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The influence of game animals on the distribution and feeding habits of *Glossina pallidipes* in the Lambwe Valley

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The role of game animals as important hosts of some species of tsetse, including Glossina pallidipes, *has been studied in detail in the Lambwe Valley area of Kenya. A large population of* G. pallidipes *existed in association with a varied community of game animals in the study area, and the investigation was designed to determine which of the hosts available to* G. pallidipes *were actively selected and whether the preferred hosts influenced the distribution of the tsetse population. Bushbuck* (Tragelaphus scriptus) *was found to be the preferred host of* G. pallidipes *and there was a positive correlation between the distribution of these two species. Buffalo and roan antelope were also selected for food but, because of their behavioural characteristics, neither was continually available to the tsetse population and they had no influence on its distribution.*

Although the significance of game animals in the maintenance of tsetse and trypanosome populations is accepted, the exact role of the great variety of potential hosts remains obscured by behavioural, physiological, and statistical complexities in the epidemiology and epizootiology of the trypanosomiases.

Between the early 1930s and the late 1950s a great deal of field research was carried out on various species of *Glossina* in many parts of Africa, and a number of reports on the influence of game animals on tsetse biology were published. Nash (1933) suggested that tsetse followed game trails, and that the fly populations concentrated and dispersed proportionally to the movements of game animals. Swynnerton (1936) elaborated on this theme and stated that tsetse fed on game animals when they found them, then left immediately to digest their meal. The same author also suggested that the regular habits of wild ungulates have enabled tsetse to adopt habits that keep them in close contact with game animals. Buxton (1955) reported that tsetse were undoubtedly carried about by grazing game animals but questioned the possibility of *Glossina* species migrating long distances to follow them.

In the past few years a considerable amount of research has been carried out on various aspects of the relationship between tsetse and game animals (see Glover, 1965), but very few attempts have been made to study the relationships between tsetse and game animals by placing equal emphasis on both elements of the association. This is largely because, whereas methods for estimating tsetse populations are highly refined, game animal populations are usually estimated from spoor counts and other imprecise methods that could reliably indicate only the presence or absence of a species.

The refinement by Weitz (1952) of the precipitin test for the determination of host utilization from blood meals opened up further possibilities for a better understanding of the tsetse–host relationship. Blood meal analyses have clearly indicated that many species of *Glossina*, *G. pallidipes* Austeni being a particular example, feed on a wide variety of non-domesticated animals (Weitz, 1963). However, by taking a census of a community of game animals in Tanzania simultaneously with the collection of *G. swynnertoni* blood meal squashes, Lamprey et al. (1962) found that although a wide variety of potential sources of food were available, the flies were

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highly selective in their choice of host, feeding on only 3 of the 11 or so larger species of game animal present in the area.

Because of the importance of the relationship between tsetse and game animals in the transmission of the pathogenic trypanosomes, it is evident that much more research is required in this field. In this respect it is worth noting that the Joint FAO/WHO Expert Committee on African Trypanosomiasis (1969) found that there was a need for clarification of tsetse–host relationships and called for the introduction of " quantitative methods that make it possible to relate the results of vector and disease surveys to the dynamics of the supporting wildlife populations, thus providing a fuller understanding of the epidemiological situation ".

The results of quantitative studies on the relationships between *G. pallidipes* and the local population of game animals in a defined locality of Kenya are described in this report.

THE STUDY AREA

General descriptions of several aspects of the Lambwe Valley area have been given by Allsopp & Baldry (1972). Briefly, the floor of the valley contains extensive *Setaria* and *Themeda* grasslands, which give way to *Hyparrhenia* grassland on the sides of the valley. Along the centre of the valley floor, following the course of the seasonal Olambwe River, these grasslands are replaced by large blocks of dense continuous thicket interspersed with isolated thicket clumps and *Acacia* woodland. The greatest concentrations of *G. pallidipes* are found within this belt of climax vegetation.

Although climatic changes and human interference, including bush burning, may cause some variation in the distribution of *G. pallidipes* in the valley, it has been established that essentially the dense continuous thickets, the isolated thicket clumps, and the grasslands with scattered acacias represent the primary, secondary, and dispersal habitats, respectively, of this species of tsetse.

Within the confines of the valley floor, where there is no influence from the shore of Lake Victoria or from the sides of the valley, the climate and microclimate within any area having a particular type of vegetation would be relatively stable and uniformly attractive to the tsetse population. A variation of the population density within any one type of vegetation can therefore be attributed to the availability of food.

Hosts of *G. pallidipes* included various species of game animal, of which certain species of Bovidae (particularly the bushbuck) and Suidae (bushpig) were most implicated by blood meal analyses (England & Baldry, 1972). The tsetse also fed on man and domestic livestock, although the blood meal analyses showed very few feeds had been taken from these hosts.

EXPERIMENTAL DESIGN

Stratification of the study area

The Lambwe Valley supports a wide variety of vegetation associations (see Allsopp & Baldry, 1972), which have a profound effect on the distribution of *G. pallidipes*. In order to standardize vegetation types for the purpose of these studies, 3 major strata were defined, as follows: dense continuous thicket, isolated thicket clumps and *Acacia seyal* woodland, and grassland with scattered *A. drepanolobium* and *Balanites aegypticum*.

Factors affecting the distribution of G. pallidipes

The factors regarded as being most important in affecting the distribution of *G. pallidipes* were vegetation, climate, microclimate, and the availability of hosts.

Selection of the study area

The Otuok thicket area was selected as being most suitable for study because it had not been involved in aerial spraying trials and because it contained all the ecological elements required for the study. Since the study area was fairly centrally located in the valley and limited in size there was little overall variation in the climatic conditions, and microclimatic conditions could also be assumed to be uniform within areas having similar vegetation. All three vegetation types were represented in this area.

Selection of specific locations for animal–tsetse censuses within the study area

It was proposed that a number of quadrats should be delineated within areas of each of the three vegetation types in the study area. Game animal and tsetse densities within each could then be monitored periodically. The limitations on this ideal situation were as follows.

Availability of materials and manpower. A game animal census in one quadrat required a minimum

of 31 men and 3 vehicles. Since manpower for quadrat counts was supplied mainly by the local Game Department, it was not possible to impose too intensive a schedule. The estimation of tsetse densities within the quadrats required tsetse traps and trained staff to operate them; the entomology staff employed for this work was already over-extended and only limited assistance could be given.

Availability of time. Weekly counts in a practice area indicated that frequent human interference affected the stability of the resident populations of game animals and the counts had therefore to be spaced over a longer period. By starting censuses in August 1970 only 7 months remained before the study area was sprayed from the air in a tsetse control trial and it then became unsuitable for further study.

The impenetrable nature of dense thickets. Clearing boundaries around a quadrat in dense continuous thicket would have been time-consuming and expensive, and a large number of beaters would have been required to ensure that all the game animals in the quadrats were flushed from the heavy cover. Even if these difficulties could have been overcome, it would have been very difficult for the beaters to make any progress through the dense vegetation, and they might have been in danger from buffalo in such confined cover.

Ultra-low density of tsetse in the grassland. The low density of tsetse in the grassland prevented an accurate estimation of the population without elaborate techniques or a prohibitive number of man-hours. In view of the shortage of tsetse traps and manpower, the possible interference with game animals, and the potentially low significance of the results, this vegetation type was abandoned.

The main part of the study was therefore confined to isolated thicket clumps, thus reducing the demands on manpower and materials. It also became possible to space out censuses with respect to time. The terrain presented relatively little difficulty for the beaters and the " counters " recording animals passing out of the quadrat had a wide field of view and consequently better opportunities for observing and recognizing species.

This vegetation type supported all the potential hosts of *G. pallidipes* to a greater extent than either of the others. Also, being more open, it was favoured for hunting by *G. pallidipes* and therefore had a greater relevance with regard to tsetse–host studies.

Selection of the quadrat size and site

Preliminary studies on marked, released, and recaptured *G. pallidipes* by one of the authors (C.R.) indicated that more than 90% of the flies travelled no further than 400 m from the point of release in thicketed areas. Based on this knowledge, a quadrat size of 0.64 km² (800×800 m) was adopted as an area within which a resident tsetse population could reasonably be expected to occur, and out of which game animals could easily be driven by the available staff.

The siting of quadrats took into account epidemiological and epizootiological considerations since this study was also part of an overall epidemiological survey. Three quadrats Ot.1T, Ot.2T, and Ot.3T were therefore placed, respectively, in the vicinity of human settlement without domestic stock, away from human settlement or domestic stock, and in the vicinity of human settlement and domestic stock.

The timing and correlation of research activities

From any one quadrat it was necessary to obtain data on the resident and transitory game animal populations, the density of the tsetse populations, and the available hosts that were selected by the tsetse population as food. Data on game animals from each quadrat were collected over a period of 7 months to establish their period of residence. Within this period fluctuations in the tsetse population density were recorded for 10 weeks. During a 3-week period counts of game animals and captures of gorged tsetse were carried out simultaneously so that squashes of *G. pallidipes* blood meals could be collected from a population in contact with a known community of game animals.

Additional studies

Although isolated thicket clumps provided the basic data in this study, particularly with respect to the distribution of game animals and tsetse, the importance of dense continuous thicket was also recognized. Complementary data were therefore obtained from a single transect cut through an area with this type of vegetation. Studies of game animals were confined to an estimation of the relative distribution of species along the transect and their relative frequency of occurrence. No attempt was made to estimate population numbers. An estimation of the tsetse distribution along the transect was obtained and gorged flies were collected when possible.

THE STUDY AREA

The study area comprised some 30 km² of the Otuok locality in the centre of the Lambwe Valley (see Allsopp & Baldry, 1972), at an elevation of 1 180 m above sea level.

Rainfall

Rainfall followed the typical bimodal seasonal pattern with peaks in March–May and October–December. The available data suggest a mean annual rainfall of approximately 890 mm. Prolonged dry periods are not exceptional.

The Olambwe River runs through the study area from south-west to north-east, but drainage is subsurface and the river carries water seasonally only. Several small streams run off the Gwasi Hills, except during extremely dry periods. These streams reached the edge of the study area, but were then absorbed into the alluvium of the valley floor.

Vegetation

The dominant vegetation type was the dense continuous thicket block along the course of the Olambwe River (Fig. 1). This was a fire climax maintained in areas where grasses had been unable to penetrate the bush association. Species of plant present in this association included *Acacia* spp., *Euclea schimperi*, *Euphorbia candelabrum*, *Grewia similis*, *Oncoba spinosa*, *Rhus natalensis*, and *Scutia myrtina*.

The periphery of the continuous thicket block was fragmented into isolated thicket clumps, the grasses *Setaria sphacelata* and *Themeda triandra* being dominant in the interstitial grasslands. The bush association of these clumps was similar to that of the continuous thicket.

Acacia seyal fistula woodland with occasional *Balanites aegypticum* also occurred amongst the isolated thicket clumps. The *Acacia* woodland was characteristic of seasonably flooded areas. The remainder of the study area was grassland with *S. sphacelata* and *T. triandra* as the dominant species. Where the study area approached the sides of the valley, the grass *Hyparrhenia filipendula* became increasingly predominant.

Localized stands of less dominant grasses occurred among the grassland and thicket clumps; they included *Sporobolus pyrimidalis*, *Cyperus*, *Pennisetum*, and *Rottboellia* spp. *Acacia drepanolobium*, and occasionally *B. aegypticum*, were dispersed throughout the grassland.

Game animals

The species of game animal present in the study area, together with their preferred habitats, are listed in Table 1. Other animals that were sometimes encountered include leopard, hyaena, serval, civet, genet, mongoose, vervet monkey, bushbaby, and aardvark.

Table 1. Game animals in the Otuok study area, and their preferred habitats

Species	Habitat [a]
bushbuck (*Tragelaphus scriptus* Pallas)	I, C
buffalo (*Syncerus caffer* Sparrman)	I, C
bushpig (*Potamochoerus porcus* L.)	I, C
grey duiker (*Sylvicapra grimmia* L.)	I, C
impala (*Aepyceros melampus* Lichtenstein)	G, I
Jackson's hartebeest (*Alcelaphus bucelaphus jacksonii* Thomas)	G, I
oribi (*Ourebia ourebi* Zimmerman)	G, I
bohor reedbuck (*Redunca redunca* Pallas)	G, I
roan antelope (*Hippotragus equinus* Desmarest)	G
topi (*Damaliscus korrigum* Ogilby)	G, I
defassa waterbuck (*Kobus defassa* Neuman)	G, I, C

[a] G, grassland; I, isolated thicket clumps; C, continuous thicket.

Species of tsetse in the study area

The study area was inhabited by large numbers of *G. pallidipes* whose primary habitat was the dense continuous (Otuok) thicket, which provided the most equable environment in times of climatic extremes. The more open thicket clump vegetation with *Acacia* woodland was used mainly by flies searching for hosts, and was considered to be a secondary habitat only. Breeding sites may have existed in some of the larger thicket clumps, but they were virtually impossible to locate. Except perhaps when following preferred or potential hosts and vehicles, flies seldom ventured far into grassland, which was mainly a wet season dispersal zone and harboured ultra-low densities of tsetse.

In addition to *G. pallidipes*, there were a few small restricted populations of *G. brevipalpis* whose density was so low as to make them irrelevant to this study.

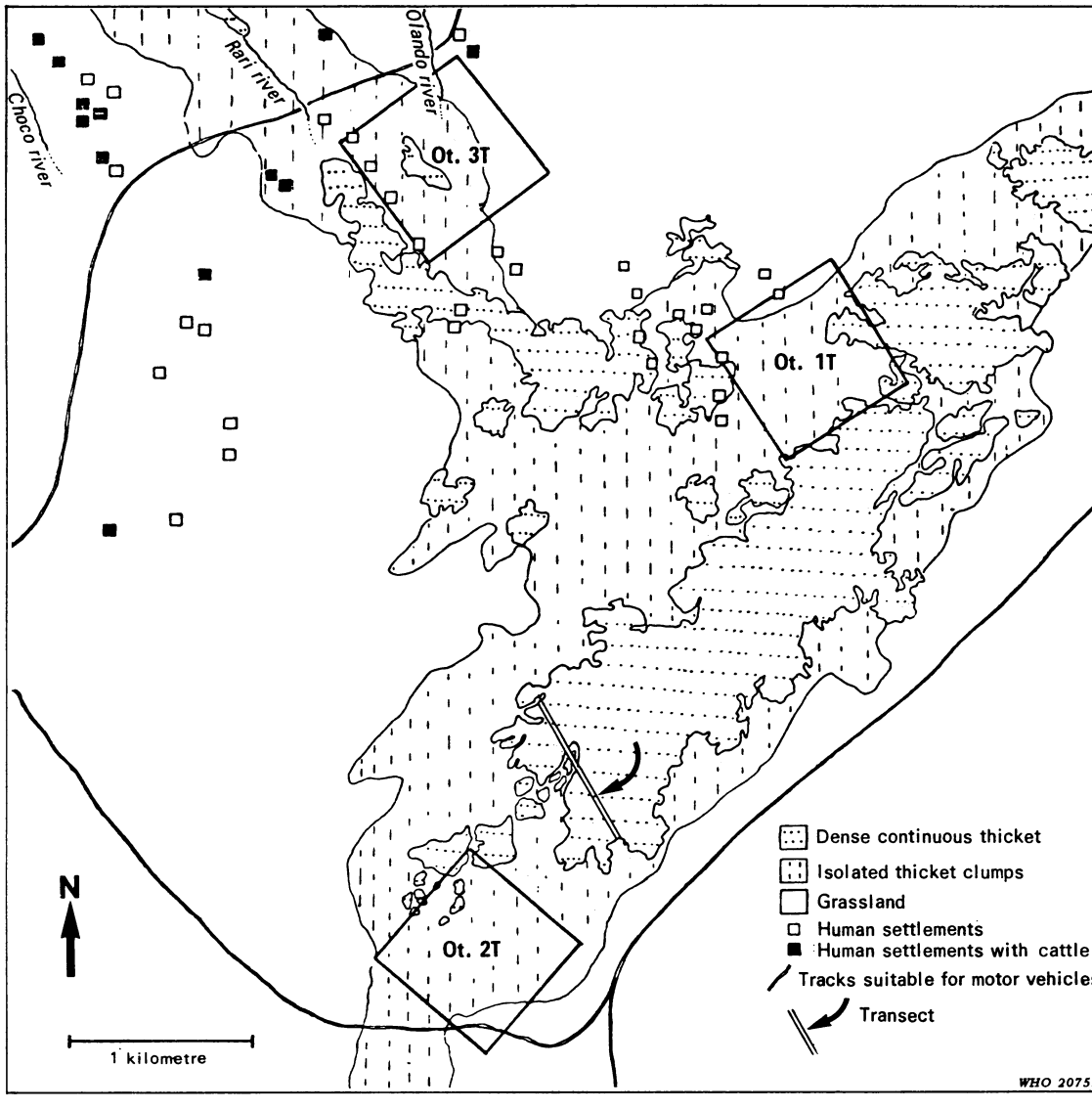

Fig. 1. The Otuok study area.

Human settlement

There was considerable human settlement along the lower slopes of the Gwasi Hills where water was available during all but the driest months of the year. In these areas, and extending into side valleys such as Rari and Wiga, the people usually kept small herds of cattle and other domestic stock. Passing from the Gwasi Hills towards the valley bottom, water became less available and the tsetse more numerous. Consequently, the number of human habitations decreased as did the number of settlements with domestic stock. The distribution of human settlements with and without cattle is shown in Fig. 1.

Many settlements were associated with cultivation, usually of maize, and quite often the natural

vegetation was disturbed by clearing and burning. Grasslands were regularly burned, particularly in areas adjacent to human habitations.

The poaching of game was common and snares were regularly found in the vicinity of settlements. Judging by the number of large wire snares found near the continuous thickets, it appears that buffalo were frequently the quarry.

MATERIALS AND METHODS

Game censuses in isolated thickets

Game censuses in isolated thickets were carried out in the 3 quadrats designated Ot.1T, Ot.2T, and Ot.3T. They were surveyed 10, 9, and 9 times, respectively.

Preliminary counts in a 0.64 km² quadrat outside the study area suggested the best method to use. This involved placing counters at intervals around three sides of the quadrat to be surveyed; altogether, 12 counters were used and they recorded the number of animals leaving the quadrat on their right only. The distance between each counter was 100 m and each counter occupied a raised position such as a tree or the top of a vehicle to give better visibility. If necessary, boundaries around each quadrat were cleared to facilitate the counting of animals. The beaters (16–20, depending on availability) were spaced evenly along the fourth side of the quadrat, and they moved through the quadrat, keeping as far as possible in line and evenly spaced. They were instructed to make a considerable amount of noise and to beat bushes and thicket clumps with sticks. All the animals leaving the quadrat were recorded on standard data sheets.

Censuses were carried out between 7 August 1970 and 5 January 1971, the period between counts in any one quadrat being 2 weeks whenever possible.

Game censuses in dense continuous thicket

A transect of 810×3 m was cut through the continuous vegetation block (Fig. 1) and was divided into 27 sectors each 30 m in length. Trails of game animals crossing the transect were recorded in each sector (Fig. 2). No attempt was made to estimate population densities of game animals in this stratum. Only the relative distribution of species along the transect and the relative daily frequency of use were studied. The method involved the clearing of 2-km² plots of earth at appropriate positions in each sector. These plots were kept clear of vegetation and the soil was kept as loose as possible. Each day for a period of 2 months the plots were examined and the presence of spoor was recorded.

Game censuses in the grassland stratum

To complete the picture of game distribution throughout the Lambwe Valley Game Reserve, plains game animals were counted each month. The reserve was divided into 6 areas of approxi-

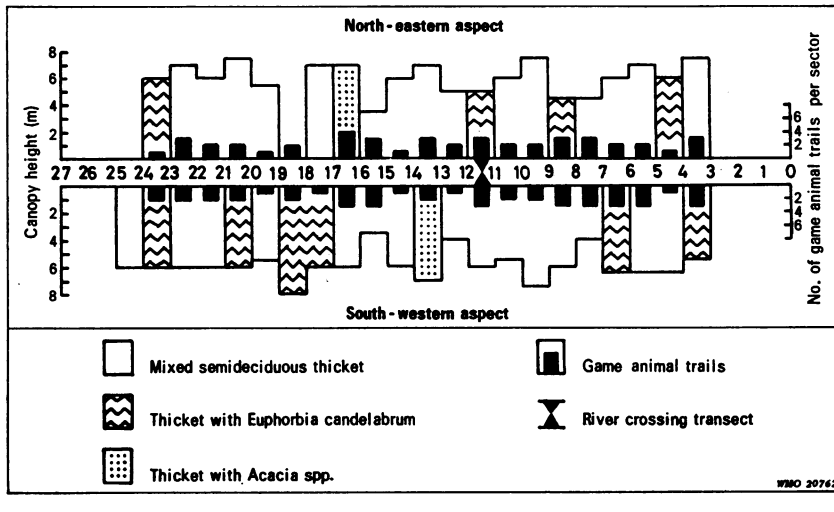

Fig. 2. Vegetation profiles and distribution of game trails along the Otuok thicket transect. The transect measured 810×4 m.

mately 7 km² and the total game animal community was counted in each area from a vehicle.

Estimation of G. pallidipes in isolated thickets

In order to obtain estimates of the *G. pallidipes* populations in the 3 Otuok quadrats, two "Langridge-type" tsetse traps (Langridge, 1972) were appropriately sited in the centre of each quadrat, and they remained in approximately the same position from 25 September to 4 December 1970, although individual traps were replaced monthly by new ones. Each pair of traps was closed for two 24-h periods each week. Two additional collections were made in each quadrat in February 1971.

Since the information required was the variation in tsetse distribution between quadrats and not absolute estimates of the population, the method outlined above was considered to be satisfactory.

Estimates of G. pallidipes in dense continuous thicket

Estimates of game animals in dense continuous thicket were limited to spoor counts that indicated the relative distribution of species along a 810-m transect. The method of estimating tsetse populations was therefore designed for correlation with these data. A 5-man screen patrol traversed the transect and spent 5 min in each sector catching, recording, and ultimately, after completing the transect, releasing the *G. pallidipes*.

Tsetse patrols were carried out simultaneously with spoor counts, starting from opposite directions on alternate days.

Collection of gorged G. pallidipes

Trained staff who were capable of collecting recently fed flies were few in number and available for only a few weeks. During the time that they were available they could be employed only on the days when counts of game animals were conducted. Consequently, the number of gorged tsetse collected specifically for the purposes of this study was small.

By carrying out a census in one quadrat and then collecting gorged flies from the same quadrat immediately afterwards, the blood meals identified could be correlated approximately with a known community of potential hosts. Gorged flies were also collected along the transect through the Otuok continuous thicket. Additional data on host utilization in the valley as a whole is available from blood-meal collections reported by England & Baldry (1972).

The gut contents of gorged flies were squashed on to filter paper disks by the method described by Baldry & Riordan [1] and sent to Dr P. F. L. Boreham, Imperial College Field Station, England, for analysis.

RESULTS

Game distribution in the three Otuok quadrats

The results of censuses of game animals conducted in isolated thickets are given in Tables 2, 3, and 4, while the percentage distribution of each species between quadrats based on the mean number per quadrat per census is shown in Table 5.

In all three quadrats reedbuck was the animal most frequently observed, although bushbuck and duiker were also common. In the Ot.3T quadrat oribi was also fairly common.

Distribution of game animals along a transect through dense continuous thicket

Bushbuck, duiker, buffalo, waterbuck, hyaena, and very occasionally bushpig, were recorded by spoor identification along the Otuok transect. The first two species were by far the most frequently recorded (Fig. 3) and were observed in all sectors. There was a tendency for these species to occur less frequently along the thicket edge and near sector 11/12 where the Olambwe River crossed the transect. Sector 11/12 was most frequently utilized by buffalo, while waterbuck were most active in the adjacent sector 9/10.

The relative frequencies of various animals obtained from 53 daily counts was as follows: bushbuck, 486 (59.35%); duiker, 269 (32.96%); buffalo, 16 (1.96%); waterbuck, 15 (1.84%); hyaena, 30 (3.67%).

Distribution of game animals in grasslands

Although no estimate was made of tsetse population densities in grassland, counts of game animals were made (Table 6) to complete the distribution survey. Briefly, these censuses indicated that Jackson's hartebeest, oribi, roan antelope, and topi were present in considerable numbers. Although they may have approached the thicket areas, they spent most of the time away from the thicket edge, nearer the sides of the valley. With the exception of roan antelope these plains game animals, together with impala, were strongly attracted to recently burned grassland.

[1] Baldry, D. A. T. & Riordon. K. (1965) *Notes on entomology*. In: WHO unpublished document PD/68.9.

Table 2. Game animal census results for the Ot.1T quadrat

Species	No. of animals recorded on the following dates:										Mean no. of animals per quadrat
	15 Aug. 1970	8 Sept. 1970	15 Sept. 1970	8 Oct. 1970 [a]	23 Oct. 1970	13 Nov. 1970 [a]	23 Dec. 1970	20 Jan. 1971	28 Jan. 1971	5 Feb. 1971	
bushbuck	8	9	1	6	9	7	10	4	2	5	6.1
reedbuck	5	10	6	4	8	9	8	5	3	4	6.2
duiker	2	6	4	4	6	7	7	3	4	8	5.1
impala	—	7	—	—	—	—	—	—	—	—	0.7
waterbuck	1	2	7	16	3	1	4	1	—	1	3.6
buffalo	2	—	—	—	—	—	—	—	—	—	0.2
bushpig	—	—	—	2	2	2	—	—	—	—	0.6
oribi	—	5	—	2	—	—	7	—	3	2	1.9
others [b]	—	—	—	—	—	—	—	4	—	—	0.4
totals	18	39	18	34	28	26	36	17	12	20	

[a] Gorged *G. pallidipes* collected immediately after census.
[b] Including topi, roan antelope, and Jackson's hartebeest.

Table 3. Game animal census results for the Ot.2T quadrat

Species	No. of animals recorded on the following dates:									Mean no. of animals per quadrat
	27 Aug. 1970	11 Sept. 1970	25 Sept. 1970	9 Oct. 1970 [a]	30 Oct. 1970 [a]	23 Dec. 1970	20 Jan. 1971	28 Jan. 1971	5 Feb. 1972	
bushbuck	5	4	3	1	2	3	3	1	7	3.2
reedbuck	9	8	11	8	10	12	7	13	6	9.3
duiker	5	2	5	4	6	6	5	5	7	5.0
impala	—	1	—	1	—	—	—	—	—	0.2
waterbuck	—	—	—	—	—	—	—	—	—	0.0
buffalo	2	—	—	—	2	—	—	—	2	0.7
bushpig	—	—	—	—	1	—	—	—	—	0.1
oribi	—	1	2	—	4	3	—	—	—	1.1
others [b]	6	8	—	—	—	—	—	—	—	1.5
totals	27	24	21	14	25	24	15	19	22	1.5

[a] Gorged *G., pallidipes* collected immediately after census.
[b] Including topi, roan antelope, and Jackson's hartebeest.

Table 4. Game animal census results for the Ot.3T quadrat

Species	No. of animals recorded on the following dates:									Mean no. of animals per quadrat
	27 Aug. 1970	8 Sept. 1970	15 Sept. 1970	12 Oct. 1970	6 Nov. 1970	23 Dec. 1970	20 Jan. 1971	28 Jan. 1971	5 Feb. 1971	
bushbuck	5	5	1	2	6	—	2	6	1	3.1
reedbuck	13	12	9	10	29	20	10	17	10	14.4
duiker	3	4	1	4	9	4	1	2	1	3.2
impala	3	6	—	—	—	—	—	—	—	1.0
waterbuck	—	—	—	5	1	—	—	—	—	0.7
buffalo	—	—	—	—	—	—	—	—	—	0.0
bushpig	—	—	2	1	—	2	—	—	—	0.6
oribi	—	—	—	1	—	3	9	—	7	2.2
others [a]	5	—	—	2	—	—	—	—	—	0.7
totals	29	27	13	25	45	29	22	25	19	

[a] Including topi, roan antelope, and Jackson's hartebeest.

The availability of game animals to G. pallidipes in isolated thickets

The availability of game animals to tsetse depends on density and dispersion, i.e., the total number and their frequency in any one area. Availability of game animals within any one quadrat has been calculated as follows: availability = (mean number per quadrat × number of times recorded)/total number of censuses made in that quadrat. The overall availability for isolated thickets was calculated by a similar formula, appropriately modified, and the estimates are given in Table 7.

Table 5. Inter-quadrat distribution of game animals based on means/quadrat/census (calculated from data in Tables 2, 3, and 4)

Species	Percentage distribution between quadrats			
	Ot. 1T	Ot. 2T	Ot. 3T	Totals
bushbuck	49.19	25.81	25.00	100.0
reedbuck	20.73	31.10	48.16	99.99
duiker	38.34	37.59	24.06	99.99
impala	36.84	10.52	52.63	100.0
waterbuck	83.72	0.0	16.28	99.99
buffalo	22.22	77.77	0.0	99.99
bushpig	46.15	7.69	46.15	100.0
oribi	36.54	21.15	42.31	100.0
others [a]	15.38	57.69	26.92	99.99

[a] Including topi, roan antelope, and Jackson's hartebeest.

Table 6. Population estimates for plains game animals in the Lambwe Valley Game Reserve, August–December 1970

Species	Mean monthly total	Mean no./km²
impala	355	7.10
Jackson's hartebeest	79	1.58
oribi	242	4.84
reedbuck	210	4.20
roan antelope	92	1.84
topi	252	5.40

In all three quadrats three species—namely, bushbuck, duiker, and reedbuck—generally contributed 80–90% availability to the tsetse population. Of these species, reedbuck was always the most available.

The availability of game animals to G. pallidipes in dense continuous thicket

In the absence of population estimates for dense continuous thicket, availability can be assumed to

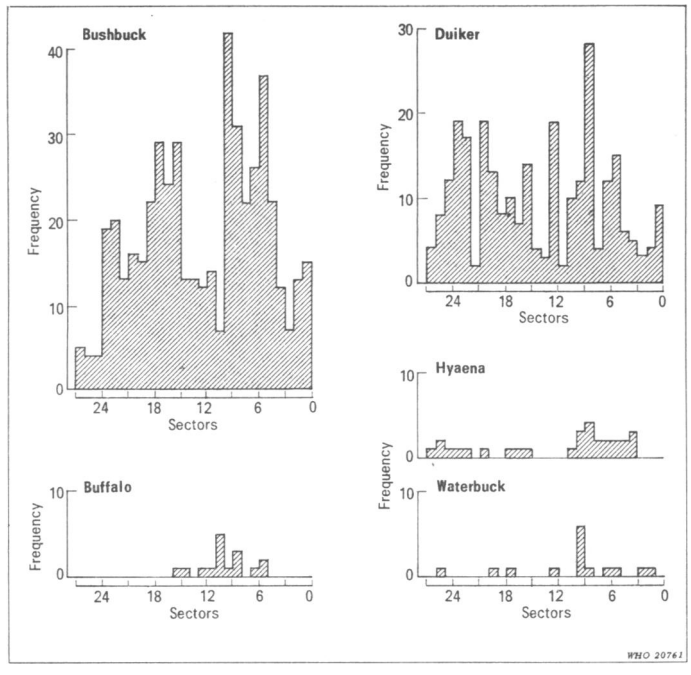

Fig. 3. The frequency of occurrence per sector of game animals along the Otuok thicket transect.

be proportional to the frequency of occurrence. In theory, one animal may feed hundreds of flies (Jackson, 1933), and therefore the presence or absence of a species is a reasonable criterion for availability.

The percentage availability of game animals to a resident population of *G. pallidipes* in areas with this type of vegetation was therefore approximately as follows: bushbuck, 60%; duiker, 32%; buffalo, 2%; waterbuck, 2%; hyaena, 4%.

The distribution of G. pallidipes in isolated thickets

The distribution and population structure of *G. pallidipes* in the three *Otuok* quadrats are shown in Tables 8 and 9. Based on the fact that nonteneral male catches are representative of the total fly population, and bearing in mind that Langridge-type tsetse traps catch more females than males, it is evident that the tsetse population in this study was fairly uniformly biased towards the Ot.1T quadrat. With the exception of the teneral female catches in the Ot.3T and Ot.2T quadrats, where the former predominated, all other components of the population were greater in Ot.1T than in Ot.2T, and greater in Ot.2T than in Ot.3T. It can therefore be assumed that between quadrats Ot.1T, Ot.2T, and Ot.3T the percentage distribution of *G. pallidipes* was about 65%, 30%, and 5%, respectively.

The percentage of females in the total catch per quadrat was smallest in Ot.1T (64.6% compared with 74.4% in Ot.2T, and 71.4% in Ot.3T).

The distribution of G. pallidipes in dense continuous thicket

The results of catches made by tsetse patrols along the Otuok transect are given in Fig. 4. Although, as would be expected, the flies were distributed along the whole transect, there was a tendency for teneral flies of both sexes to be concentrated at the south-eastern thicket edge, and to a more limited extent towards the centre of the thicket. By contrast, there was a distinct peak in the distribution of nonteneral males coinciding with the western thicket edge.

Analysis of blood meals in G. pallidipes collected in the Otuok quadrats

Immediately after the game censuses in quadrat Ot.1T on 8 and 23 October 1970, 16 and 12 gorged

Table 7. Availability of game animals to *Glossina pallidipes* in the Otuok isolated thicket clump vegetation stratum

Species	No. of times recorded/number of observations				Total no. recorded				Mean no./quadrat/census				Availability to *G. pallidipes*							
													Observed				Percentage/quadrat			
	Ot.1T	Ot.2T	Ot.3T	overall	Ot.1T	Ot.2T	Ot.3T	overall	Ot.1T	Ot.2T	Ot.3T	overall	Ot.1T	Ot.2T	Ot.3T	overall	Ot.1T	Ot.2T	Ot.3T	overall
bushbuck	10/10	9/9	8/9	27/28	61	29	28	118	6.1	3.2	3.1	4.22	6.1	3.22	2.76	4.06	27.85	17.26	12.50	20.07
reedbuck	10/10	9/9	9/9	28/28	62	84	130	276	6.2	9.3	14.4	9.86	6.2	9.33	14.44	9.86	28.31	50.00	65.40	48.74
duiker	10/10	9/9	9/9	28/28	51	45	29	125	5.1	5.0	3.2	4.46	5.1	5.00	3.22	4.46	23.29	26.79	14.58	22.05
impala	1/10	2/9	2/9	5/28	7	2	9	19	0.7	0.2	1.0	0.64	0.07	0.05	0.22	0.12	0.32	0.26	1.00	0.59
waterbuck	9/10	0/9	2/9	11/28	36	0	6	42	3.6	0.0	0.7	1.50	3.24	0.00	0.15	0.59	14.79	0.00	0.68	2.92
buffalo	1/10	3/9	0/9	4/28	2	6	0	8	0.2	0.7	0.0	0.29	0.02	0.22	0.00	0.04	0.09	1.18	0.00	0.20
bushpig	3/10	1/9	3/9	7/28	6	1	5	12	0.6	0.1	0.6	0.43	0.18	0.01	0.18	0.11	0.82	0.05	0.81	0.54
oribi	5/10	4/9	4/9	13/28	19	10	20	49	1.9	1.1	2.2	1.75	0.95	0.49	0.99	0.81	4.34	2.63	4.48	4.00
others [a]	1/10	2/9	3/9	6/28	4	14	7	25	0.4	1.5	0.7	0.86	0.04	0.34	0.12	0.18	0.18	1.82	0.53	0.89

[a] Including topi, roan antelope, and Jackson's hartebeest.

flies, respectively, were collected and the blood meals were identified as follows: (1) 8 October: 14 bushbuck, 2 unidentified bovids; (2) 23 October: 9 bushbuck, 2 unidentified bovids, 1 negative. After the game census in quadrat Ot.2T on 9 October 1970, only 3 gorged *G. pallidipes* were found; 2 had fed on bushbuck and 1 on an unidentified bovid. All 12 blood meal squashes obtained after the game censuses in quadrats Ot.2T and Ot.1T, on 30 October and 13 November 1970, respectively, were derived from unidentified bovids. Several unsuccessful attempts were made to collect gorged flies from quadrat Ot.3T.

Analysis of G. pallidipes blood meals collected along the Otuok transect

On 8 October 1970 5 blood meals were collected from gorged tsetse; 4 flies had fed on buffalo and 1 on bushbuck. On 18 October 1970 3 blood meals were collected, 1 of which was from an unidentified bovid, 1 from buffalo, and 1 from both buffalo and bushbuck.

Between 8 and 28 December 1970 a total of 47 gorged *G. pallidipes* were collected from the transect through the Otuok thicket. The blood meals were identified as follows: man, 1; bushbuck, 22; buffalo, 7; unidentified bovids, 17.

Analysis of G. pallidipes blood meals collected outside the study area

Although the results reported here were not obtained in the study area, they are significant and are discussed later.

On 12 April 1970, 40 gorged *G. pallidipes* were collected in the Rari Valley near the Ot.3T quadrat; 16 of the blood meals were identified as buffalo, 1 as buffalo or bushbuck, 1 as man or monkey, and the remaining 22 as bushbuck.

Between 16 and 27 November 1970 a total of 35 *G. pallidipes* blood-meal squashes were collected from the Ruma thicket, about 8 km north-east of the Ot.1T quadrat, in an area that had been occupied by a large herd of roan antelope during that period. Of the 35 blood meals, 4 were derived from unidentified bovids and 22 from roan antelope; 1 could not be identified.

Details of the hosts of *G. pallidipes* over a wider area of the Lambwe Valley are given by England & Baldry (1972).

Table 8. *G. pallidipes* trap catch results in the Ot.1T, Ot.2T, and Ot.3T quadrats

Quadrat	No. of trap catches	Total no. of tsetse caught	Mean trap catch	No. of non-teneral and teneral *G. pallidipes*					
				Non-tenerals			Tenerals		
				Males	Females	Total	Males	Females	Total
Ot. 1T	38	10 779	283.6	2 651	5 373	8 024	1 166	1 589	2 755
Ot. 2T	44	5 218	118.5	1 231	3 776	5 007	103	108	211
Ot. 3T	40	795	19.8	136	458	594	91	110	201

Table 9. Analysis of the *G. pallidipes* trap catches in the Ot.1, Ot.2, and Ot.3 quadrats (from data in Table 8)

Quadrat	Mean trap catches						Percentage of females		
	Non-tenerals				All flies				
	Males		Females						
	No.	%	No.	%	No.	%	Non-teneral	Teneral	Overall
Ot. 1T	69.7	69.1	183.2	64.1	283.6	67.2	66.9	57.6	64.6
Ot. 2T	27.9	27.7	88.3	30.9	118.5	28.0	75.5	51.1	74.4
Ot. 3T	3.4	3.4	14.2	5.0	19.8	4.7	77.1	54.7	71.4

DISCUSSION

The influence of the distribution of game animals on that of G. pallidipes

The studies made on the effect of the distribution of game animals on that of *G. pallidipes* were designed to eliminate as many variables as possible, so that variations in the distribution of game animals could be used to explain variations in tsetse distribution, if any were found. However, in order that these investigations could be fitted into the total epidemiological study of the Otuok area, the siting of quadrats Ot.1T, Ot.2T, and Ot.3T took into account the distribution of human settlements. Therefore, before the effect of the distribution of game animals on that of *G. pallidipes* can be assessed, the possible effects of human settlement must be considered.

Perhaps the most significant observation in this respect was the small number of human and livestock blood meals identified in gorged tsetse collected during and before the study period. Of a total of 923 blood meals that were analysed, only 2 were identified as being specifically from man, and not a single feed was specifically identified as being from oxen (England & Baldry, 1972). These findings suggest that *G. pallidipes* feeds mainly on game animals and is not highly attracted to man or cattle.

A conflicting observation worth consideration is the high incidence of pathogenic trypanosomes found in cattle in the Otuok–Rari area and in the Lambwe Valley area as a whole—namely, 65% and 17%, respectively (Robson & Ashkar, 1972). It is not known how the discrepancy between the analyses of *G. pallidipes* blood meals and the incidence of animal trypanosomiasis can be explained. The high trypanosomiasis infection rate in livestock in the Otuok–Rari area was possibly the result of mechanical transmission of trypanosomes by biting flies other than tsetse; however, this seems unlikely. A more probable explanation is that many of the cattle, most of which moved into the area after September 1969 with Maragoli settlers from the Serengeti Region of Tanzania (which, incidentally,

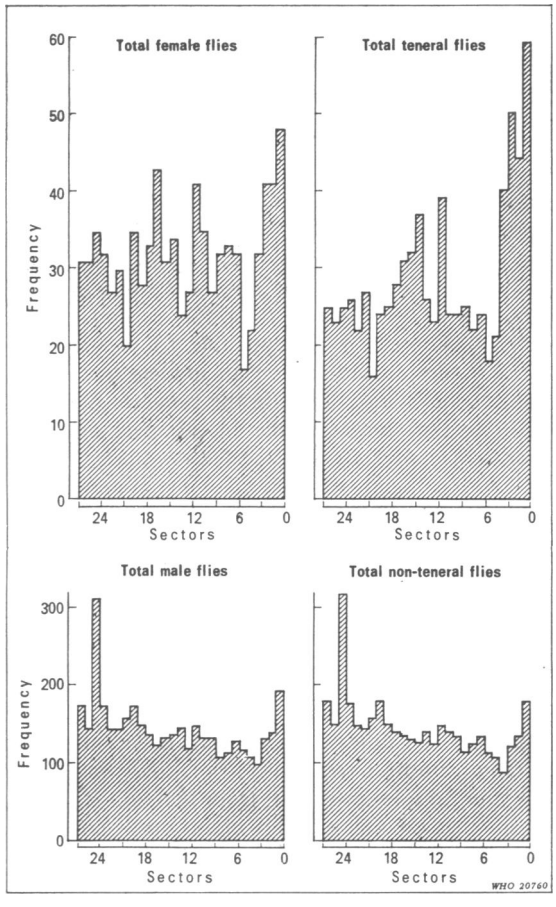

Fig. 4. The frequency of occurrence per sector of *G. pallidipes* along the Otuok thicket transect.

is an area of high trypanosomiasis endemicity), were infected prior to their arrival in the Otuok area.

As far as cattle trypanosomiasis in the area as a whole is concerned, it is very probable that livestock became infected after brief nonfocal encounters with peripheral tsetse populations and that the type of host–tsetse contact was much the same as that between plains game animals and the tsetse population. It would therefore be extremely difficult to collect gorged *G. pallidipes* that had fed on cattle unless a search was made in exactly the right place and at the right time, i.e., immediately after cattle had approached a particular part of the fly belt. Therefore, assuming that the distribution of man and cattle did not significantly affect the distribution of *G. pallidipes*, it remains only to consider the possible role of game animals in this respect.

The mean numbers of game animals recorded in quadrats Ot.1T, Ot.2T, and Ot.3T were 24.8, 21.2, and 24.9, respectively. Evidently, these numbers do not differ sufficiently to account for the variations in tsetse distribution shown in Tables 8 and 9.

With the exception of bushbuck, duiker, and reedbuck, all species of game animal could be considered to be transitory in the Otuok quadrats. The three exceptions were regularly recorded in higher numbers than the other species and consequently accounted for over 90% of the hosts available to *G. pallidipes*. Being the stable game animals in areas with this type of vegetation, it is reasonable to assume that these three species would exert the greatest influence on a stable tsetse population and that variations in tsetse distribution were correlated to variations in one or more of these species. In fact, there was a strong positive correlation between the distribution of bushbuck and that of *G. pallidipes* ($r = +0.94$), a strong negative correlation between the distribution of reedbuck and *G. pallidipes* ($r = -0.96$), and a weakly positive correlation for duiker ($r = +0.26$).

These results suggest that the distribution of bushbuck positively affected the distribution of *G. pallidipes* in isolated thickets. Support for this hypothesis was provided by the blood meal analyses, which showed that bushbuck was the species most frequently selected by *G. pallidipes*. Since the bushbuck is a highly suitable host it is to be expected that a stable tsetse population would tend to become orientated to this constant source of food.

A further consideration is the structure of the tsetse population in the various quadrats, a particular feature being that a high proportion of females was caught in Langridge-type tsetse traps. Behavioural and environmental factors do however affect this proportion in that catches in feeding grounds and generally favourable habitats tend to contain a slightly lower proportion of females in the total catch. It is therefore significant that the proportions of females in quadrats Ot.1T, Ot.2T, and Ot.3T were 64.6%, 74.4%, and 71.4%, respectively, indicating that the segment of the total tsetse population occupying Ot.1T found the habitat more suitable than the other populations found quadrats Ot.2T and Ot.3T.

Although reedbuck, bushbuck, and duiker were the most widely available hosts to the tsetse in this area, it is possible that more transitory species were

of slight significance in respect of tsetse distribution. Waterbuck were regularly recorded in quadrat Ot.1T, although the numbers were highly variable and they were also observed in Ot.3T but never in Ot.2T; in fact, there was a large group of waterbuck resident in the area between Ot.3T and Ot.1T. The extensive home ranges of these animals tended to bring them into these quadrats from time to time and in variable numbers. The frequent presence of a substantial herd of large antelope in the vicinity of Ot.1T could have attracted tsetse from adjacent areas, even if this species was not a preferred host.

The fact that no waterbuck blood meals were identified in the valley, even in tsetse collected in Ot.1T on 8 October 1970 when waterbuck (see Table 2) was the most numerous species recorded, strongly suggests that waterbuck were not attractive to *G. pallidipes*. However, they could have been involved indirectly in maintaining the greater density of tsetse in and around quadrat Ot.1T.

Buffalo and bushpig were the other species that might have been significant; however, the numbers observed were too small to permit general conclusions to be drawn. Buffalo were highly transitory, as shown by casual observations in many parts of the valley. Generations of intensive poaching might explain the frequent local migration and extremely nocturnal behaviour. Seasonal movements throughout the valley may have been determined by the poor drainage in the area and the animals' need to drink regularly. Bearing in mind the more flexible utilization of the range by this species, it is unlikely that they would have affected the distribution of a stable tsetse population.

Bushpigs were undoubtedly important hosts of *G. pallidipes*, as shown by total blood meal analyses from animals throughout the valley. In the Otuok area, however, their numbers were low and it is impossible to attach any significance to their distribution.

Considering the analyses of *G. pallidipes* blood meals broadly, all the evidence points to bushbuck being the most preferred host of this tsetse, although it is apparent that bushbuck were slightly less available than duiker and considerably less available than reedbuck.

The blood meals collected from quadrats immediately after game censuses again indicated that bushbuck was the preferred host. On one occasion—namely, 23 October 1970—in Ot.1T (see Table 2) it was the most available host, but on all other occasions when blood meals were collected from the vicinity of a known community of game animals bushbuck was not the species in the greatest density, although it was the only species identified from the blood meal analyses. Blood meals collected from Ot.2T on 9 October 1970 could have been highly significant since the bushbuck were considerably lower in number than the reedbuck and duiker. Although it was possible to collect only 3 gorged flies, 1 had fed on an unidentified bovid and 2 on bushbuck. Despite the presence of bushpig in several censuses, the blood meal analyses never indicated that tsetse had fed on Suidae.

Blood meal analyses from known communities of game animals therefore strongly suggest that bushbuck is selected as a host despite the presence of other species in greater numbers. This confirms the observations made by Lamprey et al. (1962) on the selective feeding behaviour of *G. swynnertoni* in an area where several species of game animals were present in much greater numbers than those selected by the tsetse population.

The identification of blood meals collected along the Otuok transect were derived mainly from bushbuck and, to a lesser extent, from buffalo. It is significant that on 1 day 4 of 5 blood meals collected were identified as being from buffalo. It appears that buffalo were highly preferred hosts when available, and this view is supported by the blood meals collected in the Rari Valley during an entomological survey. A large proportion of the feeds were identified as being from buffalo, although the Rari Valley was heavily settled and buffalo were seldom recorded in the area. In the Rari quadrat, Ot.3T, buffalo were never recorded and their spoor were not observed. Therefore, the blood meals were probably obtained after a recent migration of a buffalo herd through the area.

A similar phenomenon was recorded at the edge of Ruma thicket during another entomological survey. A herd of roan antelope occupied an area close to the thicket edge for several days and *G. pallidipes* blood meals identified from this same area during that period were all from roan antelope.

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RÉSUMÉ

INFLUENCE DE LA FAUNE SAUVAGE SUR LA RÉPARTITION ET LES HABITUDES TROPHIQUES DE *GLOSSINA PALLIDIPES* DANS LA VALLÉE DE LA LAMBWE

Bien qu'on admette généralement que les animaux sauvages jouent un rôle important en tant qu'hôtes de certaines espèces de mouches tsé-tsé, on ne dispose que d'informations fragmentaires sur les aspects quantitatifs de ces relations. Les auteurs ont entrepris de les étudier dans la vallée de la Lambwe (Kenya) où coexistent de nombreuses populations de *Glossina pallidipes* et une faune abondante et variée.

On a choisi au préalable une zone de fourrés épars, particulièrement riche en glossines et en gibier, d'aspect relativement uniforme. On y a délimité trois secteurs de 800 m de côté et de 0,64 km² de superficie chacun. Les animaux présents dans chaque secteur ont été dénombrés à 9–10 reprises en disposant, sur trois côtés du territoire, des observateurs chargés d'enregistrer les passages d'animaux chassés par des rabatteurs. Les glossines ont été capturées au moyen de pièges placés au centre de chaque secteur pendant environ 2 mois, le nombre de captures étant considéré comme proportionnel à la population totale du secteur. Aussitôt après le recensement des animaux sauvages, on a procédé à la recherche des glossines gorgées afin d'identifier les repas de sang et de les rapporter à une espèce animale connue.

Des renseignements complémentaires ont été obtenus par l'examen des traces d'animaux, par des sondages concernant les populations de glossines et par l'analyse des repas de sang au cours d'investigations effectuées à travers une zone de fourrés denses continus. Cette analyse a donné des résultats concordant avec ceux des analyses pratiquées dans les secteurs délimités.

On a découvert que le céphalophe (*Tragelaphus scriptus*) est de loin l'hôte préféré de *G. pallidipes*, même lorsqu'il n'est pas l'espèce prédominante, et qu'il existe une corrélation positive entre sa répartition et celle de la glossine. *G. pallidipes* prélève aussi ses repas de sang sur les buffles et les antilopes rouannes, mais ces deux espèces, en raison de leurs habitudes migratrices, n'ont aucune influence sur la distribution de l'insecte.

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