in density of the dominant species (G. palpalis). Experiments show that G. pallicera and G. nigrofusca immediately invade anthropic areas from which G. palpalis has been partially removed by trapping. These species thus appear to confront each other in a global dynamic equilibrium. This suggests that there is a 'conflicting coexistence' between the cohabiting species. Whereas the reason for such a process is quite obvious, how it occurs still remains to be explained. Other observations may provide a clue. For example, the sex ratios of both the main species fluctuate in opposite phases during the annual cycle. This strongly suggests that interspecific interactions occur through sexual mediation. Finally, the authors discuss the consequences of dynamic cohabitation on disease systems (trypanosomes, tsetse flies, hosts) and on control possibilities. © Elsevier, Paris

Tsetse fly guilds / Glossina palpalis / G. pallicera / G. nigrofusca / interspecific interaction / sexual behaviour / Côte d'Ivoire

# **1. INTRODUCTION**

Glossina only occur in Africa where they form a family consisting of a single genus and three subgenera. Two fossilized species from the Miocene period 20 to 30 million years ago have been found in Colorado, USA. These American species probably disappeared following the glaciation of the Pleistocene period [2]. There are currently 31 known taxons, species or sub-species divided between three sub-genera: 9 Nemorhina Robineau-Desvoidy, 1830 (the palpalis group), 7 Glossina s. str. Zumpt, 1935 (the morsitans group) and 15 Austenina Townsend, 1921 (the fusca group). On the whole, the species in each group have homogeneous ecological characteristics. The first group consists of riverine Glossina, the second group are savannah species and the third group comprises the forest and dusk Glossina. Many species from the fusca

group are rare and not well documented. Some seem to be rapidly declining with the disappearance of the great African forest [26].

All these species – potential vectors of various species of trypanosomes – have unusual and similar physiological characteristics [3, 16]. Both sexes feed exclusively on blood and take a blood meal every 3 to 4 days [6]. The females mate during the first few days of their life and the sperm stored in spermathecae lasts for their lifetime. The males remain sexually active throughout life. The females do not lay eggs, but deliver a mature larva (ready to pupate) after a gestation of about ten days. During gestation, the larva is fed on a secretion in the mother's uterus. This larviparity results in a relatively slow reproductive rhythm (one larva about every 9–11 days). The pupal period (25-55 days) is similar for all the species. Specimens of marked *G. palpalis* have been recaptured seven to



Fonds Documentaire ORSTOM Cote:  $B \times 16140$  Ex: 1 nine months after being released, which suggests a remarkably long life-span [5, 24]. Since the average life-span of a tsetse fly varies between one and two months depending on the climatic conditions, each female will deliver on average between 3 and 6 larvae during her life. The demographic strategy of tsetse flies is therefore a K-strategy, which is extremely rare for Diptera. This strategy is probably the result of adaptation to competition [1].

The term guild is used here to mean a group of species in the same taxonomic group that exploit the same class of resources [1]. This definition is similar to that used by MacNally and Doolan [70]: "a set of closely related species (usually coordinal or confamilial) that are both sympatric and synchronously active, and that forage on similar items in similar ways" (for a complete review of the guild concept, see Simberloff and Dayan [86]). Tsetse fly guilds usually comprise two or three species. The presence of only one species in a given area is generally related to anthropic modifications of the habitat, such as deforestation and elimination of wild hosts [48]. Few publications report on the cohabitation of three or four species. This has been observed in areas inhabited by wild game (nearly always wild animal reserves) where the presence of one or several species of the *fusca* group has been noted. During field work in the Vavoua sleeping sickness focus in Côte d'Ivoire, we caught up to five species in the same site, representing the three sub-genera of Glossina. This situation is extremely rare and to our knowledge has never been recorded in the literature. It is indicative of a very rich ecosystem with contrasting and varied botanical characteristics.

In the past, detailed studies have always been monospecific, even if several species were present in the zone considered. However, all tsetse fly species are potential vectors of trypanosomes. The problems related to the cohabitation of several species with very similar behavioural characteristics have been generally neglected. In this paper, we first present the characteristics of the tsetse fly populations of the Vavoua sleeping sickness focus in Côte d'Ivoire. Secondly, we show how the observed facts suggest that these species confront each other permanently in a global dynamic equilibrium. Using these results and other data from the literature, we put forward a hypothesis in an attempt to understand this conflicting coexistence. Finally, we discuss the consequences on the disease systems (hosts/tsetse flies/ trypanosomes) and on their control.

# 2. MATERIALS AND METHODS

# 2.1. Study zone

The zone in which various bio-ecological studies were conducted on tsetse flies between 1977 and 1982

is situated near the Vavoua sleeping sickness focus  $(7^{\circ}25' \text{ N}, 6^{\circ}24'30'' \text{ W})$  in the preforest area east of central Côte d'Ivoire (*figure 1*). The area is a mosaic of semi-deciduous forest, plantations (coffee and cacao) and savannah (including savannah on compact lateritic soil or 'Bowal') with Sudano-Guinean vegetation. It is furrowed with troughs where evergreen trees grow. The bioclimatic characteristics have been described in Gouteux et al. [36], Gouteux and Laveissière [31] and Hervouët and Laveissière [52].

#### 2.2. Sampling and analysis

All the data were obtained from *Glossina* captured with biconical traps [9] simplified by Gouteux et al. [34], some of which were used with a permanent capture system [34]. The details of the protocol and methods of analysis used for the various observations reported here are given in publications cited in *table I*.

#### **3. OBSERVATIONS**

# **3.1.** The species present

The three sub-genera (or groups) of the *Glossina* genus were found (*table I*): *G. palpalis palpalis* (Robineau-Desvoidy, 1830) and *G. pallicera pallicera* (Bigot, 1891) belong to the *palpalis* group whereas *G. nigrofusca nigrofusca* (Newstead, 1910) and *G. fusca fusca* (Walker, 1849) belong to the *fusca* group. *G. longipalpis* (Wiedemann, 1830), the least common species, belongs to the *morsitans* group. For simplicity, we use the binominal nomenclature instead of the more usual trinominal nomenclature (in addition, the specific or sub-specific status for *G. palpalis palpalis* and *G. palpalis gambiensis* is still under discussion [10]).

# 3.2. Adult size

From the point of the proboscis to the end of the wings, G. nigrofusca measures about 20 mm (17– 22 mm), G. pallicera 15 mm (12–16 mm) and G. palpalis 12 mm (10–14 mm) (figure 2). G. pallicera and G. longipalpis are of comparable size, as are G. nigrofusca and G. fusca, the latter being slightly smaller in the study zone. Female Glossina are usually larger than the males. Thus, a male G. pallicera can be smaller than a large female G. palpalis and female G. nigrofusca are often twice as big as male G. palpalis.

# 3.3. Abundance

*G. palpalis* and *G. pallicera* are the two most abundant species. *G. palpalis* is always the dominant species near human dwellings, villages and plantation settlements (seasonal or permanent encampments) [22,

2



Figure 1. The region of Vavoua and the study sites. Vavoua is situated near the west branch of the 'Baoulé V', the indentation of the savannah zone into the Côte d'Ivoire forest south of Bouaké.

Vol. 19 (5) 1998

7

Study Site	Biotopes Present	Species Captured	(1)	References	
Gatifla	village area	G. palpalis	AC	Gouteux [25]	
	(forest paths, plantations, troughs)	G. pallicera	AD	Gouteux et al. [44]	
		G. nigrofusca	PD	Gouteux and Buckland [29]	
		G. fusca	EC	Gouteux et al. [40]	
,			PH	Gouteux et al. [35]	
			RS	Gouteux and Dagnogo [30]	
				Gouteux et al. [38]	
				Gouteux et al. [49]	
				Gouteux and Laveissière [31]	
				Gouteux et al. [43]	
				Gouteux et al. [37]	
				Gouteux and Monteny [33]	
lantations south	settlements, plantations	G. palpalis	AD	Gouteux and Buckland [29]	
of Gatifla		G. pallicera	PD	Gouteux et al. [49]	
		G. nigrofusca	EC		
		G. fusca			
Doka encampment	settlement, forest paths	G. palpalis	AD	Gouteux [21]	
	plantations, troughs	G. pallicera	PD	Gouteux et al. [35]	
		G. nigrofusca	EC		
		G. fusca	RS		
Kaloufla	village	G. palpalis	EC	Gouteux et al. [35]	
	-	G. pallicera			
		G. nigrofusca			
Biriba encampment	settlement, forest paths, plantations	G. palpalis	AD	Gouteux [22]	
-	· · · ·	G. pallicera	EC	Gouteux [23]	
		G. nigrofusca	PH	Gouteux et al. [43]	
		G. fusca			
		G. longipalpis			
Koudougou crossroads	village area, forest paths	G. palpalis	AD	Challier and Gouteux [8]	
	plantations, troughs	G. pallicera	EC	Gouteux [21]	
		G. nigrofusca	CT	Gouteux et al. [39]	
		G. fusca	PH	Gouteux et al. [44]	
		G. longipalpis	FH	Gouteux et al. [43]	
Dé Forest	plantation	G. palpalis	AD	Challier and Gouteux [8]	
	-	G. pallicera	EC	Gouteux [20]	
		G. nigrofusca	PH	Gouteux et al. [43]	
		G. fusca			
		G. longipalpis			
La Léraba (2)	forest galleries	G. gambiensis	СТ	Laveissière and Couret [64]	
	Torost Buildings	G. morsitans		Sateronice and course [04]	
		J. morantino			

Table I. Species, biotopes and studies carried out in the sites mentioned in the text. The situation of the study sites is shown in figure 1.

 (1) Types of study. Studies conducted over an annual cycle: EC, ecodistribution; PD, population dynamics/capture-recapture; AD, population dynamics/ apparent densities; RS, resting sites; AC, activity; PH, pupal habitat. Single studies: CT, control trials; FH, flight height. Studies conducted systematically in all sites: estimation of the apparent densities, feeding preferences (origin of the blood meals), structure of the populations by physiological age group.
 (2) This site is situated in the north of Côte d'Ivoire in the Guinean savannah zone.

31, 38]. This species is considered to be the principal sleeping sickness vector in the Côte d'Ivoire foci. *G. nigrofusca* and *G. fusca* are respectively the third and fourth most abundant species. These two species usually account for less than 20% of flies. *G. longipalpis* is only captured east of the study zone (figure 1, table I) and always in small numbers.

### **3.4. Ecodistribution**

We have not been able to show a significant difference between the distribution of the pupae of the three species in the different types of habitat. In the village area, 67% of the pupae belonged to *G. palpalis*, which corresponds to the dominance of this species in this area [43].

As for adults, the study of ecodistribution using trapping data has shown that the distribution is aggregative for all species. The ecodistribution of *G. nigrofusca* and *G. fusca* is even more aggregative than that of the dominant species and their tendency to aggregate increases with density. In contrast, for the two dominant species, *G. palpalis* and *G. pallicera*, the tendency to aggregate disappears for brief periods corresponding to maximum density peaks [23].

All the species have several common behavioural characteristics. The insects concentrate along flight lines which follow the edge of the forest [38–40], and in particular, forest paths. The four principal species cohabit in most of the biotopes [8]. In the forest-plantation mosaic zone, G. pallicera may dominate G. palpalis depending on the period and the biotope sampled. Thus, around a one-family permanent settlement (Biriba, *figure 1*, *table I*) where the five species were represented, G. palpalis dominated, except for a short period during which G. pallicera was dominant. Of the 100 371 tsetse flies captured around this settlement continuously between January 1978 and April 1980, 55 % were G. palpalis, 35 % G. pallicera, 8 % G. nigrofusca, 2 % G. fusca and 0.3 % were G. longipalpis. In the village of Gatifla (300 inhabitants), G. palpalis accounted for 100 % of the captures; on the outskirts of the village, this species still represented 96 % of the captures (Shannon index H' = 0.34) and at the watering place, it only represented 74 % (H' = 1.07). Several kilometres from the village, in the plantation paths, G. pallicera (67 %) dominated G. nigrofusca (19.5%) and G. palpalis (13.5%) and the Shannon index reached 1.24 [38]. In plantation zones, the biodiversity was less in coffee plantations (H' = 0.99) than in cacao plantations (H' = 1.23). Far from human dwellings, the species composition in coffee plantations varied markedly according to the age of the plantation (figure 3). The biodiversity was greatest in young plantations (3 years) with H' = 1.63, versus H' = 1.07 for the new ones (1 year) and H' = 1.27 for the oldest (7 years or more) [20]. The 3year old coffee trees form low cover for small antelopes (*Cephalophus* sp. and *Tragelaphus scriptus*) and cane rat (*Thryonomys* sp.). The appearance of coffee plantations does not change after 6–7 years and the diversity of this *Glossina* community is maintained at a lower level once the environment has stabilized.

The ecodistribution of tsetse flies has long been considered to be relatively simple [16]. However, a more detailed study of the ecodistribution of *G. palpalis* in a village setting has shown that this apparent simplicity masks an unsuspected complexity [25]. Indeed, both sexes are distributed quite differently in the habitat. The young nulliparous females and the males occupy shady damp areas, whereas the parous females are in the clearings and at the edge of the forest. The older the female, the more they prefer the sunny areas. Old females are also the group most involved in the dispersal of flies [20, 21, 38, 39]. Considerable movement of both *G. palpalis* and *G. pallicera* female flies has been observed in plantation zones [22, 23].

# 3.5. Diurnal and nocturnal resting sites and flight height

The diurnal and nocturnal resting sites of the three principal species of the guild seem to be similar [44]. Experiments involving trapping at different heights have been conducted to determine whether flight height could be used to distinguish between the species. The results found a similar distribution in the captures of *G. palpalis*, *G. pallicera*, *G. nigrofusca* and *G. fusca*. The maximum number of flies (nearly 90%) were captured at 15–50 cm (normal height of the trap opening). At 1 m from the ground, the captures represented less than 10% of the total, at 1.5 m, they represented less than 1% and above 1.5 m, no captures were recorded [44].

# 3.6. Circadian activity

G. palpalis and G. pallicera are two exclusively diurnal species. For G. palpalis, the activity and aggressiveness are greatest in the middle of the day [30, 33]. G. pallicera tends to be active throughout the day with a peak in the morning around 9h00 and in the afternoon around 15h00. This species remains active in the evening after 17h00. G. nigrofusca differs from the other two species in that it is active at dusk (figure 4). These types of activity vary according to the season and the biotope. In the hot dry season and in sunny biotopes, the circadian cycle of G. palpalis presents a peak at the end of the morning and the beginning of the afternoon; the bimodal aspect of the circadian cycle of G. pallicera is even more marked [33]. In the village area, the male G. palpalis are active

J.-P. Gouteux, M. Jarry



Figure 2. Scale drawings of the five species in the Glossina guild present in the study zone.

Acta Oecologica

458

**Figure 3.** Variations in the number of *Glossina* captured in plantations of different ages. Trapping was carried out five times for 7 to 10 consecutive days using 10 to 17 traps per plantation, in July, September and December 1979 and January and March 1980. Botanical characteristics of the plantations: 1 year, trees planted on burnt stubble; 3 years, low copse; 7 years and more, permanent appearance, trees 2–3 m high with low growing sparse vegetation. Site: Dé forest [20].





Figure 4. Circadien cycle activity: the percentage per hour of the daily catch of *G. palpalis* ( $\Box$ ), *G. pallicera* (O) et *G. nigrofusca* ( $\blacklozenge$ ). Results obtained over an annual cycle from February 1981 to February 1982 (6 239 *G. palpalis*, 1 160 *G. pallicera* et 960 *G. nigrofusca*). Site: Gatifla [33].

about a quarter of an hour later than the females, whereas the opposite is true for *G. pallicera*.

Vol. 19 (5) 1998

#### 3.7. Annual population dynamics

# 3.7.1. Seasonal trends

When G. palpalis accounts for nearly all the flies in the guild in a village area, a single peak is observed (in October) during the annual cycle [29, 31]. When the number of G. pallicera is relatively high, two peaks are observed for both G. palpalis and G. pallicera, the first in May-June and the second between September-December (figure 5). There is a remarkable similarity in the overall seasonal trend in the number of individuals of these two species studied in different annual cycles, in different zones and with different methods of evaluation. In the plantation zone south of Gatifla (figure 1, table I), the absolute number of individuals were estimated by the capture-recapture method in 1981-82 [29]. In the plantation zone of the Vavoua focus (Biriba, figure 1, table 1), the apparent trap densities were obtained during a permanent trap experiment conducted over 28 months (in 1978-1980) in which 12 traps were arranged in a circle of 40 m radius around a one-family settlement and the contents recorded every 3 to 4 days (figure 5A [22, 23]). The overall similarity can be explained by abiotic factors, in particular by the distribution of rainfall [31].

The overall annual population dynamics of G. palpalis and G. pallicera are similar, but there is always a slight time-lag between the density peaks, the

459

2



Figure 5. Trend in the number of *G. palpalis* ( $\Box$ ), *G. pallicera* (O) (A), *G. nigrofusca* ( $\blacklozenge$ ) (B), *G. fusca* (D) and *G. longipalpis* (+) (C) in the plantation zone. Continous captures with 12 traps recorded every 2–3 days for two annual cycles (over 100 000 *Glossina* captured). The control programme was carried out in a nearby zone (4 km) in December–January 1978–79, over an area of 870 ha. Site: Biriba encampment [22].

460

peak of the dominant species immediately preceding that of the dominated species. The dominant species is *G. palpalis* in the Biriba settlement (*figure 5A*) [22] and *G. pallicera* in the plantation zone south of Gatifla [29]. The zones are comparable in both cases (coffee plantations). In the Biriba settlement, 77 % of the density variations of *G. pallicera* are accounted for by the variations of *G. palpalis* in the previous month, whereas the variations of *G. palpalis* are independent of *G. pallicera* ( $R^2 = 0.03$  [22]). Peaks of *G. nigrofusca* and *G. fusca* occur when the numbers of *G. palpalis* and *G. pallicera* decrease (*figure 5B*). *G. longipalpis* are captured occasionally, but a peak is recorded when the densities of the other species, especially *G. nigrofusca*, are very low (*figure 5C*).

# 3.7.2. Differences related to sex

When G. palpalis is the dominant species, the females are always more numerous than the males. This was observed in the captures (figure 6A) done in the Biriba settlement (figure 1). This difference is less marked in the middle of the dry season -a period of high mortality which evens out the numbers in each sex [31]. In general, females account for 60 to 70 % of the individuals of this species [29]. For G. pallicera, the dominated species, the difference in the number of flies in each sex is not so clear (figure 6A). On the other hand, when G. pallicera is the dominant species, the difference in number of each sex is greater for this species than for G. palpalis [29]. In this case, only G. pallicera presents a difference between males and females regarding the correlation of the number of flies with climatic factors [29]. There is very little difference between the proportion of sexes for the other three species, which are always numerically dominated. The study in the Biriba settlement showed spectacular fluctuations in the apparent densities of G. palpalis and G. pallicera: the proportion of females varied symmetrically in opposite phases over two annual cycles (figure 6B). It is of interest to note that when the change-over of dominance occurred (between October and November 1978 and between December 1978 and January 1979), the spatial pattern of each species was similar whereas the rest of the time each species occupied separate parts of the habitat [22].

#### 3.8. Feeding hosts

*G. palpalis* is a species with opportunistic feeding habits [72]. It is generally more anthropophilic than *G. pallicera* or *G. nigrofusca*. For both *G. palpalis* and *G. pallicera*, the males usually take a higher proportion of human blood meals than do the females [41, 42]. When swine are present, they are the principal hosts for *G. palpalis*. *G. pallicera* and *G. nigrofusca* feed frequently on bovids, mainly small ante-

lopes (duiker and bushbuck) which are numerous in the study zone (table II). In coffee plantations where there are no pigs (they remain in the village), the range of hosts is different. The proportion of meals taken on man is higher, and bovids are the principal hosts for all species; the proportion of blood meals on bovids reaches 82 % for G. nigrofusca. This species can however be anthropophilic in certain cases. For example, where there is a high density of this species, G. nigrofusca may bite farmers during their evening occupations (e.g. washing) (Gouteux, unpubl.). Bovids provide more meals in coffee plantations than in cacao plantations. This is because, unlike in cacao plantations, there are still thickets in coffee plantations in which antelopes can hide [41]. The differences in the choice of hosts correspond therefore to differences observed in the ecodistribution of these three species. It is not known whether these species have true feeding preferences or whether they feed on the most accessible hosts in their respective areas. Given the wide range of hosts, it is not possible to determine precise ecological niches for the different species studied. Instead, there are large overlaps.

# 3.9. Parasitism

A new species of the tsetse fly parasite Mermithidae was discovered during these studies [77]. In March-April 1979, this parasite, *Hexamermis glossinae*, presented the highest infection rate in *G. nigrofusca* (7.7%), the lowest in *G. pallicera* (2.4%) and intermediate in *G. palpalis* (5.6%). The difference between the infection rates of *G. palpalis* and *G. pallicera* is statistically significant. The numbers of *G. nigrofusca* were insufficient to allow a statistical comparison. This difference might be due to a site of infection in one of the pupal habitats around the village, Indeed, infection occurs mainly during the larval stage and when young flies emerge. Infection of adults is possible but is more rare [37].

# **3.10.** Experimental demonstration of interspecific equilibria by intensive trapping

In the Biriba plantation settlement (*figure 1*), the abnormally low densities observed after the dry season (December 1978–February 1979), presented in *figure 5*, are the indirect consequence of control trials over 400 ha in a zone situated 4 km further southwest [22, 66]. The densities of *G. nigrofusca* were particularly affected (*figure 5B*), those of *G. fusca* and *G. longipalpis* much less (*figure 5C*); the latter even presented a slight peak in June-July-August 1979 when this species became more numerous than *G. nigrofusca* and *G. fusca*.

Ļ

In the village of Gatifla (*figure 1*), a one-week trapping experiment produced a regular decrease in the apparent density from 16 to 7 *G. palpalis* per trap per day and a gradual increase from 0.45 to 1.5 *G. pallicera* per trap per day [35]. Before these experiments, the populations were estimated by capture-recapture techniques at 7 000 for *G. palpalis*, but the

populations of *G. pallicera* and *G. nigrofusca* could not be assessed because the numbers were too small. In another experiment, the population of *G. pallicera* was estimated at a few hundreds [38].

In the Doka plantation (*figure 1*), an isolated coffee plantation in the forest, this observation was more spectacular [21]. From the fourth day of trapping, the



Figure 6. Variation in the sex ratio, expressed as the percentage of females for each species (A) and for the total number of flies (B). Trapping of *G. palpalis* ( $\Box$ ) et *G. pallicera* (O) was carried out over two annual cycles. The percentages are shown with 95 % confidence intervals. Site: Biriba encampment [22, 23].

[].								
Zone	Tsetse fly species	Man	Bovids	Suids	Other	n (1)		
Whole area	G. palpalis	14.4	25.4	56.2	28.0	694		
	G. pallicera	9.3	59.6	23.7	7.2	97		
	G. nigrofusca	10.7	64.3	21.4	3.6	28		
Coffee plantations	G. palpalis	35.6	45.8	11.9	6.8	59		
	G. pallicera	13.3	76.7	6.7	3.3	30		
	G. nigrofusca	0.0	81.8	18.2	0.0	11		
Cacao plantations	G. palpalis	25.0	27.5	42.5	5.0	40		
	G. pallicera	6.3	68.8	25.0	0.0	32		
	G. nigrofusca	0.0	66.7	33.3	0.0	9		

Table II. The hosts of the three principal *Glossina* species in 1977–1981 (%) in the whole study zone (Vavoua focus), in the coffee plantations and the cacao plantations [42].

(1) Sample size

sizes of the captures became reversed. *G. pallicera* became the dominant species and the number of *G. nigrofusca* captured was greater than the number of *G. palpalis* (*figure* 7A and B). Thus, the elimination of the dominant species *G. palpalis* by intensive trapping (46 traps) was immediately followed by an increase in the number of captured *G. pallicera* and *G. nigrofusca*. The populations estimated by capture-recapture techniques were 4 000 *G. palpalis*, 17 000 *G. pallicera*, 5 000 *G. nigrofusca* and a few hundred *G. fusca* [35].

In the north of Côte d'Ivoire, where *G. tachinoides* is the dominant species and *G. gambiensis* the dominated species, trapping control experiments conducted by another team from 1977 to 1982 modified considerably the existing equilibrium [64]. The densities which were approximately 60 *G. tachinoides* per trap per day versus 3 *G. gambiensis* per trap per day stabilized at respectively 34 and 28 flies per trap per day [64]. Furthermore, it was observed that the sum of the density of these two species remained constant throughout these experiments (between 58 to 63 flies per trap per day).

#### 4. INTERPRETATION

The coexistence of tsetse flies is organized by sharing time, space and feeding hosts.

#### 4.1. Time sharing

In the ecology of animal communities, time is an important partitioning factor between species [85]. Time is shared between species over the circadian cycle. The existence of differences in the activity cycle of *G. palpalis* and *G. caliginea*, two species which cohabit in the mangrove swamps near Douala (Southern Cameroon), were highlighted by Eouzan and Ferrara [15]. In the present study, separation in time

was observed but there was a broad overlap, especially between the two principal species, *G. palpalis* and *G. pallicera*.

Over an annual cycle, the opposite phases observed between the apparent density peaks of G. palpalis and G. pallicera seem to be a normal occurrence. Rogers and Randolph [79] reported such fluctuations between G. palpalis and G. tachinoides in an area of Nigeria: "each species reaches a peak in numbers at a different time of the year, when the other species is scarce" (data from Onyia [76] on G. palpalis and from Morris and Morris [73] on G. tachinoides). They also observed this for G. fuscipes, G. pallidipes and G. brevipalpis in Uganda (data from Okoth, unpubl.). For Rogers and Randolph [79], this separation in time minimizes interspecific competition: "The flies would not escape competition completely, but its effect would be minimized through temporal separation". In reality, this seasonal factor, which is clearly an abiotic determinant of the fluctuations in the number of tsetse populations, can not easily account for the time-lag observed between G. palpalis and G. pallicera over a few weeks, which interchanges according to the dominant species. The cohabitation of tsetse flies involves more complex mechanisms, which are completely biotic and density-dependent.

Before going further, it must be noted that the origin of the fluctuations observed here or reported in the literature is not fully understood. Indeed, the *Glossina* population dynamics are characterized by a low reproduction rate (*K*-strategy) related to larviparity [59]. A model for isolated populations suggests that population dynamics are close to equilibrium [59, 60]. The high density peaks observed are therefore difficult to explain by a local increase (in the Biriba settlement in November 1978 for *G. pallicera* and April–May and October–November 1978 for *G. palpalis, figure 5*). These peaks are nearly all due to females. Since

.

females have a tendency to disperse, unlike males [38], these peaks could correspond to immigration waves of females in the dispersal phase, crossing the 'continuum' formed by the forest-plantation mosaic.

The absence of a decrease effect of trapping in this study is due to the low number of traps and the high number of fly populations. These fly populations do not have well-defined geographic limits in this forest-plantation continuum and are not fixed by particular concentrations of hosts (human or animal). This sector only consists of small scattered plantation settlements. There has not been a short-term trapping effect on the composition of the species (as in other experiments shown in *figure 7*) or a long-term effect on the physiological age of the females [22]. According to Utida [93] and Janzen [58], the stability of a system of

several cohabiting species could be enhanced by the presence of predators which do not have a particular preference for any of the species. The twelve traps in the Biriba settlement could have acted as immobile predators which are insensitive to fluctuations of the prey and exert a similar and constant pressure on the various species of *Glossina*. Under this hypothesis, the traps would have become an integral part of the local ecosystem, the equilibrium of which would not be modified but reinforced. This is probably no longer true after the drastic reduction in *Glossina* populations following the control experiments conducted 4 km from this camp (figure  $\overline{I}$ ); indeed, given that these populations disperse evenly over large areas in the forest-plantation continuum, they will have been affected far from the study zone.



Figure 7. Trend in the number of *G. palpalis* ( $\Box$ ), *G. pallicera* ( $\bigcirc$ ), and *G. nigrofusca* ( $\blacklozenge$ ) during continuous trapping experiments (48 traps) in September 1978 (A) and November 1978 (B). Site: Doka encampment [35].

#### 4.2. Sharing space

The control trials which considerably reduced G. palpalis and G. nigrofusca populations in the Biriba settlement seem to be responsible for the increase in apparent density of G. longipalpis. This relatively rare species is much more abundant in the savannah east of the study zone [7]. Together with G. fusca, which is the dominant species further south [65], G. longipalpis may be a replacement species when the local dominant species becomes scarce. This situation is well known for maintaining biodiversity in other ecological systems (e.g. aquatic systems [68]). These observations, and the more or less immediate replacement of G. palpalis by G. pallicera in the village zone or by G. pallicera and G. nigrofusca in the plantations, demonstrate the intensity of the competition for occupation of space. They suggest the involvement of demographic pressure related to the size of the different populations (density-dependent effect). A large population of one species produces a demographic excess which exerts pressure on the populations of the other species. Glossina thus share space in a dynamic equilibrium. Trapping in the preferred habitat of a species might thus disturb this fragile equilibrium between populations.

#### 4.3. Sharing hosts

These observations reveal the existence of an 'equilibrium ratio' between the populations of the different species in the guild. This equilibrium assumes that the maximum carrying capacity of the environment has been reached. In the plantation zone, the notion of the carrying capacity seems well established for G. palpalis and G. pallicera. Indeed, the total number of flies estimated over an annual cycle remained constant during the climatically favourable seasons, the considerable specific fluctuations being mutually compensated [29]. The difficulty is in defining the concept of carrying capacity in this case. An excess of bites produces a reaction in the host which reduces the success rate of blood meals according to the density of flies. This has been reported by Vale [94] as a factor of intraspecific competition for tsetse flies, and the same observations were made by Waage and Davies [97] for tabanids. In the plantation zone, small antelopes are the principal hosts of these two species and it is probably their densities which limit the densities of their 'predators'. In the north of Côte d'Ivoire, G. tachinoides and G. palpalis gambiensis presented a similar phenomenon of variations in their apparent densities [64] which finally led to a stable and constant mean density. These two species both seem to be as opportunist in the choice of hosts and as well adapted to this bioclimate. The observed supremacy of G. tachinoides (20 times greater in number than control), a smaller species than *G. gambiensis*, might be due to a slightly better ability to adapt during difficult periods (severe drought, bovine plague). *G. tachinoides* would have taken advantage of these periods to gradually establish its dominance in numbers. The dominance of *G. tachinoides* over *G. gambiensis* in this study zone may thus reflect the previous local history of these two species, when random events probably played a significant role.

Competition of G. nigrofusca with the opportunistic species of the *palpalis* group is reduced because of its dusk specialization which could be an adaptation of the fusca group species to the forest antelope. In the daytime, bushbuck (Tragelaphus scriptus) and duiker (Cephalophus sp.), the major hosts of G. nigrofusca in the study zone, hide in the thicket which tsetse flies can only penetrate with difficulty. They emerge at sunset at the peak activity of G. nigrofusca. These antelopes are abundant in the plantation zones and are also present in large numbers around the village. Unlike pigs, these hosts probably become more nervous in the presence of a high density of tsetse flies, therefore less accessible and they may even run away. This may be a major mechanism for the densitydependent regulation of the tsetse fly populations most dependent on these antelopes (in this case G. nigrofusca, G. fusca and to a lesser extent G. pallicera). The disappearance of game leads to the disappearance of species in the *fusca* group [26, 61] whereas G. palpalis can survive with meals taken on reptiles, rodents and man. Anthropic activities, deforestation and scarcity of game in this zone is probably responsible for the spectacular decrease in six years (1984-1990) of G. nigrofusca and G. pallicera to the advantage of G. palpalis as reported by Dagnogo et al. [13].

#### 4.4. The effect of size

The difference in size between the three principal species might also reflect a slight adaptation to a particular niche. In the Nola focus in the Central African Republic, *G. palpalis*, which occupies coffee plantation zones, is much smaller than *G. fuscipes*, a species from the surrounding forest (Gouteux, unpubl.). This fact is interesting because these two mutually exclusive species are not known to be particularly different in size. Such differences are often observed in cohabiting species. For example, *G. palpalis* sensu lato is much bigger than *G. tachinoides* and slightly smaller than *G. submorsitans*. *G. palpalis* s.l. and *G. fuscipes* s.l. are much smaller than the species in the *fusca* group.

#### 4.5. Unexplained competition

All these differences in the activity cycle, annual fluctuations, ecodistribution, size etc. are probably

adaptations required for the coexistence of the species. But this coexistence remains a conflicting coexistence in that these species are ubiquitous and present large overlaps in activity cycles, range of hosts and habitats. The mechanisms by which the resources are shared and the manner in which this equilibrium is organized are not yet understood. In other words, how is this density-dependent pressure exerted on the various species?

No satisfactory explanations for the mechanisms of competition between the different Glossina species have been put forward in the past [3, 69]. Vale [94] suggested that the reactions of the host may account for competition between individuals of the same species where density-dependent regulation occurs. For Glossina specialists such as Jackson [55] and Buxton [3], competition for food or habitat does not account for the interspecific competition in tsetse flies. The abundance of hosts in the village studied (Gatifla) including a herd of about 250 pigs makes the village a choice zone for all tsetse flies. The exclusion of the other species by G. palpalis is all the more difficult to understand because pigs accept a very high load of Glossina. Apparent densities of over 200 G. palpalis per trap per day were recorded at the edge of the village studied.

## 4.6. The sexual activity of the male flies as a working hypothesis

The fact that the sex ratios of the two principal species G. palpalis and G. pallicera fluctuate symmetrically in opposite phases (figure 6A) suggests the existence of interactions related to sex. Interspecific 'sexual harassment' might therefore be the basis for this mysterious regulation. This is in agreement with the experimental observation that: "intertaxon mating occurs extensively among tsetse flies under laboratory conditions" (Gooding [17] commenting on the famous experiments carried out by Vanderplank [95, 96] and Curtis [12]). Similar observations have been made in natural conditions (with G. swynnertoni and G. morsitans centralis [54, 95]). The tsetse fly sex hormones are contact hormones [4, 63]. The sexual behaviour of the males starts with an active visual search for females. Recognition only occurs after physical contact (male tarsi on the female cuticle) after which the male may or may not be stimulated by the sex hormones [53]. Male tsetse flies are attracted to small decoys (knots on string or small nylon rectangles) and will try to copulate with them if they are impregnated with the sex hormone [11, 50, 51]. While studying the sexual behaviour of male G. pallidipes, Jaenson [57] observed that they attempted to copulate with recently killed females and that copulation succeeded 40 times out of 64. This author also observed that "live females very often exhibited rejection responses when mounted by a male, and the males often did not manage to link genitalia". The high sexual aggressiveness of the males is thus coherent in terms of evolution. The shorter life-span of males encourages the strategy of giving priority to finding a partner and mating before finding a feeding host, as demonstrated experimentally by Langley and Hall [62]. The hypothesis put forward here for *G. palpalis* and *G. pallicera*, that habitat is divided up according to interspecific sexual aggressiveness, can be applied to other situations. Three types of sex-related interactions can be distinguished, as follows:

# 4.6.1. 'Sexual harassment'

This is the situation described for the guild studied in this paper and applied to cohabiting species for which the ecological niches are not identical but present large overlaps. According to this hypothesis, the sharing of space would be based on the sexual activity of the males of the dominant species. For example, because of the high concentration of male G. palpalis in the shady biotopes (forest, watering places), these males would be able to drive the female G. pallicera out of these favourable areas by harassing them with repeated attempts at heterologous copulation. Such attempts have been observed with flies in tubes (Gouteux unpubl.). When G. pallicera is the dominant species, the males of this species drive out the female G. palpalis. In the dominant position, G. pallicera reaches its density peaks before G. palpalis and then presents a greater density-dependent mortality for males than for females [29]. 'Sexual harassment' therefore seems to occur between G. palpalis and G. pallicera, two species belonging to the same sub-genus. Such interactions seem improbable for G. nigrofusca, a species belonging to a different sub-genus, because of the structure of the genitalia and the difference in size. However, interspecific interactions do exist between G. nigrofusca and G. palpalis, as shown in figure 7A and B. These indirect observations of 'sexual harassment' must obviously be confirmed by direct ethological observations.

#### 4.6.2. Fatal heterologous copulation

This occurs in the case of two very similar species, which have similar (or only slightly differentiated) ecological niches and which are completely mutually exclusive. This is the case for *G. fuscipes* and *G. palpalis* [45, 46]. It has already been suggested that heterologous mating could have been the cause of the total exclusion of *G. palpalis* and *G. quanzensis* observed in Congo [27]. Experimentally, such mating occurs frequently and, according to certain observations, is more frequent than homologous mating [80]. It usually leads to the death of the female, killed by the

heterologous male's claspers [71, 80, 96]. It is known that these two taxa do not produce hybrids in the wild [27, 69] or experimentally [71]. These interspecific boundaries can be unstable, especially when anthropic modifications occur. We have thus observed the advance of *G. palpalis* towards Brazzaville to the detriment of *G. quanzensis* [27] and the invasion of the *G. palpalis* zone in Cameroon by *G. fuscipes* via the great rivers [74].

## 4.6.3. Harmful heterologous copulation

This occurs in the case of non-cohabiting 'sub-species' (more exactly 'juxta-species') which present a narrow belt of hybridization along their 'interspecific' boundary. These are species which may have identical niches but which generally present different bioclimatic preferences. This is the case for G. palpalis and G. gambiensis, the former being more a forest species, the latter more a savannah species. But both are in competition in the humid savannah; when one is absent, the other occupies the preferred habitat of the absent species (e.g. G. gambiensis in Guinea/Sierra Leone and G. palpalis in north Nigeria). Heterologous mating between these two species occurs spontaneously. Hybrids have been observed both in the wild [10, 32] and experimentally [18, 19, 32, 88]. The male hybrids are very sexually active and copulate so violently that they often kill their partner [88]. The difficulty in separating probably also makes these heterologous couples extremely vulnerable to predators. The fact that male hybrids are sterile [18, 19, 88] adds to the mortality as a factor for extinction. This accounts for the exclusion of these two species, for which cohabitation is limited to a very narrow hybridization band at the interspecific boundary [10, 32, 75].

#### **5. DISCUSSION**

Sexual competition exists for parasites such as schistosomes [98], which are Trematodes resembling flukes. This has been clearly demonstrated for Schistosoma mansoni and S. intercalatum [90]. When these two species cohabit in the same host, the males of the former species dominate those of the latter and the probability of homologous mating for S. intercalatum is very low. This dominance has been demonstrated experimentally. This would account for the low distribution of *S. intercalatum* in Africa [91]. Thus, for this parasite, we find the same explanation which accounts for the exclusion of closely related tsetse fly species, for example G. palpalis and G. fuscipes (previously considered to be the same species) and G. palpalis and G. gambiensis (still considered as sub-species). For these Diptera, a lesser form of sexual competition ('sexual harassment') would, on the other hand, account for the time-lag and the separate occupation of the habitat of cohabiting species in the guild.

One of the aspects which has not been covered in this study is the relationship between the size of guilds and the available resources. This would involve exploring different *Glossina* guilds with this objective. Publications on research into tsetse fly guilds are extremely rare; it has been more usual to focus on the exhaustive study of a single species, carefully ignoring the other cohabiting tsetse fly species. On the other hand, this type of study exists for other Diptera, for example *Drosophila*, some of which have produced interesting models [87].

Another aspect not covered is the mating behaviour of both sexes. This is a very complex subject, as for many Brachycera, which has not been much studied in tsetse flies. The work of Saunders [83], Saunders and Dodd [84] and especially Jaenson [56, 57] can be cited however. The males often swarm towards the moving hosts - the 'following swarms' mentioned by Swynnerton. The apparent absence of mating attempts between males seems to be due to the recognition of the females' flight characteristics (especially speed), as established for other Diptera [14] or certain characteristics of the female's resting posture (observed in G. pallidipes by Jaenson [57]). Once the males reach the females and recognize them by the contact pheromones, they try to mate but will be accepted or rejected by the females according to precise stimuli produced by appropriate wing vibrations. These 'nuptial songs' are essential in other Diptera, such as the housefly [92]. According to Saini [81], sound may be a very elaborate means of communication in tsetse flies, during mating and also for other purposes, for example in the formation of swarms or during feeding [82]. This whole area remains to be explored, in particular to understand interspecific sexual interactions.

# 6. CONSEQUENCES ON DISEASE SYSTEMS AND THEIR CONTROL

In the Vavoua sleeping sickness focus, as in other forest foci in Côte d'Ivoire, *G. palpalis* is considered a priori as the major vector. However, here, man is not faced with a single species but with a complex *Glossina* guild. The richness of the ecosystem is due to the diversity of its botanical features. Between 1975 and 1984, human beings were still few in number and only exerted a moderate predatory pressure on small game. Anthropic modifications have increased further this biodiversity with the introduction of zones as different as coffee and cacao plantations into the forest and the creation of artificial savannah for cultivating food-producing crops on burnt stubble. With regard to the *Glossina* guild, this has resulted mainly in conflicting dynamics between *G. palpalis* and *G. pallicera*; *G. pallicera* could sometimes be more abundant than *G. palpalis* depending on the place and the season. A relationship between the size of the settlements and the ecodistribution of these species was demonstrated: *G. pallicera* is more frequently associated with small settlements, and *G. palpalis* with larger ones [49]. However, workers living in the smaller settlements are those most affected by sleeping sickness [89]. So, what role does *G. pallicera* play in the transmission of the disease?

In epidemiological models, the proportion of blood meals on man is a key factor in transmission [28]. Whereas the densities of these two species are in general comparable, G. pallicera takes 13.3 % of its blood meals on man in the high risk part of the Vavoua focus compared with 35.6 % for G. palpalis [28]. The number of blood meals taken on man is thus 2.7 times greater for G. palpalis than for G. pallicera, which corresponds to an epidemiological importance 7 times greater and confirms the principal role of G. palpalis [28]. However, the 13 % of G. pallicera are not negligible. Without a precise knowledge of the 'vectoral competence' of G. pallicera (as defined by Rodhain [78] or the 'intrinsic vectoral capacities' of Le Ray [67]), the fact that this species may play a local role in the transmission of sleeping sickness can not be excluded [24].

In the north of Côte d'Ivoire, *G. gambiensis* has taken advantage of a control programme which targeted essentially *G. tachinoides* to balance its populations with those of the latter species, whereas it had previously been dominated by a ratio of 20 to 1. The vectoral competence of these two species are different. If *G. palpalis* is a better vector than *G. tachinoides* for local strains of *Trypanosoma brucei gambiense*, this new epidemiological situation might be more dangerous than the previous state.

In the Nola focus, in the Central African Republic, two species, G. fuscipes and G. palpalis, transmit sleeping sickness. They each show a well-defined preference: coffee plantations for G. palpalis and the surrounding forest for G. fuscipes. The epicentre of the focus is situated in the G. palpalis zone [47]. This species is found in a residual pocket in the Central African Republic, far from its area of distribution [45]. Since populations of G. palpalis and G. fuscipes mutually exclude each other, they are permanently confronted in a dynamic equilibrium. However, a trapping experiment started in March 1992 in 14 villages has involved mainly the peridomestic populations of G. palpalis [46]. The interspecific equilibrium will very probably be modified by the vectoral control trials which will follow. It is likely that a new epidemiological situation will be established which must be closely monitored.

Biodiversity produces the possibility of the replacement of the targeted species by another which can become a new potential vector, possibly even more dangerous than the first. In the most anthropic zones where this biodiversity is lost, it is easier to control a single tsetse fly species than a complex *Glossina* guild. The *Glossina* biodiversity is destroyed naturally with the increase in human population which results in the destruction of forests and the elimination of game [13, 26, 48, 61]. In fact, a vector control programme should take into account the whole guild and not focus on a single species suspected a priori of being the major vector.

# 7. CONCLUSION

Tsetse flies have yet to reveal all their mysteries. The role of 'sexual harassment' has been suggested from several indirect observations. This may provide a better understanding of the cohabitation of closely related species, the mechanisms of which have yet to be explained. However, it needs to be validated by direct observations in the field, to be studied experimentally in detail and possibly modelled. This new hypothesis perhaps does not explain all the mechanisms of interspecific competition. It is likely that visual and sound recognition signals are involved in these extremely complex behaviours. What these signals are, and how they intervene, are open questions which remain to be answered.

#### Acknowledgments

These studies were supported by GDR-CNRS n° 1107 CoReV ('Modèles et théories pour le contrôle des ressources vivantes et la gestion de systèmes écologiques') and Orstom - I.R.D.E.C. (UR7 Santé et Politiques de Développement).

# REFERENCES

- [1] Barbault R., Écologie des peuplements. Structure, dynamique et évolution, Masson, Paris, 1992, 273 p.
- [2] Brunhes J., Cuisance D., Geoffroy B., Hervy J.P., Lebbe J., Les glossines ou mouches tsé-tsé. Logiciel d'identification Glossine Expert, Orstom, Didactiques, Paris, 1994, 160 p.
- [3] Buxton P.A., The natural history of tsetse flies, in: Lewis H.K. (Ed.), Mem. Lond. Sch. Hyg. Trop. Med., n° 10, London, 1955, 816 p.
- [4] Carlson D.A., Langley P.A., Huyton P., Sex pheromone of the tsetse fly: isolation, identification, and synthesis of contact aphrodisiacs, Science 201 (1978) 750–753.
- [5] Challier A., Écologie de Glossina palpalis gambiensis Vanderplank, 1949 (Diptera - Muscidae) en savane d'Afrique occidentale, Mémoires Orstom n° 64, Paris, 1973, 274 p.

- [6] Challier A., The ecology of tsetse (*Glossina* spp.) (Diptera, Glossinidae): A review (1970-1981), Insect Sci. Applic. 3 (1982) 97-143.
- [7] Challier A., Gouteux J.P., Enquêtes entomologiques sur les glossines du complexe sucrier Sérébou-Groumania (République de Côte d'Ivoire), Doc/Tech/OCCGE n° 6.624/78, Centre Muraz, Burkina Faso, 1978, 8 p.
- [8] Challier A., Gouteux J.P., Ecology and epidemiological importance of *Glossina palpalis* in the Ivory Coast forest zone, Insect Sci. Applic. 1 (1980) 77–83.
- [9] Challier A., Laveissière C., Un nouveau piège pour la capture des glossines (*Glossina*, Diptera: Muscidae): Description et essais sur le terrain, Cah. Orstom Sér. Entomol. Med. Parasitol. 15 (1973) 283–286.
- [10] Challier A., Gouteux J.P., Coosemans M., La limite géographique entre les sous-espèces Glossina palpalis palpalis (Rob.-Desv.) et G. palpalis gambiensis Vanderplank (Diptera: Glossinidae) en Afrique occidentale, Cah. Orstom, Sér. Entomol. Med. Parasitol. 21 (1983) 207–220.
- [11] Coates T.W., Langley P.A., The causes of mating abstension in male tsetse flies, *Glossina morsitans*, Phys. Entomol. 7 (1982) 235-242.
- [12] Curtis C.F., Sterility from crosses between sub-species of the tsetse fly *Glossina morsitans*, Acta Trop, 29 (1972) 250–268.
- [13] Dagnogo M., Lohuirignon K., Traore G., Diversity of *Glossina* in the forest belt of Côte d'Ivoire, Acta Trop. 65 (1997) 149– 153.
- [14] Downes J.A., The swarming and mating flight of Diptera, Annu. Rev. Entomol. 14 (1969) 271–298.
- [15] Eouzan J.P., Ferrara L., Habitat et rythme d'activité de Glossina caliginea dans une zone littorale du Sud-Cameroun. Comparaison avec G. palpalis palpalis, Cah. Orstom Sér. Entomol. Med. Parasitol. 16 (1978) 243-250.
- [16] Glasgow J.P., The distribution and abundance of tsetse, Pergamon Press, London, 1963, 241 p.
- [17] Gooding R.H., Tsetse genetics: a review, Quaest. Entomol. 20 (1984) 89–128.
- [18] Gooding R.H., Preliminary analysis of genetics of hybrid sterility in crosses of *Glossina palpalis palpalis* (Robineau-Desvoidy) and *Glossina palpalis gambiensis* Vanderplank, Can. Entomol. 120 (1988) 997-1001.
- [19] Gooding R.H., Genetic analysis of hybrid sterility in crosses of the tsetse Glossina palpalis palpalis and Glossina palpalis gambiensis (Diptera: Glossinidae), Can. J. Zool. 75 (1997) 1109-1117.
- [20] Gouteux J.P., Observations sur les glossines d'un foyer forestier de trypanosomiase humaine en Côte d'Ivoire. 4. Peuplement de trois plantations de caféiers d'âges différents, Cah. Orstom Sér. Entomol. Med. Parasitol. 20 (1982) 29–39.
- [21] Gouteux J.P., Observations sur les glossines d'un foyer forestier de trypanosomiase humaine en Côte d'Ivoire. 5. Peuplement quelques biotopes caractéristiques: plantation, forêt et galerie forestière, en saison des pluies, Cah. Orstom Sér. Entomol. Med. Parasitol. 20 (1982) 46-61.
- [22] Gouteux J.P., Écologie des glossines en secteur préforestier de Côte d'Ivoire. 6. Etude comparative des populations de quatre espèces en zone de plantations, Cah. Orstom Sér. Entomol. Med. Parasitol. 21 (1983) 18'1-197.
- [23] Gouteux J.P., Écologie des glossines en secteur préforestier de Côte d'Ivoire. 7. Analyse de la distribution spatiale des glossines en activité dans une plantation de caféiers, Cah. Orstom Sér. Entomol. Med. Parasitol. 21 (1983) 231–239.

[24] Gouteux J.P., Écologie des glossines en secteur pré-forestier de Côte d'Ivoire. Relation avec la trypanosomiase humaine et possibilités de lutte, Ann. Parasitol. Hum. Comp. 60 (1985) 329– 347.

- [25] Gouteux J.P., Écodistribution de *Glossina palpalis palpalis* (Rob.-Desv.) en secteur préforestier de Côte d'Ivoire. Sexe, rythmes ovaro-utérins et utilisation de l'espace, Acta Oecol. Oec. Applic. 8 (1987) 27–38.
- [26] Gouteux J.P., La raréfaction des tsé-tsé du groupe *fusca* en Afrique Centrale (Diptera, Glossinidae), Bull. Soc. Entomol. Fr. 96 (1992) 443–449.
- [27] Gouteux J.P., Un cas d'exclusion géographique chez les glossines (Diptera): L'avancée de Glossina palpalis palpalis vers Brazzaville (Congo) au détriment de G. fuscipes quanzensis, Insect. Sci. Applic. 13 (1992) 59-67.
- [28] Gouteux J.P., Artzrouni M., Faut-il ou non un contrôle des vecteurs dans la lutte contre la maladie du sommeil? Une approche bio-mathématique du problème, Bull. Soc. Pathol. Exot. 89 (1996) 299–305.
- [29] Gouteux J.P., Buckland S.T., Écologie des glossines en secteur pré-forestier de Côte d'Ivoire. 8. Dynamique des populations, Cah. Orstom Sér. Entomol. Med. Parasitol. 22 (1984) 19–34.
- [30] Gouteux J.P., Dagnogo M., Écologie des glossines en secteur pré-forestier de Côte d'Ivoire. 11. Comparaison des captures au piège biconique et au filet. Agressivité pour l'homme, Cah. Orstom Sér. Entomol. Med. Parasitol. 24 (1986) 99–110.
- [31] Gouteux J.P., Laveissière C., Écologie des glossines en secteur pré-forestier de Côte d'Ivoire. 4. Dynamique de l'écodistribution en terroir villageois, Cah. Orstom Sér. Entomol. Med. Parasitol. 20 (1982) 199–229.
- [32] Gouteux J.P., Millet P., Observation sur le contact entre Glossina palpalis palpalis (Rob.-Desv., 1830) et G. palpalis gambiensis Vanderplank, 1949 (Diptera), dans la région de Bouaké (Côte d'Ivoire), Tropenmed. Parasitol. 35 (1984) 157–159.
- [33] Gouteux J.P., Monteny B., Écologie des glossines en secteur pré-forestier de Côte d'Ivoire. 10. Activité, Cah. Orstom Sér. Entomol. Med. Parasitol. 24 (1986) 83–97.
- [34] Gouteux J.P., Challier A., Laveissière C., Modifications et essais du piège à glossine (Diptera : Glossinidae) "Challier-Laveissière", Cah. Orstom Sér. Entomol. Med. Parasitol. 19 (1981) 87–99.
- [35] Gouteux J.P., Couret D., Bicaba A., Observations sur les glossines d'un foyer forestier de trypanosomiase humaine en Côte d'Ivoire. 2. Effectifs des populations et effets du piégeage, Cah. Orstom Sér. Entomol. Med. Parasitol. 19 (1981) 209–222.
- [36] Gouteux J.P., Laveissière C., Challier A., Stanghellini A., Observations sur les glossines d'un foyer forestier de trypanosomiase humaine en Côte d'Ivoire. 1. Présentation du foyer de Vavoua, Cah. Orstom Sér. Entomol. Med. Parasitol. 19 (1981) 199–207.
- [37] Gouteux J.P., Mondet B., Poinar G.O., Écologie des glossines en secteur pré-forestier de Côte d'Ivoire. 1. Parasitisme par *Hexamermis glossinae* (Nematoda, Mermithidae), Cah. Orstom Sér. Entomol. Med. Parasitol. 19 (1981) 285–295.
- [38] Gouteux J.P., Dongo P., Coulibaly D., Observations sur les glossines d'un foyer forestier de trypanosomiase humaine en Côte d'Ivoire. 3. Dispersion et distribution des populations autour d'un village, Tropenmed. Parasitol. 33 (1982) 119–128.
- [39] Gouteux J.P., Challier A., Laveissière C., Couret D., L'utilisation des écrans dans la lutte anti-tsétsé en zone forestière, Tropenmed Parasitol. 33 (1982) 2163–168.

469

ŧ

- [40] Gouteux J.P., Challier A., Laveissière C., Stanghellini A., Le foyer de trypanosomiase humaine de Vavoua, Côte d'Ivoire. Données récentes sur l'épidémiologie de la maladie en relation avec l'écologie des glossines, Dakar Méd. 27 (1982) 271–285.
- [41] Gouteux J.P., Laveissière C., Boreham F.L., Écologie des glossines en secteur pré-forestier de Côte d'Ivoire. 2. Les préférences trophiques de *Glossina palpalis* s.l., Cah. Orstom Sér. Entomol. Med. Parasitol. 20 (1982) 3–18.
- [42] Gouteux J.P., Laveissière C., Boreham F.L., Écologie des glossines en secteur pré-forestier de Côte d'Ivoire. 3. Les préférences trophiques de *Glossina pallicera* et *G. nigrofusca*. Comparaison avec *G. palpalis* et implications épidémiologiques, Cah. Orstom Sér. Entomol. Med. Parasitol. 20 (1982) 109–124.
- [43] Gouteux J.P., Laveissière C., Couret D., Écologie des glossines en secteur pré-forestier de Côte d'Ivoire. 5. Les lieux de reproduction, Cah. Orstom Sér. Entomol. Med. Parasitol. 21 (1983) 3–12.
- [44] Gouteux J.P., Bois J.F., Laveissière C., Couret D., Mustapha A., Écologie des glossines en secteur pré-forestier de Côte d'Ivoire.
  9. Les lieux de repos, Cah. Orstom Sér. Entomol. Med. Parasitol. 22 (1984) 159–174.
- [45] Gouteux J.P., D'amico F., Kounda-Gboumbi J.C., Noutoua L., Bailly C., *Glossina fuscipes fuscipes* New and *G. palpalis palpalis* (Rob.-Desv.) as joint vectors of sleeping sickness in the focus of Nola-Bilolo in the Central African Republic, Acta Trop. 51 (1992) 163–166.
- [46] Gouteux J.P., Kounda-Gboumbi J.C., Noutoua L., D'amico F., Bailly C., Roungou J.B., Man-fly contact in the Gambian trypanosomiasis focus of Nola-Bilolo (Central African Republic), Trop. Med. Parasitol. 44 (1993) 213–218.
- [47] Gouteux J.P., Kounda-Gboumbi J.C., Noutoua L., D'amico F., Wagner C., Bailly C., Enquête pour la recherche des lieux de contamination probable dans un foyer Centrafricain de maladie du sommeil, Bull. OMS 71 (1993) 605–614.
- [48] Gouteux J.P., Blanc F., Pounekrozou E., Cuisance D., Mainguet M., D'amico F., Le Gall F., Tsé-tsé et élevage en République Centrafricaine: Le recul de *Glossina morsitans submorsitans*, Bull. Soc. Pathol. Exot. 87 (1994) 52–56.
- [49] Gouteux J.P., Jarry M., Wagner C., Étude de la structure spatiotemporelle d'un peuplement de *Glossina palpalis*, *G. pallicera* et *G. nigrofusca* (Diptera: Glossinidae) à l'aide de l'analyse triadique en secteur pré-forestier de Côte d'Ivoire, J. Afr. Zool. 111 (1997) 121-136.
- [50] Hall M.J.R., The orientation of males of *Glossina morsitans* morsitans Westwood (Diptera: Glossinidae) to pheromonebaited decoy "females" in the field, Bull. Entomol. Res. 77 (1987) 487–495.
- [51] Hall M.J.R., Characterization of the sexual responses of males tsetse flies *Glossina morsitans morsitans*, to pheromone-baited decoy "females" in the field, Phys. Entomol. 13 (1988) 49–58.
- [52] Hervouët J.P., Laveissière C., La campagne pilote de lutte contre la trypanosomiase humaine dans le foyer de Vavoua (Côte d'Ivoire). 1. Présentation de la zone d'intervention, Cah. Orstom Sér. Entomol. Med. Parasitol. 23 (1985) 149–165.
- [53] Huyton P.M., Langley P.A., Carlson D.A., Schwarz M., Specificity of contact sex pheromones in tsetse flies, *Glossina* spp., Physiol. Entomol. 5 (1980) 253–264.
- [54] Jackson C.H.N., Pairing of *Glossina morsitans* with *G. swyn-nertoni*, Proc. Roy. Entomol. Soc. Lond. (A) 20 (1945) 106.
- [55] Jackson C.H.N., The biology of tsetse flies, Biol. Rev. 24 (1949) 174–199.

- [56] Jaenson T.G.T., Mating behaviour of *Glossina pallidipes* Austen (Diptera, Glossinidae): genetic differences in copulation time between allopatric populations, Entomol. Exp. Appl. 24 (1978) 100-108.
- [57] Jaenson T.G.T., Mating behaviour of males of *Glossina pallidipes* Austen (Diptera: Glossinidae), Bull. Entomol. Res. 69 (1979) 573-588.
- [58] Janzen D.H., Herbivores and the number of tree species in tropical forests, Am. Nat. 102 (1970) 592–595.
- [59] Jarry M., Khaladi M., Gouteux J.P., A matrix model for studying tsetse fly populations, Entomol. Exp. Applic. 78 (1996) 51-60.
- [60] Jarry M., Gouteux J.P., Khaladi M., Are tsetse fly populations close to equilibrium? Acta Biotheor. 44 (1996) 317–333.
- [61] Jordan A.M., The distribution of the *fusca* group of tsetse flies (*Glossina*) in Nigeria and West Cameroon, Bull. Entomol. Res. 54 (1963) 307~327.
- [62] Langley P.A., Hall J.R., Aspects of the regulation of mating behaviour in tsetse, Insect. Sci. Applic. 5 (1984) 351–355.
- [63] Langley P.A., Pimley R.W., Carlson D.A., Sex recognition pheromone in tsetse fly *Glossina morsitans*, Nature 254 (1975) 51-53.
- [64] Laveissière C., Couret D., Conséquences d'essai de lutte répétés sur les proportions des espèces de glossines reiveraines, Cah. Orstom Sér. Entomol. Med. Parasitol. 21 (1983) 63–67.
- [65] Laveissière C., Kiénou J.P., Effets de l'accroissement des activités humaines sur la forêt du Sud-Ouest de la Côte d'Ivoire. Enquête sur les glossines de la forêt de Taï, Doc/Tech/OCCGE n° 7.249/79, Centre Muraz, Burkina Faso, 1979, 8 p.
- [66] Laveissière C., Gouteux J.P., Couret D., Essais de méthodes de lutte contre les glossines en zone pré-forestière de Côte d'Ivoire. 5. Note de synthèse, Cah. Orstom Sér. Entomol. Med. Parasitol. 18 (1980) 323–328.
- [67] Le Ray D., Vector susceptibility to African trypanosomes, Ann. Soc. Belge Méd. Trop. 69 (suppl. 1) (1989) 165–171.
- [68] Lévèque C., Role and consequences of fish diversity in the functioning of African freshwater: a review, Aquat. Living Resour. 8 (1996) 59–78.
- [69] Machado A. de Barros, Nouvelles contributions à l'étude systématique et biogéographique des glossines (Diptera), Publ. Cult. Co. Diam. Angola Lisboa 46 (1959) 17–90.
- [70] MacNally R.C., Doolan J.M., An empirical approach to guild structure: habitat relationships in nine species of eastern-Australian cicadas, Oikos 47 (1986) 33–46.
- [71] Maillot L., Les variétés de Glossina palpalis en Afrique Equatoriale Française, Bull. Soc. Pathol. Exot. 46 (1953) 1066– 1080.
- [72] Moloo S.K., The distribution of *Glossina* species in Africa and their natural hosts, Insect. Sci. Applic. 14 (1993) 511–527.
- [73] Morris K.R.S., Morris M.G., The use of traps against tsetse in West Africa, Bull. Entomol. Res. 39 (1949) 491–528.
- [74] Mouchet J., Gariou J., Rateau J., Distribution géographique et écologique de Glossina palpalis palpalis (Rob.-Desv.) et Glossina fuscipes fuscipes Newst. au Cameroun, Bull. Soc. Pathol. Exot. 51 (1958) 652-661.
- [75] N'Képeni E.B., Dagnogo M., Eouzan J.P., Détermination de la limite géographique entre deux sous-espèces de glossines en Côte d'Ivoire: *G. palpalis palpalis* (Robineau-Desvoidy, 1830) et *G. p. gambiensis* Vanderplank, 1949, Trop. Med. Parasitol. 40 (1989) 12–15.

5

- [76] Onyia J.A., Fluctuations in numbers and eventual collapse of a *Glossina palpalis* (R.-D.) population in Anara Forest Reserve of Nigeria, Acta Trop. 35 (1978) 253–261.
- [77] Poinar G.O., Mondet B., Gouteux J.P., Laveissière C., Hexamermis glossinae sp. nov. (Nematoda: Mermithidae), a parasite of the tsetse flies in West Africa, Can. J. Zool. 59 (1981) 858– 861.
- [78] Rodhain F., Relations arbovirus-vecteurs, Bull. Soc. Pathol. Exot. 78 (1985) 763–768.
- [79] Rogers D.J., Randolph S.E., Distribution and abundance of tsetse flies (*Glossina* spp.), J. Anim. Ecol. 55 (1986) 1007– 1025.
- [80] Roubaud E., Expériences d'intercroisement de glossines (tsétsé) du groupe *palpalis* effectué à l'Institut Pasteur de Paris, Ann. Inst. Pasteur 86 (1954) 537-561.
- [81] Saini R.K., Communication by sound in tsetse? Span 24 (1981)
   1-3. -
- [82] Saini R.K., The pattern of sound production by the tsetse fly Glossina morsitans morsitans Westwood, 1850 (Diptera, Glossinidae), Insect Sci. Applic. 1 (1981) 167–169.
- [83] Saunders D.S., Reproduction of *Glossina*, in: Mulligan H.W., (Ed.), The African trypanosomiases, Allen & Unwin Ltd, London, 1970, pp. 327–344.
- [84] Saunders D.S., Dodd C.W.H., Mating, insemination, and ovulation in the tsetse fly, *Glossina morsitans*, J. Insect Physiol. 18 (1972) 187-198.
- [85] Schoener T.W., Resource partitioning in ecological communities, Science 185 (1974) 27–39.
- [86] Simberloff D., Dayan T., The guild concept and the structure of ecological communities, Ann. Rev. Ecol. Syst. 22 (1991) 115– 143.
- [87] Shorrocks B., Rosewell J., Guild size in drosophilids: a simulation model, J. Anim. Ecol. 55 (1986) 527-541.
- [88] Southern D.I., 14. Chromosome diversity in tsetse flies, in: Blackman R.L., Hewitt G.M., Ashburner M. (Eds.), Insect

\$ \$141

Cytogenetics, Symposia of the Royal Entomological Society of London, Blackwell Sci. Pub., Oxford, 1981, pp. 225–241.

- [89] Stanghellini A., Duvallet G., Épidémiologie de la trypanosomiase humaine à *Trypanosoma gambiense* dans un foyer de Côte d'Ivoire. I. Distribution de la maladie dans la population, Tropenmed. Parasitol. 32 (1981) 141-144.
- [90] Tchuem Tchuenté L.A., Southgate V.R., Imbert-Establet D., Jourdane J., Change of mate and mating competition between males of *Schistosoma intercalatum* and *S. mansoni*, Parasitology 110 (1995) 45-52.
- [91] Tchuem Tchuenté L.A., Morand S., Imbert-Establet D., Delay B., Jourdane J., Competitive exclusion in human schistosomes: the restricted distribution of *Schistosoma intercalatum*, Parasitology 113 (1996) 129–136.
- [92] Tobin E.N., Stoffolano Jr J.G., The courtship of *Musca* species found in North America. 1. The house fly, *Musca domestica*, Ann. Entomol. Soc. Am. 66 (1973) 1249–1257.
- [93] Utida S., Interspecific competition between two species of bean weevil, Ecology 34 (1953) 301–307.
- [94] Vale G.A., Feeding responses of tsetse flies (Diptera: Glossinidae) to stationary baits, Bull. Entomol. Res. 67 (1977) 635– 649.
- [95] Vanderplank F.L., Experiments on hybridization of tsetse-flies and the possibility of a new method of control, Trans. Roy. Entomol. Soc. Lond. 98 (1947) 1–18.
- [96] Vanderplank F.L., Experiments in cross-breeding tsetse-flies (*Glossina* sp.), Ann. Trop. Med. Parasitol. 42 (1948) 131–152.
- [97] Waage J.K., Davies C.R., Host-mediated competition in a bloodsucking insect community, J. Anim. Ecol. 55 (1986) 171– 180.
- [98] Wright C.A., Southgate V.R., Hybridization of schistosomes and some of its implications, in: Taylor A.E.R., Muller R. (Eds.), Genetic aspects of host-parasite relationships, Symp. British Soc. Parasitol. 14, 1976, pp. 55–86.

Vol. 19 (5) 1998

.

1944 C L 1949 3