RESTING SITES AND PREDATION LEVELS OF ADULT *GLOSSINA PALLIDIPES* AUSTEN AT NGURUMAN, KENYA

By

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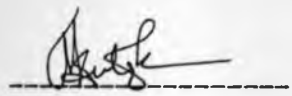
A thesis submitted in part fulfilment for the Degree of Master of Science of the University of Nairobi

1988

Declaration

This thesis is my original work and has not been presented for a degree in any other University.



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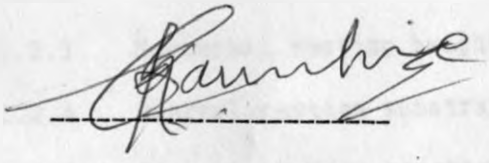

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Acknowledgements

This work would not have succeeded except for the assistance from various persons. I am indeed grateful to Dr R.D. Dransfield without whose invaluable assistance this project would not have made a first or final move. I appreciate the guidance and useful comments made by Dr G.R. Karuhize while supervising this study. Many thanks also go to Prof R.W. Mwangi and Dr Nyamasyo for their words of encouragement especially when the going got tough.

I acknowledge the invaluable field and laboratory assistance provided by Tsetse Research Programme and the then Biostatistics & Computer Service Unit of the ICIPE. This study was, however, hosted at the Department of Zoology of the University of Nairobi.

Lastly, my sincere gratitude go to the National Council for Science and Technology for financing this project, Miss Leah Ndung'u for typing the initial drafts of this thesis and the German Academic Exchange Service (DAAD) without whose scholarship I would not have read for a Master of Science degree.

Abstract

This study aimed at investigating the resting sites and assessing the amount of predation done on resting adult tsetse flies of the genus Glossina pallidipes Austen.

Tsetse flies were trapped in the field using Zimbabwean F3 traps baited with cow urine and acetone. Flies used for nocturnal resting site studies were dusted with flourescent powder and released in the bush at dusk. When it was fully dark, one-hour long searches were then made using long wave ultra-violet light. This was done from August 1986 to May 1987. Daytime resting sites were investigated during the hot dry and long rainy seasons. It involved searching for resting tsetse flies in a large field cage at four different times of the day, namely early in the morning (05.45 to 06.30 h), late in the morning (10.30 to 11.30 h), early afternoon (13.30 to 14.30 h) and late in the afternoon (16.30 to 17.30 h). For each fly observed, its resting substrate and resting height were recorded. Temperature and relative humidity were also measured.

Nocturnal resting substrates were leaves, twigs, branches and tree trunks. Strong preferences were shown for twigs and small branches during the cool dry, short rainy and hot dry seasons. Leaves were preferred during the long rains. Mean nocturnal resting heights were lowest in the cool dry season (1.5 m), intermediate and equal in the two rainy seasons (1.7 m), and were remarkably high during the hot dry season (2.3 m).

Branches and tree trunks were used as daytime resting substrates. During the afternoons of the hot dry season, the ground was preferred, while branches were preferred during the wet season at the same times. No tsetse were found on the ground during the wet season. The nocturnal resting substrates were the ones observed in the very early morning search. Diurnal mean resting heights varied greatly during the hot dry season depending on the time of the day. There was a gradual decrease from 2.03 m early in the morning to 1.21 m late in the morning, and eventually to 0.25 m in the early afternoon. During the long rainy season resting heights fluctuated from 1.74 m to 1.38 m to 1.51 m and eventually to 1.34 m during the four times of the day respectively.

Generally tsetse rested higher at night than in the daytime. It was observed that temperatures above 25°C and relative humidity below 40% were apparently responsible for resting low down on thick substrates, and even on the ground.

The amount of predation of resting tsetse flies was assessed at three different resting sites namely leaves, branches and tree trunks, and at three different localities. The method adopted was that developed by Rogers (1974). It involved tethering tsetse flies within a 'metre cube' of the resting substrate. The predatory behaviours of vertebrates, mainly birds and lizards were watched from a distance while those of invertebrates were done by inspections at experimental sites. Samples of invertebrate predators were preserved in

alcohol for species identification later in the laboratory. The amount of predation occurring in the daytime was distinguished from that which occurred at night. The effects of prey density on predation levels was also investigated. Results obtained were normalized by arcsine square root tranformation and then subjected to multivariate analysis of variance.

Field observations showed that daytime predators largely included birds, lizards and jumping spiders of the family Salticidae. Ponerine ants were the main nocturnal predators. The level of total predation on the various resting substrates, i.e leaves (44%), branches (47%) and tree trunks (56%) were not significantly different. Vertebrate predation was however much higher on thick substrates than on thin ones (i.e 37% on tree trunks and 17% on leaves). Predation by ants was indifferent of the sites. Level of predation in the daytime (54%) was much higher than that at night (43%). Mean levels of predation at the three locations were 43%, 61% and 52%. These were shown to be significantly different. These results were caused by the existing local differences in the abundance, distribution and movements of the predator populations.

Vertebrate predation showed direct density dependence at low densities of up to 8 tsetse flies per metre cube of vegetation.

CHAPTER 1

GENERAL INTRODUCTION AND LITERATURE REVIEW

1.1 Introduction

1.1.1 Taxonomy and Distribution of Tsetse flies

Tsetse flies are blood sucking two winged insects which belong to the genus Glossina Wiedemann 1830. 'Tsetse' is a Setswana (Botswana) word meaning a fly destructive to cattle. Features of their antennae and wings distinguish tsetse flies from other flies. The antennae each have 3 segments and the hairs of their aristae bear secondary branches. The wings possess a hatchet shaped discal cell between the 4th and 5th longitudinal veins.

Newstead et al. (1924) first placed the genus in the family Muscidae together with other flies. It is now placed in a separate monogeneric family called Glossinidae (Brues et al., 1954; Haeselbarth et al., 1966). The genus contains 30 living taxa, comprising of 22 species and 8 subspecies. Based on the morphology of the male and female genitalia, the species are arranged in three groups namely fusca, palpalis and morsitans. Some authors have accorded these the status of subgenera (Zumpt, 1936; Haeselbarth et al., 1966) namely Austenina, Nemorhina and Glossina respectively.

Glossina pallidipes Austen 1903 belongs to the morsitans group. It is differentiated from the closely related G. longipalpis by its uniformly pale colour of the last tarsal

segment of the foreleg. The tip of the same segment in G. longipalpis is dark. G. pallidipes also has a narrower 3rd segment of its antennae as compared to that of G. longipalpis (Potts, 1970).

Tsetse flies are limited to Africa and confined between latitudes 15°N and 28°S. In general, species of the fusca group inhabit the forests, the palpalis group inhabits riverine areas and the morsitans group occupies the savannah woodlands. The first tsetse distribution maps were drawn by Potts (1953/54) and revised by Ford and Katondo (1975, 1977). In an interim report of the revision of their 2nd edition, Katondo (1984) advised that for many species, surveys are done on a national basis, and hence the maps for the overall distribution are approximations that are not updated.

Rogers (1979) defined the distribution limits of a species by the inequality $\sum_{n=1}^{n=12} \log. fn \geq \sum_{n=1}^{n=12} Kn$ where fn is the fertility for each month, n, of the year and Kn is the corresponding monthly mortality (K-value) due to abiotic conditions. Using the empirical approach, Rogers and Randolph (1986) found that the northern distribution limits of Glossina palpalis and G. fuscipes in West and Central Africa best correspond with the joint condition that temperature and saturation deficit do not exceed 27°C and 14 mm Hg respectively, while the southern cooler limit is set by the line of 6/7 mm Hg saturation deficit.

The Kenyan tsetse belt is shown in Fig. 1. It is estimated at 138,000 Km^2, nearly 24.2% of the land surface (National Atlas of Kenya, 1970). Glossina pallidipes is the

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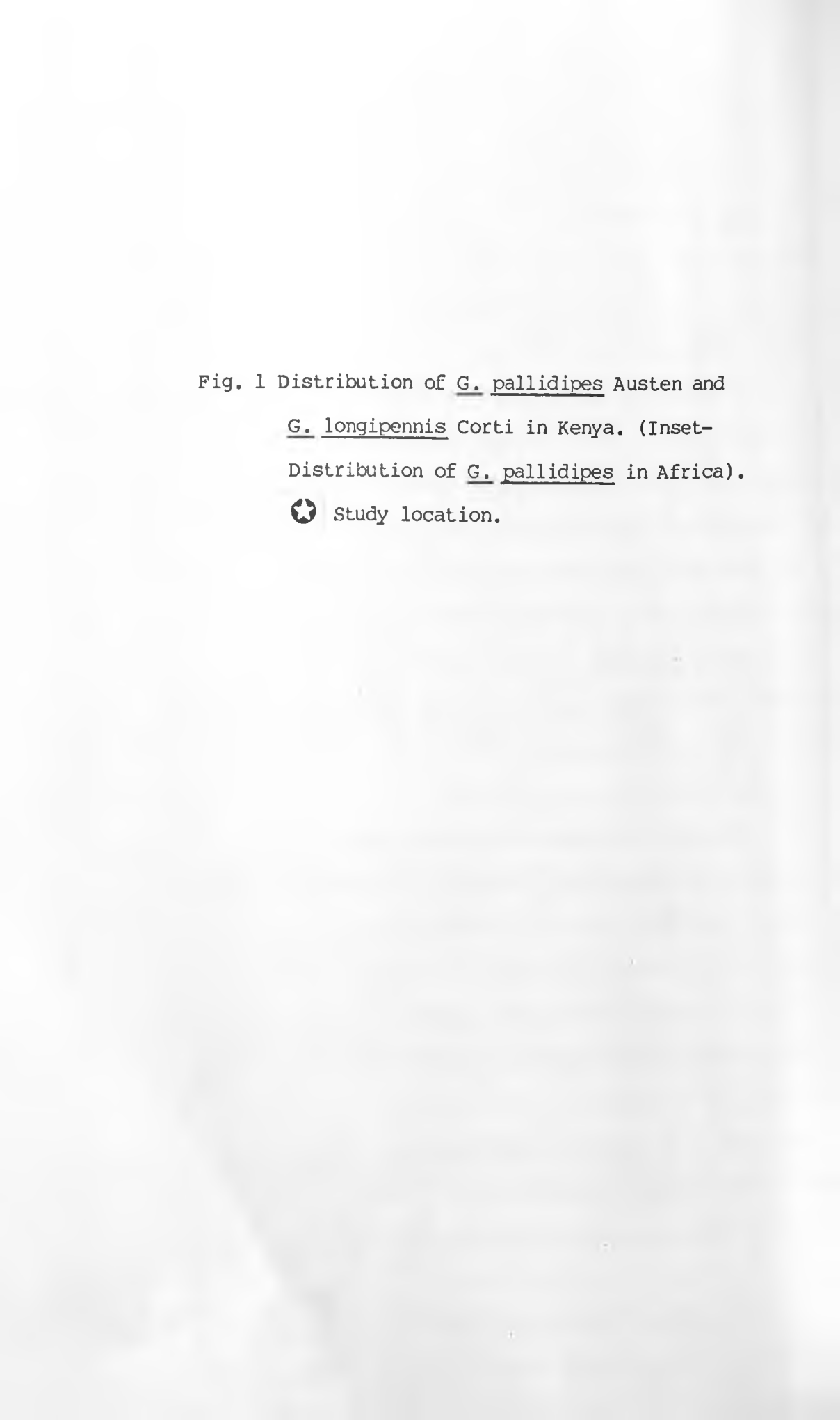
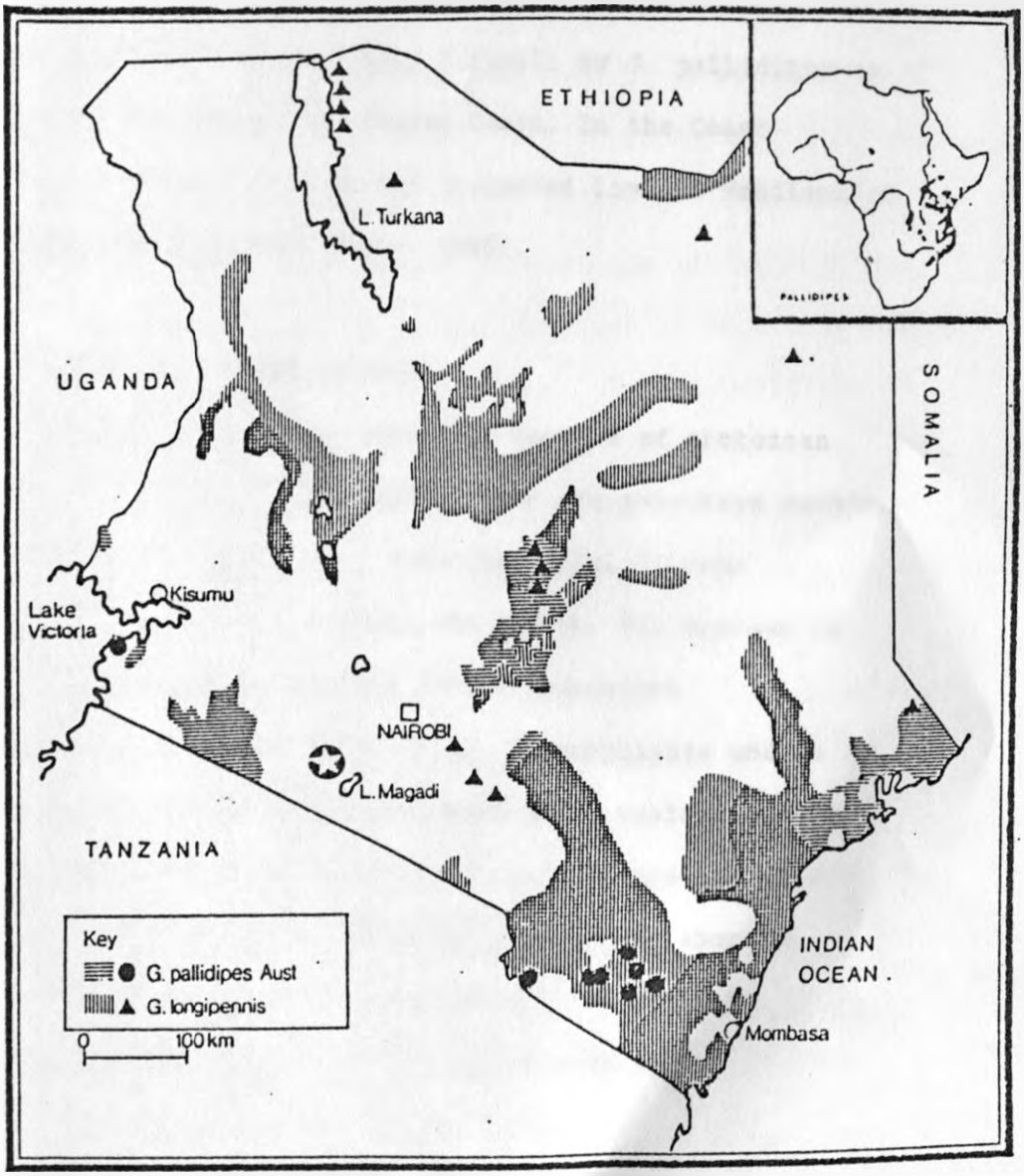


Fig. 1 Distribution of G. pallidipes Austen and G. longipennis Corti in Kenya. (Inset- Distribution of G. pallidipes in Africa).
✪ Study location.


ETHIOPIA
L. Turkana
UGANDA
SOMALIA
Kisumu
Lake
Victoria
NAIROBI
L. Magadi
TANZANIA
INDIAN
OCEAN
Mombasa
Key
G. pallidipes Aust
G. longipennis
0
100 km

most common and widely distributed species (Jaenson, 1981). According to Ford (1970) G. pallidipes is found in areas associated with bushbuck but is now widely distributed in habitats ranging from savanna thickets to man-made plantations. Turner (1980) reported the colonisation of coniferous plantations bordered by Euphorbia tirucali by G. pallidipes in the Lambwe Valley and at the Kenyan Coast. In the Coast Province it is common in both the thicketed lowland woodland or forest/grassland interface (Snow, 1980).

1.1.2 Tsetse and Trypanosomiasis

Glossina species are important vectors of protozoan parasites of the genus Trypanosoma. These are causative agents of trypanosomiasis, a serious, sometimes fatal disease affecting both domestic livestock and humans. The disease in cattle is called Nagana. In East Africa, livestock trypanosomiasis is caused by T. vivax, T. congolense and to a lesser extent T. brucei brucei. Susceptible livestock bitten by infective tsetse flies develop severe parasitaemia and anaemia, become weak and lose weight. Breeding animals may abort or become infertile. Many infected animals die; others may eventually recover but their growth and productivity are severely reduced (ILRAD Reports, 1983; 1984).

Livestock trypanosomiasis is one of the most pervasive problems in livestock production in Africa. It is impossible to estimate, even approximately the direct losses that it causes (ILRAD Reports, 1984) but several facts give some indication of the magnitude of the problem. It excludes an area of 10.8M Km^2

from supporting 120M head of cattle that would produce an additional 1.5M tons of meat every year (Odhiambo, 1976). It has further incurred the use of 25M doses of trypanocidal drugs a year, and associated poor public health. In Southern Somalia alone, Hendy et al. (1986) estimated that it is responsible for about 30% of all cattle mortality, 10% of sheep and 8% of goats.

The disease in man is called sleeping sickness. In Kenya, it is caused by T. brucei rhodesiense (ILRAD Reports, 1983). Lambwe valley in the Nyanza Province is an example where sleeping sickness is endemic. Moreover, there is evidence of disease transmission taking place within the communities inhabiting the Lake Victoria shores through the agency of a different vector called G. fuscipes fuscipes. This is also the main vector of T. b. gambiense in Uganda (Turner, 1980).

Several attempts have been made over the years to control the problem of trypanosomiasis. Some of the methods have included surveillance, use of trypanocidal drugs both for animals (e.g berenil, novidium) and man (e.g suramin) and follow-up procedures. Despite these measures, Turner (1986) has cited over 200 human cases in the Lambwe valley and several deaths by mid 1984. One immediate problem is that there is a general shortage of these drugs and again their administration tends to be poorly controlled (Hursey, 1985).

Another problem lies in the highly evolved protective mechanism of these trypanosomes. Both metacyclic and bloodstream forms are coated with a dense layer of variable surface glycoproteins (VSGs). This is a thick coat of surface antigens that prevents antibodies produced by the host from

reaching other parts of the parasite. Trypanosomes have a large number of VSG genes which code for the protein component of the surface glycoprotein. Only one of the genes is expressed at any one time (ILRAD Reports, 1983). Thus the parasite can change its surface coat. Before all the parasites are eliminated, some are produced which display new VSGs and thus evade the hosts' immune response.

Given these problems, chemotherapy has therefore been regarded as a temporary measure only. Another feasible alternative to the disease control entails removal of tsetse from the infested areas. Tsetse control has hence been an integral part of the suppression of trypanosomiasis.

1.1.3 Tsetse control

In the early days, tsetse populations were reduced by eliminating game animals and thereby removing their food supply, or by destroying their preferred habitats by bush clearance, and human settlements. Such traditional methods, however, had several disadvantages. Game destruction has not only been wasteful of Africa's natural resources but tsetse have often found other hosts, including man. The agricultural potential of the land has also deteriorated through soil erosion as a result of reduced cover. Other methods were therefore developed.

Following the discovery of the insecticidal properties of DDT, the control of many insect pests, including tsetse, became increasingly dependent upon the use of chemicals. The methods of insecticide application are thoroughly reviewed by

Allsopp (1984). The earliest of these methods was ground spraying, and thereafter aerial application using light aircraft.

In the 1940's large volumes of aqueous suspensions of DDT and other persistent chlorinated hydrocarbon insecticides were applied to trees and bushes in the tsetse habitats (Allsopp et al., 1985). Based on the knowledge of the resting sites of flies in these habitats, ground spraying of DDT played an important role in the tsetse eradication campaigns in Zimbabwe. In the early 1970's, tsetse were eliminated from the south eastern region while between 1980 and 1984, eradication was achieved in 40% of the treated area in the western region (Shereni, 1985). This low percentage was largely due to reinvasion. By a single selective ground application of the residual pyrethroids permethrin, cypermethrin and decamethrin on G. palpalis and G. tachinoides in Nigeria, no flies were caught within 450 days after spraying (Spielberger et al., 1979). Spielberger et al. (1977) has reviewed the aerial spraying using helicopters of the persistent insecticides dieldrin, and endolsulfan in northern Nigeria from 1969 to 1976 where some degree of success was achieved.

Because these residual insecticides are environmentally hazardous, emphasis was later placed on the use of aerial sequential application of non-residual insecticides from fixed wing aircrafts. These applications are aimed at killing all tsetse on the first spraying with further sprays eliminating those which emerge from puparia in the ground at the commencement of spraying before they can breed. The duration of spraying is thus determined by the pupal period, and the interval betwe

sprays by the time taken by the female to produce an offspring. Recent research has shown that it is the smaller droplets of an aerial spray drifting through the habitat and penetrating through the canopy that has the greatest immediate effect on the adult tsetse flies (Allsopp et al., 1985). Moreover, the method has minimal risk of non-target contamination. Some degree of success has been achieved.

In 1978, 98-100% of tsetse population was eliminated following ULV fixed wing aerial application of endosulphan in southern Zambia (Kalimina, 1983). In Tanzania, an area of 1700 Km^2 chiefly inhabited by G. m. centralis and isolated pockets of G. pallidipes and G. brevipalpis was treated with five aerial sprays of endosulphan as an aerosol. It achieved 90-96% reduction in tsetse populations. Failure to achieve eradication was due to uneven distribution of aerosol caused by the rugged terrain (Gao and Mwashala, 1983).

Some of the above methods have also been integrated. For example, five aerial applications of endosulphan to eradicate G. pallidipes and G. morsitans from a 2400 Km^2 area of rugged hilly terrain in Zimbabwe in 1982 achieved total elimination of tsetse for at least 90 days after final application. Reinvasion was prevented by ground-spraying the perimeter with 5% DDT before the aerial spraying (Hursey and Allsopp, 1983). These operations were continued in 1983 and this area was increased to 10000Km^2 (Hursey and Allsopp, 1984).

Sequential aerial application of endosulfan was supplemented by ground application of residual dieldrin and bush clearance in Lambwe Valley for eradication of

G. pallidipes. After nine sprays of comparatively heavy doses of insecticide, the tsetse population was eventually reduced by 99 to 99.9% in the main habitats of thicket and acacia woodland and by about 90% in coniferous plantations. However, it recovered within one year to original levels despite the fact that the tsetse belt is quite small and isolated (Turner, 1984; Turner and Brightwell, 1986).

A predictive model was developed to attempt to explain this rapid recovery in terms of the number of flies (adults and puparia) present initially and the probable effectiveness of the spray (Turner and Brightwell, 1986). It was estimated that the aerial spraying was 90% effective in killing adults per application with several thousand flies probably remaining after spraying. This was confirmed by the similarity between observed and expected times to recovery of the population following spraying. It was considered unlikely that tsetse caught during and immediately after spraying were re-invaders from unsprayed gulley thickets.

The effects of insecticidal application programmes are now shown to depend very strongly on the characteristics of the population ecology of the tsetse (Randolph et al., 1984). For example, the sprayed population has often recovered to a large extent through density dependent emigration and immigration. Such population resilience has been evidenced in Cote d'Ivoire and on a local scale within the Lambwe Valley. In the former, insecticides killed a higher proportion of the local, mainly resident population in sites with high G. p. palpalis numbers than those with low numbers. Large re-invasions from the

neighbouring areas caused rapid recovery (Randolph et al., 1984). In the latter, only the thicket population initially showed any sign of recovery but when the numbers finally reached their pre-control levels, trap catches in the woodland and plantation suddenly increased (Turner, 1984).

Further use of insecticides is today being reconsidered with a view to eliminating, restricting, or integrating their use with other methods. This is because not only do these insecticidal applications often fail to achieve their aims but they are also expensive, can cause environmental pollution and upset the ecosystems operating in tsetse habitats. For example, in Zimbabwe it was shown that DDT residues from tsetse fly control programmes, and with relatively minor contribution from mosquito control, commercial agriculture and traditional farming readily accumulated in insectivorous birds and bats in amounts sufficient to cause eggshell thinning in certain avian predators (Matthiessen, 1985).

Alternative methods to the use of insecticides include the sterile insect technique (SIT) and the use of traps and screens. SIT has been used in Burkina Faso where 650000 sterile G. p. gambiensis males were released along a 32 Km stream linear habitat in riparian vegetation. Eradication was achieved in 16 to 20 months after release began according to the release strategy employed (Politzar and Cuisance, 1982). In Tanzania, 351000 sterile males were released over 195 Km^2 of mixed savannah woodland. It achieved an average of 81% control of G. m. morsitans over a 15 month period. Failure to achieve eradication was attributed to reinvasion from outside the area (Williamson et al., 1983).

In Nigeria, reinvasion from nearby infestations was prevented by using blue screens impregnated with 0.05% a.i solution of deltamethrin and a 3 Km long 40% e.c dieldrin barrier. Three forests were then first subjected to different methods of population suppression after which SIT kept the population of G. p. palpalis under control for 2 years using a flooding ratio of three sterile males for each wild male. Eradication was achieved after this ratio was raised to 10:1 (Oladunmade et al., 1986).

Theoretical studies have suggested (Overseas Development Administration and University of Bristol, 1986) that sterilizing and releasing wild flies of both sexes in the field is always more superior than sterilizing males only. The method, however, has a few problems. It is technologically demanding and automatic sterilizing traps made are far too complex, expensive and hazardous for routine use (House, 1982; cited in Vale et al., 1985). Results obtained by Hall and Langley (1987) with various autosterilizing systems for G. pallidipes and G. m. morsitans in Zimbabwe, however, suggest that it may be possible to develop a cheap, safe and efficient autosterilizer for use on tsetse traps.

Traps or insecticide impregnated targets are far cheaper and safer, but would they control tsetse over the whole of the infested areas ? The development of the biconical trap provided a standard tool for sampling most tsetse species populations in many African countries and was a first step in this regard. Many such traps have since been exploited for purposes of control through removal trapping. For example, six

weeks of continuous removal trapping using biconical traps reduced the population of G. palpalis by more than 90% in Central Nigeria but failed to eradicate it. Eradication was expected when this method was combined with sterile male release (Takken et al., 1986).

More tsetse have been observed to visit and alight on the trap than those that actually enter it (Hargrove, 1972; Vale and Hargrove, 1979). Treating their surfaces with persistent insecticides to kill tsetse that alight on it without entering enhances their efficiency. This was demonstrated in Cote d'Ivoire where G. p. gambiensis and G. tachinoides were almost eradicated in an area of about 1700 Km^2 (Kupper and Douati, 1986).

Together with traps, simple visual targets that consist of screens of blue or black cloth coated with insecticides offer the advantages of considerably reduced costs, are non-polluting and could form a new approach to tsetse control. In a pastoral area in Burkina Faso for instance, a successful control campaign against G. p. gambiensis, G. tachinoides and G. m. morsitans integrated insecticide impregnated screens in the dry season and release of sterile males in the rainy season. No tsetse were thereafter found for more than eight months of regular and systematic checks (Cuisance et al., 1986).

Dosages required to kill tsetse are also quite low. Susceptibility studies of wild caught G. pallidipes females to fresh aqueous suspensions of 3% dieldrin w.p., 3% dieldrin e.c., 5% DDT w.p., and 0.0625% deltamethrin flowable concentrate sprayed on a cotton canvas at 0.36 $l\ m^{-2}$ killed 95% of the tsetse that rested for 45 seconds on these deposits

within 72 hours. Tsetse flies colliding with terylene netting immersed in 0.75 to 6.0% suspension of dieldrin w.p. and 0.01 to 0.1% suspension of deltamethrin flowable concentrate produced mortalities of 100% (Torr, 1985).

Vale et al. (1985) estimated that the quantities of insecticide needed for the targets are about 1% of those for ground or aerial application; hence they are less environmentally hazardous and require little foreign currency. Whereas tsetse re-invade sprayed areas during seasons when the spray is no longer effective, the greatest advantage, perhaps, is that once the targets have cleared an area of tsetse, they can hold it free against invasion.

Traps and targets impregnated with insecticide are nevertheless associated with a few problems. Like most other insects, there is a possibility of tsetse developing resistance against the insecticides. The servicing of the several screens or traps laid in the field is expensive especially where a landrover is used to negotiate the rugged tsetse habitat. Theft of screens/traps is also common especially where the cloth used to construct them is fancied by the local community for their clothes. Effective tsetse control operations have to be as cheap as possible. One solution to the former problem is to use traps exclusively while that of the latter two problems has been seen in having local community involvement in tsetse control (Okoth, 1986).

On a large scale, what impact has tsetse control had and what is the current thought ? The continued presence of tsetse flies in the continent only shows that they have taken

advantage of the loopholes and weaknesses that existed in the prior control methods used against them. Rogers and Randolph (1985) have shown that Glossina species still infests 40% of tropical Africa and that this figure has not changed much in at least the last 30 years. Tsetse control now requires a novel approach.

The Report of the Second Consultation of the Programme for the Control of African Trypanosomiasis from 5 to 7 December 1978 (FAO of the United Nation, Lusaka, Zambia, 1979) noted that the rational control of tsetse flies is not possible without a thorough knowledge of the ecology of the target species. For most of the species, we still lack this thorough knowledge about them. At the 19th meeting of the Organisation of African Unity/International Scientific Council for Trypanosomiasis Research and Control (OAU/ISCTRC) held in Lome, Togo from 30 March to 3 April 1987, it was noted that a multidisciplinary approach appeared to be the best means of acquiring this knowledge, and thereafter achieving a significant measure of success in tsetse and trypanosomiasis control.

1.1.4 Objectives of current study

In 1983 ICIPE scientists initiated the multidisciplinary Nguruman Tsetse and Trypanosomiasis Project which aimed at developing new approaches to tsetse and trypanosomiasis control through a greater understanding of the vector and disease dynamics and more appropriate control strategies. The target species is Glossina pallidipes and the

major approaches are population modelling, and the development of cost effective technologies for tsetse control with maximum community participation.

A simple population model of G. palliaipes has already been developed which exposed missing links in our knowledge suitable for further collaborative research. In particular, data were lacking on predation of adult tsetse flies at the resting sites. In 1974 a Scientific advisory Group meeting at the Memorial University of Newfoundland, St. Johns', Canada noted the growing recognition of the importance of safeguarding such natural regulatory factors as predators and insect parasites bearing upon tsetse populations, and their possible use in biological control (IDRC, 1974).

Bursell (1959) determined that tsetse flies were active for only 30 minutes in a day and analysis of their energy budget by Bursell and Taylor (1980), and Randolph and Rogers (1978) confirmed this finding. Since adult tsetse therefore spend most of their time at resting sites, most of their predation would occur there. It is therefore important to know the actual predators, their ecology and their predatory potentials. This would help to evaluate the status of biological control for tsetse flies.

This information was required to improve the predictive power of the model and thereby assist to design integrated control strategies that would enhance the beneficial role of these predators. Some ways of achieving this could be through increasing the predator populations or by designing control measures that would not kill them, for example, by the use of selective tsetse traps for removal trapping.

These investigations were therefore initiated with the following objectives in mind:

1 to determine, and explain the diurnal and nocturnal resting sites of Glossina pallidipes at Nguruman

2 to identify the common predators attacking this tsetse species at its resting sites

3 to quantify the level of predation of resting tsetse flies, and to assess the contribution of such mortality to the natural population regulation of G. pallidipes.

1.2 Literature Review

1.2.1 Techniques used to study resting sites

Davies (1967) categorised resting sites broadly into true resting sites and watching sites. The latter included hunting and following sites while the former included day and night resting sites. Movement from day to night resting sites undoubtedly takes place at dusk and the reverse at dawn. A resting tsetse is totally immobile, has the legs rather widely spread and the wings crossed flat over the back (Buxton, 1955). Most workers (eg Jewell, 1956; Minter, 1971; Scholz et al., 1976; Turner, 1980b) have noted little difference in the selection of resting sites between male or female, engorged or hungry flies. Nash (1952) found that resting tsetse directed their heads upwards immediately after taking a bloodmeal and thereafter they were directed downwards.

Several methods have been used in resting site studies. At night, marking techniques have largely been used. Reninson et al. (1958), Pilson and Leggate (1962), Robinson (1965), and Pilson and Pilson (1967) initially used reflective paints or glass spheres. Flourescent powders either mixed with gum arabic or dissolved in isopropyl alcohol have also been used (Jewell, 1956, 1958; MacDonald, 1960; Scholz et al., 1976; Spielberger and Barwinek, 1978; Turner, 1980a,b).

In the daytime unaided vision has been used (e.g. Nash and Davey, 1950; Chadwick, 1964; Oloo, 1984), but the dull colour and muted pattern of resting tsetse has often made observation difficult. Other methods of overcoming this problem

include the use of large field cages erected over cut back vegetation (Swynnerton, 1936), radioactive isotopes (Bois et al., 1977) and tanglefoot (Okiwelu, 1976; 1977; 1981; 1982; 1983). The latter is a clear, odourless and colourless sticky substance on which resting tsetse may get trapped.

1.2.2 Nocturnal resting substrates

Minter (1971) observed that the majority of G. pallidipes showed a marked preference for leaves and twigs of less than 2 mm diameter and few (10% or under) made use of tree trunks or branches. Spielberger and Barwinek (1978) found 84.6% of G. tachinoides mainly on the upper surface of leaves and only 11.5% on creepers and twigs. Oloo (1984) found most G. fuscipes fuscipes on leaves, then stems, twigs and climbers. Scholz et al. (1976) found that the nocturnal resting sites of G. palpalis palpalis did not differ during three observational seasons. Their distribution was 72% on leaves, (with 50% on the upper surface), 20.2% on creepers, twigs and branches of less than 5 mm diameter; and 4.8% on those of more than 5 mm diameter. Okiwelu (1981) noted strong preferences for fallen logs by G. palpalis gambiensis in all seasons and that there was a progressive increase in the percentage of tsetse at this site from the warm rainy through the warm dry to the hot dry season.

Using tanglefoot, preference for resting on fallen logs (37.9%), boles (27.6%), bushes (24.1%) and Branches (10.3%) was shown by G. morsitans morsitans during the dry season in Zambia (Okiwelu, 1976). Their distribution in the wet season was boles

57%, canopies 16% and bushes 15% (Okiwelu, 1977). By marking the flies, overwhelming preference for leaves (75%) and particularly the upper surface was noted for the same species, while 23% were on twigs, petiole and very thin branches in Mozambique (Turner, 1981). If other factors were constant, it appears that the methods used here gave different results. This is further supported by observations in Mali during the warm dry season on a closely related species G. m. submorsitans where the only ten tsetse found at night were restricted to boles (60%) and fallen logs (40%) (Okiwelu, 1982).

1.2.3 Nocturnal resting heights

A range of nocturnal resting heights have been demonstrated for various species. In Mozambique for example, Turner (1980b) found a fairly even height distribution of G. m. morsitans from the lowest up to about 4.5 m. Around the Lake Victoria region Oloo (1984) found G. f. fuscipes at a mean resting height of 0.81 m. Similarly, Minter (1971) found the majority of G. pallidipes at a range of 1 to 3 m above the ground. A small proportion were found up to a maximum height of 7 m while a relatively large minority were below 1 m. Whereas no gross effects of place and season were observed from Otuok, Roo, and Kiboko study sites over the wet and dry seasons, Scholz et al. (1976) found that the mean resting heights of 3.78, 2.95, and 1.52 m for G. p. palpalis over the seasons mid-rains, late rains, and the dry season respectively differed.

1.2.4 Diurnal resting substrates

Diurnal resting sites have ussually been studied at various times of the day. Between 09.00 and 15.00 hours, Chadwick (1964) found G. swynnertoni in Western Tanzania during the wet season resting on the underside of branches (64.6%), on large boles (15.4%) and beneath fallen trees (7.8%). In Niger, Turner (1980b) found G. tachinoides resting between 10.00 and 16.30 h and with a slight peak at 14.00 h. Their distribution was 77% on tree trunks, 13% on undersurface of low horizontal branches and 10% on exposed roots. Searches for G. m. submorsitans from 08.30 to 18.00 h (Turner, 1980b), however, revealed no resting tsetse before 11.00 and after 17.00 h. The majority were found between 12.00 and 16.00 h with 75% resting on the undersurface of horizontal and inclined branches and the remainder on tree trunks.

In Zambia Okiwelu (1976) found that the numbers of resting G. m. morsitans at different times of the day also varied, the highest numbers were stuck on tanglefoot between 06.00 and 09.00 h. Site type preferences were also shown between different times, boles being preferred from 06.00 to 09.00 h and thereafter, bushes were preferred for the rest of the day. During the wet season boles were highly utilised for the whole day; the next in importance being bushes and canopies. Higher numbers were found in open shaded bushes. Aardvark holes were least preferred, and were only important from 09.00 to 12.00 h (Okiwelu, 1977). Random searches for the same species in Mozambique (Turner, 1980b) showed that 93% rested on the underside of horizontal branches, on the woody

parts over 5 cm in diameter and 7% on tree trunks. Okiwelu (1982) observed its strong preference for low heights on tree trunks in all seasons: warm and dry, warm and rainy, and hot and dry. This implied that it was apparently not a seasonal adaptation but a characteristic of the species.

In Mali a marked preference for fallen logs by G. p. gambiensis was noted throughout the day. There was a progressive increase in the percentage of tsetse on these fallen logs from the warm rainy (90%) to the hot dry (95%) season (Okiwelu, 1981). Further observation on the species during the hot and dry season showed the order of importance of resting substrates as fallen logs, boles, and undergrowth; but at 12.00 to 15.00 h, fallen logs and boles were equally important (Okiwelu, 1983).

In a diurnal and seasonal study of the resting behaviour of G. pallidipes (Pilson and Leggate, 1962) in the Zambezi valley in Zimbabwe, a variety of resting sites were employed during the late dry season. The distribution of fed tsetse among the three major site types, viz branches, boles and rot holes indicated that clearly defined preferences were exhibited at different times of the day. Rot holes were highly preferred at 11.45 to 12.45 h, boles at 14.45 to 15.45 h, branches were preferred at two different times: 06.45 to 09.45 h and 16.45 to 17.45 h. During the rainy, cool and early dry seasons, there was exclusive preference for branches.

MacLennan and Cook (1972) observed that movement from day- to night-time resting sites takes place at the time of the rapid drop in light intensity. The reverse occurs during

movement from night to day resting sites. Preference for woody parts during the day and leaves at night does not, however, seem to be the general rule. For instance Kernaghan (1950-1960) (cited in Glover, 1967) observed that G. tachinoides in Northern Nigeria perched more often on stems than on leaves at night. Also the change in preference of G. p. gambiensis from woody parts during the day to green leaves at night deduced by Challier (1973) and Bois et al. (1977) based on two separate studies using marked flies was not observed by Scholz et al. (1976) and Okiwelu (1981).

1.2.5 Diurnal resting heights

A range of heights are usually given for tsetse resting in the daytime. The largest number of G. swynnertoni were, for example, found resting between 1.73 to 2.30 m (Chadwick, 1964). Turner (1980) demonstrated this for a few species: in Niger, 84% of G. tachinoides were found resting below 0.40 m and with a mean resting height of 0.32 m. Those of G. m. submorsitans ranged narrowly from 1.25 to 2.25 m with a mean of 1.75 m. A wider range from one to just over 4 m was recorded for G. m. morsitans in Mozambique, where 56% rested between 2 and 3 m and the mean height was 2.6 m.

Seasonal variations have also been demonstrated for G. pallidipes where in the hot dry season, the percentage observed below three feet was significantly greater (49%) than in any of the other seasons (10-19%) while that observed over 2.60 m was greatest during the cool season (Pilson and leggate, 1962). Okiwelu (1981) also noted an increase of G. p. gambiensis

resting low on fallen logs from the warm rainy (90%) to the hot dry (95%) season in Mali.

With regard to the general pattern of vertical height distribution, it can be inferred that a) there is a decrease in number of flies with increasing height, b) resting heights are lower in the daytime than at night, and c) resting heights are lower in the dry than in the wet season (Challier, 1982).

1.2.6 Factors affecting the choice of resting sites

Certain trees or woody parts have been found to be most attractive as tsetse resting sites. For example, Chadwick (1964) found 80% of G. swynnertoni at one location resting on Acacia mellifera whose individuals composed 31% of all trees. At another location 91% of the flies were resting on Commiphora schimperi which composed 92% of the trees. It was further noted that A. mellifera at the first location grew well and had open easily accessible branches whereas in the second location, it formed a tangled bush and C. schimperi grew better. Diallo (1984) studying the diurnal resting places of G. m. submorsitans during the hot dry season in Mali showed that 58% of the tsetse favoured the plant species Tamarindus indica, Vitellaria paradoxa or Khaya senegalensis.

In most cases such species were the most abundant in the area or their shape and growth habits provided better environmental conditions. It therefore seemed that it was the form of a tree rather than its species that is important in determining it's suitability as a resting site. In this regards, Okiwelu (1976) found no significant differences in the

distribution of G. m. morsitans on various tree species thereby suggesting a random selection of trees.

Minter (1971) noticed that the choice of resting sites by G. pallidipes was strongly influenced by the seasonal effects on the physical condition of the vegetation especially where at Kiboko study site there was a long dry season. Whenever and wherever leaves were sufficiently abundant, they were strongly preferred but when they decreased during the dry seasons, then small twigs became progressively more important as resting sites and finally predominated. Despite this, there also seems to be some directed choice to resting sites.

Challier (1982) explained the preference of thin twigs and creepers, and thick branches and trunks of plants by the fact of the utilisation of whatever is available. Species living in dense thickets or gallery forests therefore have the possibility of choosing their resting sites from the great numbers of twigs and creepers occuring in these types of vegetation whereas those living in more open vegetation are attracted to conspicuous isolated trunks constrasting with the background. He further noted that these two types of behaviours were in accordance with the laboratory observation on vision in G. m. morsitans by Turner and Invest (1973) that tsetse were sensitive to high contrasts and non-complexly shaped objects (trunks) and appreciate linearity of forms (twigs and creepers).

Scholz et al. (1976) noted a decreasing proportion of flies perched on small twigs during periods of dewfall in the rainy season. They noted that liquid droplets collected more easily on small surfaces like twigs rather than on large

leaves. Leaves could therefore be favoured as resting sites because they were drier. This was further supported by findings of Spielberger and Barwinek (1978) who observed that the proportion of flies on small twigs was lowest (6.6%) during the short rains when dewfall occurred. If this explains the seasonal change in nocturnal resting sites, then it still remains to determine what factors influence the diel and diurnal choice of resting sites. This could include predator avoidance, selection of vantage points for food searching and weather factors.

The earliest work documented to substantiate that the avoidance of predators could be a factor that determined the choice of resting sites is that by Swynnerton (1936). In a very large mosquito net erected over cut-back vegetation, he observed that females of G. morsitans, G. pallidipes and G. brevipalpis possessed procryptic resting habits, because rough-barked stems were selected in preference for smooth ones. Holes in tree trunks and grooves in the bark were also used for hiding in. Colour harmonisation also occurred because black tsetse (morsitans) chose black and grey barks, while brown ones (brevipalpis) chose brown bark. These behaviours were accounted to the avoidance of various bark hunting species of spiders that hid in crannies, and which were probably the female tsetse's most important enemy.

There has been a suggestion (Minter, 1971) that the shift to leaves and thin twigs at night is an adaptation to predator avoidance. While at daytime tsetse use the power of sight and their homochromy while on resting sites to escape

predators, at night they are warned of any approaching predators by the vibrations caused by the disturbances of these leaves and small twigs by the spiders and predatory beetles. Why then should they go for thicker substrates at daytime ?

Okiwelu (1976, 1977, 1981, 1982) noted that the choice of lower levels on boles, branches and canopies may be an adaptation for efficient host finding by the fly as watching sites. Since their preferred suid hosts (warthog and bushpig) are ground dwellers, the resting behaviour certainly brings them closer to their hosts. No arboreal mammals have been detected as providing bloodmeals. The movement of G. m. morsitans with the rising sun/temperatures onto the undersurface of more lateral and horizontal branches with a preference for those nearest the ground and free of foliage was also presumed to afford unobstructed vantage points to view movements of potential hosts (Turner, 1980).

The use of low thick trunks as true resting sites may help in the avoidance of harsh climatic conditions. Pilson and Leggate (1962) observed exclusive utilisation of the boles of large trees, rot holes and fallen logs as resting sites by G. pallidipes only in the very hot dry season when the temperatures were 34.3^{o}C mean maximum and 22.2^{o}C mean minimum. Temperatures above 32^{o}C, made flies to move to particular well shaded refuge sites, such as ant-bear holes, rot holes in trees and under fallen logs. MacLennan and Cook (1972) further asserted that a temperature above 36^{o}C was apparently required to oblige the majority of flies to move from the branches onto the trunks at low heights. Further evidence is where a large

proportion of flies were found low down on trunks during the hottest part of the day than at any other time (Okiwelu, 1976). Resting heights of G. tachinoides in the daytime decreased with an increase in environmental temperatures and no tsetse were found at a resting site where temperatures were above 36°C (Gruvel, 1977).

Humidity may also be an important factor. G. p. palpalis for example, rested lower in the dry than in the wet season (Scholz et al., 1976). When the relative humidities of the air at ground level were above 60% flies rested at 1.80 m high and when RH was below 60%, a height of 1.05 m was recorded. Spielberger and Barwinek (1978) also found that the average night resting heights of G. tachinoides were lowest (1.3 m) during the early rains when the temperatures were higher and humidities lower than other periods. In the mid-rains, it was observed that flies rested higher during the early part of the night (2.6 m) than during the second half (1.3 m), probably due to the higher humidities (ca 97%) during this second part of the night. This high humidity caused more dewfall on leaves higher up, than on those close to the ground. Drier ones were preferred. In the wet season, Scholz et al. (1976) recorded lower temperatures and higher humidities in tree canopies than on the ground. He explained that these may have caused G. p. palpalis to seek lower resting heights. During the dry season, temperatures recorded in the tree canopy were practically the same as those recorded during the mid-rains (23.9 cf 22.5°C). Relative humidity was however almost four times greater during the wet season (95.5%) than

during the dry season (25.6%). It therefore seemed likely that low humidity in the tree canopy during this latter period might have compelled the tsetse to seek lower sites where the humidity was more favourable.

However, weather parameters cannot always adequately account for preferred resting heights. Turner (1980) reported some instances of this. For example, the steady drop of temperatures from around 27°C to 16°C between sunset and 21.00 hours, and the doubling of the relative humidity from 36 to 70% did not have any apparent influence on the vertical distribution of G. tachinoides. There was only a slight variation between the ground and a height of 6 m (temperature varied by 2°C only, RH was only slightly higher at the ground).

In the daytime, Turner (1980) recorded lower temperatures and higher relative humidities in the G. tachinoides resting site than in the ambient habitat during the dry season. Thus they utilised a more favourable microclimate during the hottest part of the day and therefore avoided rigors of climatic stress. A different situation was experienced in the G. m. submorsitans woodland habitat where resting site and ambient temperature profiles were almost identical, but the exterior, ambient and resting site relative humidities all fell below 15% for 5 hours during the middle part of the day. In this habitat, the species was found not to be exploiting a favourable microclimate when at rest. During the cool dry season in Mozambique, there was no indication that these factors influenced the resting behaviour of G. m. morsitans (Turner, 1980).

Besides determining the choice of resting sites, weather factors can also affect the recovery rate of marked flies released for resting site studies. Scholz et al. (1976) demonstrated that during observation periods when unfavourable temperatures and relative humidities were recorded, the recovery rate of G. palpalis dropped from 30.2% in the rainy season to 14.4% in the dry season. Spielberger and Barwinek (1978) also reported that during the early rains higher temperatures saw a 26.2% recapture rate of G. tachinoides compared to 30.7% during the mid rains that had lower temperatures. Hostile weather may have caused tsetse to disperse resulting in a low recovery rate. According to Okiwelu (1981) low recovery rates during the rainy season may be due to the easier penetration of the released tsetse through the thin undergrowth to rest on the abundant fallen logs where their detection is often difficult.

1.2.7 Techniques used to study predation of insects

The ultimate aim of studies of predation and other population processes is to provide a basis of understanding the dynamics of animal populations (Holling, 1961). In the book 'The Biology of Predation' Curio (1976) considered predation as a universal factor important towards an understanding of the habits and structures of animals. He defined it as a process in which an animal spends some effort to locate a live prey and in addition spend another effort to mutilate or kill it. It is best distinguished from other forms of foraging in that it concludes with the mutilation, or total destruction of an

animal that offers some resistance against being discovered and/or being harmed.

The earliest method used to identify the predatory species and evaluate their predation of tsetse flies was the direct observation of the incidences of predation (Swynnerton, 1936). The rapidity with which the phenomenon may occur reduced the probability of making many such observations. An alternative is the examination of gizzard (and by the same argument stomach) contents of these predators. However, the work of Hartley (1939) (cited in Buckner, 1966) on the assessment of the food of birds showed that samples were so variable in volume, time and locality that an unobtainable number of samples were required to give the necessary statistical dependability in order to draw justified conclusions.

Southon (1958) further noted that interpretation of data collected from direct observation of predation can be ambiguous. In view of this, other methods have been developed to study predation, in particular the serological method by which the specific proteins of Glossina may be identified in the stomach contents of predators. Boreham and Ohiagu (1978) have thoroughly reviewed the use of serology in evaluating invertebrate prey-predator relationships. Service and Elouard (1980) successfully identified the natural predators of larvae and pupae of the complex of Simulium damnosum Theobald (Diptera, Simuliidae) in the Cote d'Ivoire. Adabie (1987) also demonstrated the agar gel precipitin test was specific for Glossina. The advantage of the use of serology is that it helps

identify the most important predators but on the other hand, it is difficult to quantify the impact of prey without knowing predator densities. This problem is solved by the method of tethering known numbers of prey first developed by Rogers (1974).

1.2.8 Predators of tsetse flies

Tsetse predators observed are varied. They include mammals, birds, reptiles, spiders and entomophagus insects. Swynnerton (1936) observed three species of birds actively searching and feeding on tsetse from twigs, tree trunks and thicket stems. These included the common drongo (Dicrurus adsimilis divaricatus), the mimetic flycatcher (Melaeornis pammelaina) and the mouse coloured flycatcher (Bradornis pallidus murinus). Other predators recorded include lizards, jumping and web building spiders.

Most observations have been on predation of flying tsetse or those attracted to a catching party. These records have included birds, dragonflies (Cacergetes leucostictus, Orthetrum chrysostigma), robber flies and bembicid wasps (Southon, 1956; 1958). Numerous species of asilids lie in ambush at various heights at tips of small isolated branches from which they keep watch of their prey flying from its resting site. In a study on predation by Asilidae over a period of six months, G. swynnertoni formed 15% of 330 Asilidae taken with prey (Southon, 1958).

Records of predation of resting tsetse are extremely rare; they only refer to bark-hunting spiders capturing tsetse resting on trees (Southon, 1958). A survey of the fauna of the trees on which G. swynnertoni were commonly found resting showed that it included numerous predators of the families Mantidae and Reduviidae, several families of spiders and possible predators like ants, beetles and Tettigonidae. A small non web-building spider Hersilia (Araneae, Hersilidae) is reported to pounce on G. swynnertoni resting adults and rapidly envelop them in strands of silk. A few spiders of the family Salticidae were also found with prey that included G. swynnertoni. In Upper Volta, Challier (1973) found spiders belonging to the families Theriidae and Clubionidae grasping G. p. gambiensis individuals at night.

The effects of predation by spiders are undoubtedly important. Nash (1969) reported that spiders of the genus Nephilia built strong and wide webs between trees around Lake Victoria, and that their invasion apparently caused the disappearance of G. palpalis from Sumba Island. It was estimated that of the total daily mortality of G. swynnertoni, 30% could have been due to predation by Hersilia.

Minter (1971) reported that dead and moribund G. pallidipes were eaten by ants, spiders and scorpions on the ground, while spiders and spider webs caught tsetse at higher heights. He further suspected that the bush-baby might have been a good predator as well. Vasserot (1986) has also proposed that carnivorous larva of the family Myiodactylidae (Neuroptera: Planipennia) endemic to the Australian

biogeographic region has behaviours particularly fitted for catching tsetse that shelter under leaves. This is because they hunt by ambush, clinging to the underside of leaves.

By using serological methods, Adabie (1987) showed that 25% of Asilidae, 12.9% of Gryllidae, 15.8% of Hymenoptera and 5.2% of Odonata had taken tsetse, suggesting that they could be the most important natural predators in the habitat of G. pallidipes in Nguruman.

1.2.9 Natural regulation of tsetse populations

The Scientific Advisory Group convened at the Memorial University of Newfoundland, St. John's, Canada, 25-29 March 1974 considered (IDRC, 1974) that the activities of these predatory animals were generally accidental or seasonal rather than being specifically directed. Their ecology has not been adequately studied and it has been difficult to judge their real importance and their efficiency in contributing to the natural limitation of tsetse populations (Gruvel, 1977).

Long term records show that the tsetse numbers, however, fluctuate very little about their characteristic population levels. This stability is caused by one or more of the four demographic processes namely birth, death, immigration and emigration being density dependent. Rogers and Randolph (1984) pointed out that only one of the demographic processes needs to depend on density for regulation to occur, but more than one may actually do so.

Density dependent factors are usually biotic, among which death due to predation is most frequently encountered in natural field situations. Ants of the genus Pheidole were identified as a major cause of pupal mortality in Uganda, and they took a constant number of puparia at lower densities and an increasing number at higher densities (Southon, 1958; Rogers, 1974). Puparial burying experiments at Nguruman, however, showed no evidence of density dependent mortality due to predation (Adabie, 1987).

On adult tsetse, tethering experiments of G. f. fuscipes in Uganda (Rogers, 1974) showed that predation by invertebrates (ants and spiders) was density independent while vertebrate predation, mainly by birds was strongly density dependent. On the whole, Rogers et al. (1984) estimated the natural mortality at 0.036 tsetse per day.

CHAPTER 2

STUDY AREA

2.1 Location

These studies were conducted at Nguruman which is about 160 Km to the southwest of Nairobi and 30 Km to the southwest of Magadi in the southern Kenyan Rift Valley. The main study area, which is about 100 Km^2 is shown in Fig. 2. It lies at latitude $1^0 55'$S and longitude $35^0 05'$E (altitude 700-900m). It spreads from the Ewaso Ngiro River to the east, the Nguruman escarpment to the west, Olkeramatian plains to the north and Mt. Shompole to the south.

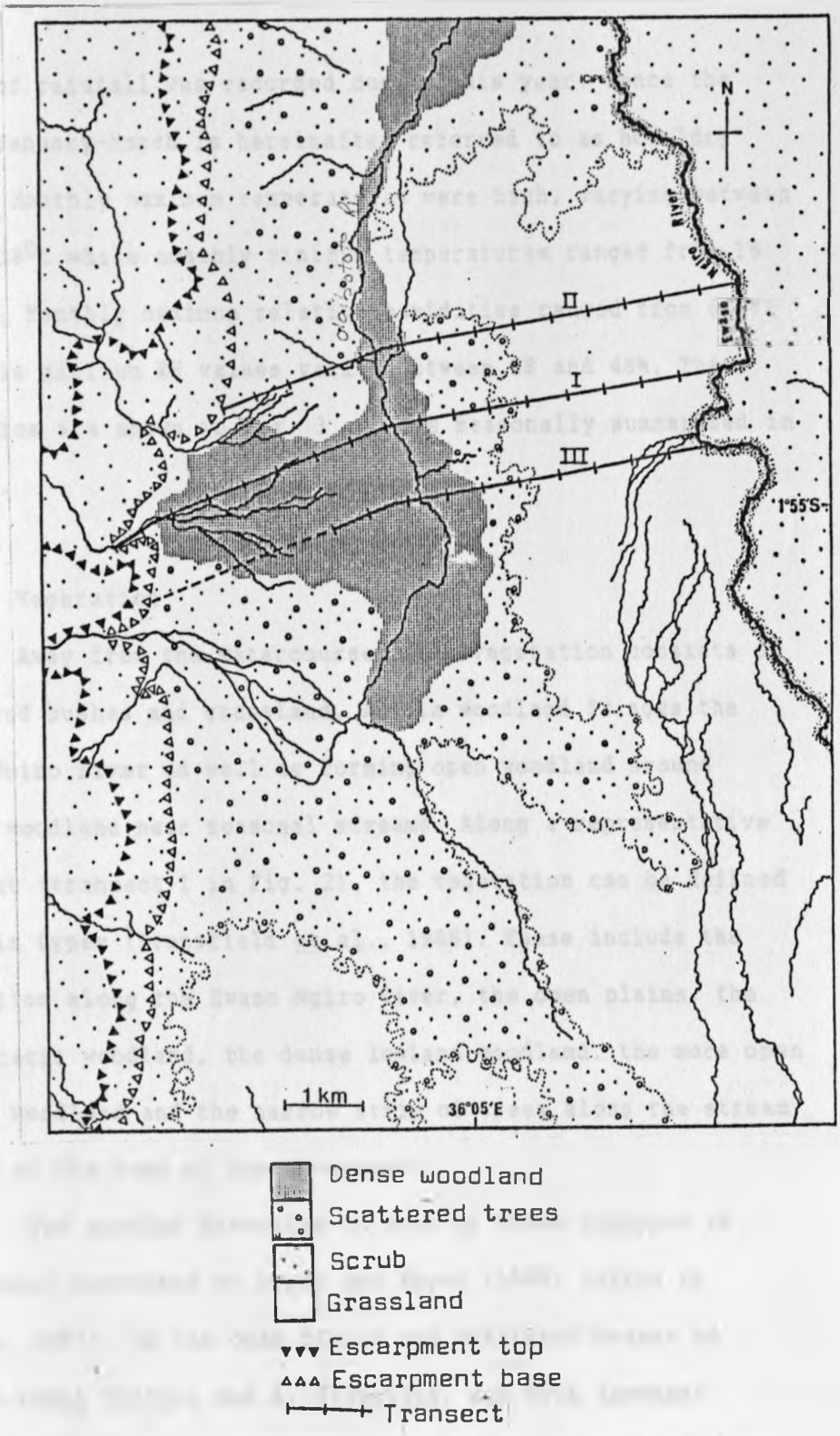
2.2 Climate

The weather conditions were monitored during the entire period of study i.e over the cool dry (July-October 1986), short rains (November-December 1986), hot dry (January-March 1987), and the long rainy (April-June 1987) seasons. Temperature and relative humidity were measured using a thermohygrograph in a Stevenson screen and placed at a height of 1.5 m. Its accuracy was checked by running alongside it a wet-dry and a maximum-minimum thermometer.

The area is generally dry for most of the year. The amount of rain received during the period of this study (July 1986- June 1987) was 512.3 mm, with two peaks in January and April. January is usually a hot dry month but an unusually high

1km
Dense woodland
Scattered trees
Scrub
Grassland
Escarpment top
Escarpment base
Transect

Fig 2


N
II
I
III
1°55'S
1 km
36°05'E
Dense woodland
Scattered trees
Scrub
Grassland
Escarpment top
Escarpment base
Transect

amount of rainfall was recorded during this year, hence the period January-March is hereinafter referred to as hot 'dry' season. Monthly maximum temperatures were high, varying between 32 and 38^{0}C while monthly minimum temperatures ranged from 15 to 21^{0}C. Monthly maximum relative humidities ranged from 60 to 90% while minimum RH values varied between 28 and 48%. These statistics are shown in Fig. 3 and are seasonally summarised in Table 1.

2.3 Vegetation

Away from the watercourses, the vegetation consists of scattered bushes and grassland. Acacia woodland fringes the Ewaso Ngiro river as well as forming open woodland around denser woodland near seasonal streams. Along a representative transect (transect 1 in Fig. 2), the vegetation can be defined into six types (Dransfield et al., 1986). These include the vegetation along the Ewaso Ngiro River, the open plains, the open acacia woodland, the dense lowland woodland, the more open upland woodland and the narrow strip of trees along the stream valley at the base of the escarpment.

The species diversity in each of these ecotypes is adequately described by Sayad and Sayad (1980) (cited in Adabie, 1987). In the open plains are scattered bushes of Acacia seyal fistula and A. siberiana, and with abundant grasses during the rainy season. In the acacia woodland, the bushes are thicker, and the tree species are more diverse i.e., in addition, there are Acacia albida and A. tortilis.

Fig. 3 The climate of Nguruman during the study period July 1986 to July 1987

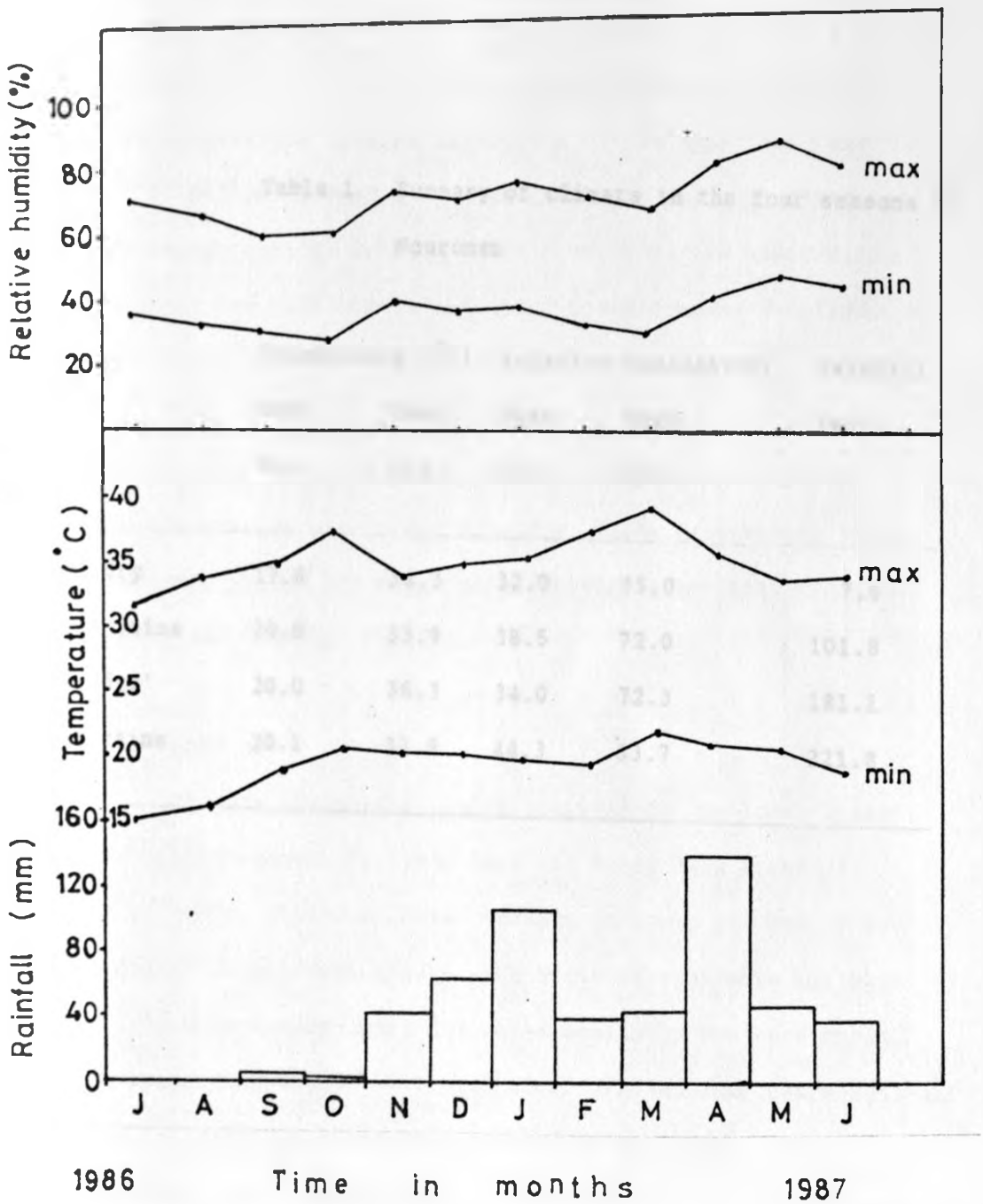

Relative humidity (%)
100
80
60
40
20
max
min
Temperature (°C)
40
35
30
25
20
15
max
min
Rainfall (mm)
160
120
80
40
0
J A S O N D J F M A M J
1986
Time in months
1987

Table 1 Summary of climate in the four seasons at Nguruman

Season	Temperature (^{0}C) Mean min.	Mean max.	Relative humidity(%) Mean min.	Mean max.	Rainfall (mm)
Cool dry	17.6	34.3	32.0	85.0	7.6
Short rains	20.0	33.9	38.5	72.0	101.8
Hot 'dry'	20.0	36.3	34.0	72.3	181.1
Long rains	20.1	33.9	44.3	83.7	221.8

The lowland woodland is mainly a belt of riverine vegetation along the seasonal streams Sampu and Oloibototo. Hence the vegetation here is rich in species diversity, and trees often go over 10 m. These include Euphorbia candelabrum, Acacia pennata and Cassine aethiopica. It is made thick and bushy by shrubs of Sautia myrtina, Scolopia spp., Aloe spp. and other thorny bushes. Outside these river beds and towards the escarpment are tall acacia and other trees forming woodland, with an abundance of grass during the rains.

The vegetation at the valley and base of the escarpment comprises tall trees, mainly Ficus capensis and the shrubs, Salvadora persica and Cordia sinensis. These intersperse with the grasses Sporobilis consimulis, Setaria spacelata, Cynodon dactylon and Themeda triandra.

2.4 Land use

The area is predominantly occupied by the local Maasai, a pastoralist community. They keep the local Zebu breed of cattle, goats, sheep and a few donkeys in group ranches. These are grazed on the open plains when grass is available but move into the more wooded areas and occasionally up the escarpment in drought conditions, like that of 1983/1984. Some years ago, a small irrigation scheme was started at the base of the escarpment which produces fruits and vegetables for sale. Livestock farming, however, remains the economic mainstay for the majority of people.

The area supports a rich variety of wild game species. The most common ones include Grants gazelle (Gazella granti),

giraffe (Giraffa camelopardalis), impala (Aepyceros melampus) buffalo (Syncerus caffer), warthog (Phacochoerus aethiopicus) and baboon (Papio anubis) (Dransfield et al., 1986). Their potential as a source of income has not been realized so far because no tourist resorts exist there.

2.5 Tsetse and trypanosomiasis at Nguruman

Both G. pallidipes and G. longipennis (a member of the fusca group) are present in the Nguruman area. Attempts to understand the factors determining and regulating G. pallidipes population size and the disease situation in Nguruman has been made. Changes in apparent density of the male and female G. pallidipes have been studied in the six different vegetation types (Dransfield et al., 1985). Apparent density was shown to be highest in the lowland woodland followed by upland woodland, acacia woodland, valley, plains and river in this order.

Relative humidity has been demonstrated as the key density independent mortality factor determining population change of adult tsetse. Low humidity is associated with high mortality. It further causes nutritional stress of the parent flies that culminates in them producing smaller offspring. Mortality at time of emergence is size dependent. From a comparison of subsequent size distributions of male and female flies of different ages, there is little evidence of size dependent mortality (Dransfield et al., 1988).

Other factors are also believed to be causing mortality. Rainfall of over 100 mm a month may increase pupal mortality. Flooding also causes a shift in larviposition sites

from low lying areas in the dry season to hilly slopes during the rains. Overall loss rate of pupae is density dependent although none of the individual causes of non-emergence viz. developmental failure, fungal attack and parasitism are density dependent. The bombylid pupal parasitoids namely Exhylanthrax beckerianus (Bezzi) and E. lugens (Loew) have emerged from field collected pupae that had been held in the laboratory until emergence. Their rates of parasitism are low and therefore less important in overall pupal mortality.

As regards developing more appropriate technologies for control, a novel trap based on the Zimbabwean F3 trap and called the NG2B has been developed at Nguruman for the control of G. pallidipes. Details on its construction are found in Brightwell et al. (1987). It is cheap, can be easily constructed in the Maasai manyattas (homesteads) and when baited with acetone (dispensed at 50 mgh^{-1} dose rates) and cow urine, is on average three times as effective for female G. pallidipes as a similarly baited biconical trap. The index of increase is however dependent upon temperature. This trap is currently used to suppress the tsetse population in an area of about 100 Km^2.

So far (a period of nine months since trap deployment), there has been a depression in daily trap catches amounting to a 99% reduction in the tsetse population. A shift in age distribution of the flies has also been observed, and these effects have also extended outside the experimental area (Dransfield, 1988).

In Nguruman, wild game are important reservoir hosts of trypanosomes. Disease transmission between wild game and domestic animals is possible because all are fed on by tsetse. Studies on the source of bloodmeals of G. pallidipes (Tarimo et al., 1986) demonstrated that the most preferred hosts were suids (primarily warthog) and buffalo.

The disease situation showed that G. pallidipes is the most important vector of livestock trypanosomiasis. Tarimo et al. (1986) estimated that the overall infection rates in the tsetse were 4.6% for G. pallidipes and 1.6% for G. longipennis. The tsetse infection rates for various trypanosomes were T. vivax 3.5%, T. congolense 0.8% and T. brucei 0.03%. Very high trypanosome infection rates were recorded in cattle, going up to 45% (Tarimo and Golder, 1985). This has caused much cattle mortality. In view of the fact that the local community derive their livelihood from livestock farming, the problem required immediate attention and thus justified this research.

CHAPTER 3

RESTING SITES OF GLOSSINA PALLIDIPES

3.1 Introduction

The diurnal resting sites of G. pallidipes have been studied in the Zambezi Valley, Zimbabwe (Pilson and Leggate, 1962) and the nocturnal resting sites in Kenya (Minter, 1971). Different resting sites for Glossina species are utilized in different vegetation zones (MacLennan, 1967). Rogers et al. (1984) considered that information on tsetse ecology obtained in one area for one purpose cannot be transferred wholesale to another area and for a different purpose.

With specific reference to resting behaviour, Turner (1980) considered that such information could have general applicability, but by taking a case analysis of the night resting behaviour of G. tachinoides he demonstrated several contradictions found in the literature by different workers, and suggested that this could apply to other species. This was ascribed to several factors, among them the different methods used to detect flies, seasonal influences or the nature of the vegetation in the area studied (whether trees have a low and high canopy or whether the site was natural or artificially isolated or enclosed). Such differences therefore justified obtaining information from the Nguruman study area for G. pallidipes.

3.2 Materials and methods

3.2.1 Microclimatic data

For the duration of the resting site studies, the vertical distribution of temperatures was recorded using a Grant's automatic meteorological recorder. In August (part of the cool dry season), hourly recordings of temperature were made at 0.20 and 2.50 m above the ground while relative humidity was recorded at 1.5 m.

Inside the large field cage used for diurnal resting sites, hourly recordings of temperature were made at 0.5 m, 1.5 m, 2.5 m, and 3.5 m from the ground while relative humidity was recorded at 1.5 m height. This was done in January and February (part of hot 'dry' season) and in May (long rainy season).

3.2.2 Tsetse trapping

G. pallidipes used in these studies were caught in the field using two Zimbabwean F3 traps (Plate 1). These are royal blue versions of the F2 trap (Flint, 1985). Catches were increased by baiting the traps with odour attractants. Cow urine and acetone were dispensed from separate containers at dose rates of 1000 mgh^{-1} and 2500 mgh^{-1} respectively (Dransfield et al., 1986). Moist cotton wool was put in the cages which were frequently changed to maintain healthy tsetse.

Plate 1. Trapping tsetse flies at Nguruman using an F3 trap baited with cow urine and acetone.

3.2.3 Nocturnal resting sites

For nocturnal resting sites, tsetse were caught in the afternoon of the same day and marked with flourescent powder. This was done by insufflating them with 'Daylight' flourescent powder so that they could be observed from all visual angles (Scholz et al., 1976). The colour of powder used was rocket red. At least 15 minutes were allowed for powder adherence to the tsetse. Cages with the tsetse were covered with wet black cloth to reduce their activity and minimise stress. At dusk, the active tsetse were released in the natural habitat by opening the cages. Healthy ones flew out while weak ones were destroyed.

When it was fully dark, one hour long searches were made to detect resting tsetse using a portable battery powered 'black light' tube that emitted long wave ultra-violet light (Scholz et al., 1976). This was done at least one and a half hours after release. Searches were made by walking systematically in the bushes to avoid recording the same tsetse more than once. Under a beam of ultra-violet light resting tsetse glowed the red colour of the powder used to dust them.

For each tsetse detected, its height above the ground and the nature of the resting site were recorded. These included leaves, small branches, larger branches, tree trunks and the ground. Twigs were defined as those thin woody parts of the vegetation with a diameter of up to 0.5 cm, small branches had a diameter of up to 3 cm, larger branches up to 10 cm and tree trunks were over 10 cm in diameter. Searching at high

altitudes of the vegetation was facilitated by climbing up a 5 m high ladder. A spotlight of white light was used very briefly to ascertain that it was a marked tsetse that glowed and not marks left behind by tsetse that had rested there temporarily.

These studies were conducted throughout the year. Data collected were analysed in relation to prevailing weather conditions, specifically temperatures and relative humidity.

3.2.4 Diurnal resting sites

Diurnal resting sites were investigated using a large field cage erected over a natural larviposition site (Plate 2). The dimensions of the cage were 4 x 4 x 4 m. The sides and roof had green mosquito netting to prevent tsetse from escaping. Sacking was used to cover part of the sides of the cage formerly shaded by vegetation.

Since no feeding took place inside the cage, tsetse were fed on rabbit ears in some experiments before release. This improved survival rate, and thereby reduced the need for frequent releases. For each experiment, between one and two hundred tsetse were introduced into the cage using a tunnel made at ground level below its base frame.

Searches were made at least two hours after tsetse were released into the cage. This was done from outside the cage so that resting tsetse were not disturbed. The observer moved round the four vertical faces of the cage; the time spent on one face depended on the amount of resting surfaces observable from it. It was possible to see the tsetse through the netting

Plate 2. A large field cage erected on a natural larviposition site used to study the diurnal resting sites of Glossina pallidipes at Nguruman. (D- entrance to cage, S- struts supporting roof flame of cage, L- ladder to facilitate observations at higher altitudes)


S
L
D

despite their cryptic colouration, but this was made easier with the release of tsetse marked with flourescent powder. This was done in later experiments. Use of a 5 m long ladder made searching at higher altitudes feasible. Tsetse found at or near the netting of the cage were not considered since this was not a natural resting site.

These studies were conducted during the hot 'dry' and the long rainy seasons. Data for the same variables as for nocturnal resting sites was collected during one hour long searches at various times of the day viz: very early in the morning at 05.45-06.30, late morning at 10.30-11.30, early afternoon at 13.30-14.30, and late afternoon at 16.30-17.30 hours. These studies were also extended into the night to give comparable data with the night time resting studies.

3.3 Results

3.3.1 Monthly microclimatic data.

The mean temperatures recorded at one hour intervals and at various heights are shown in Figs. 4, 5 and 6 for the months August, January, and February respectively. In May, the automatic recorder gave results for only 24 hours i.e. from 12.30 hours of the first day (02/05/87) to 11.30 hours of the next day (03/05/87) and then broke down. The results shown in Fig. 7 are therefore actual values and not means recorded over several days.

During August, January and February, temperatures were much higher (over 30^{o}) from 12.00 to 18.00 hours, while they never rose beyond this figure in May. Peak temperatures occurred at 16.00 to 17.00 hours while minimum temperatures were recorded at 06.00 to 07.00 hours. They did not however, vary much between 23.00 and 07.00 hours in May. Temperature gradients between the various heights considered were more pronounced in the daytime than at night, with temperatures up to three degrees lower close to the ground in the first three months and five degrees in May. Relative humidity was inversely correlated with temperatures.

Fig. 4 Vertical distribution of the mean air temperatures at the heights 0.2 m (•——•) 2.5 m (- - - -) and relative humidity (•——•) 1.5 m above the ground in August.

Fig 4

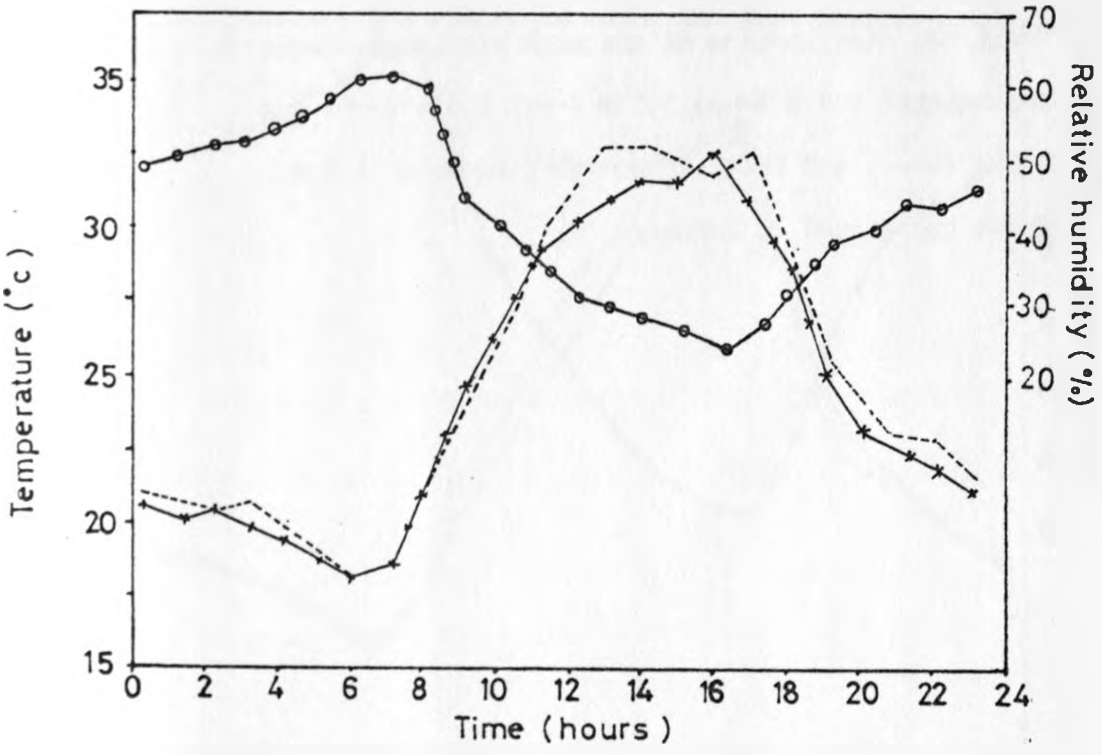

Temperature (°c)
Relative humidity (%)
Time (hours)
35
30
25
20
15
70
60
50
40
30
20
0
2
4
6
8
10
12
14
16
18
20
22
24

Fig. 5 Vertical distribution of the mean air temperatures at the heights 0.5 m (•—×) 1.5 m (·····) 2.5 m (- - -) and 3.5 m (-·-·-), and relative humidity (•—•) at 1.5 m above the ground in January.

Fig 5

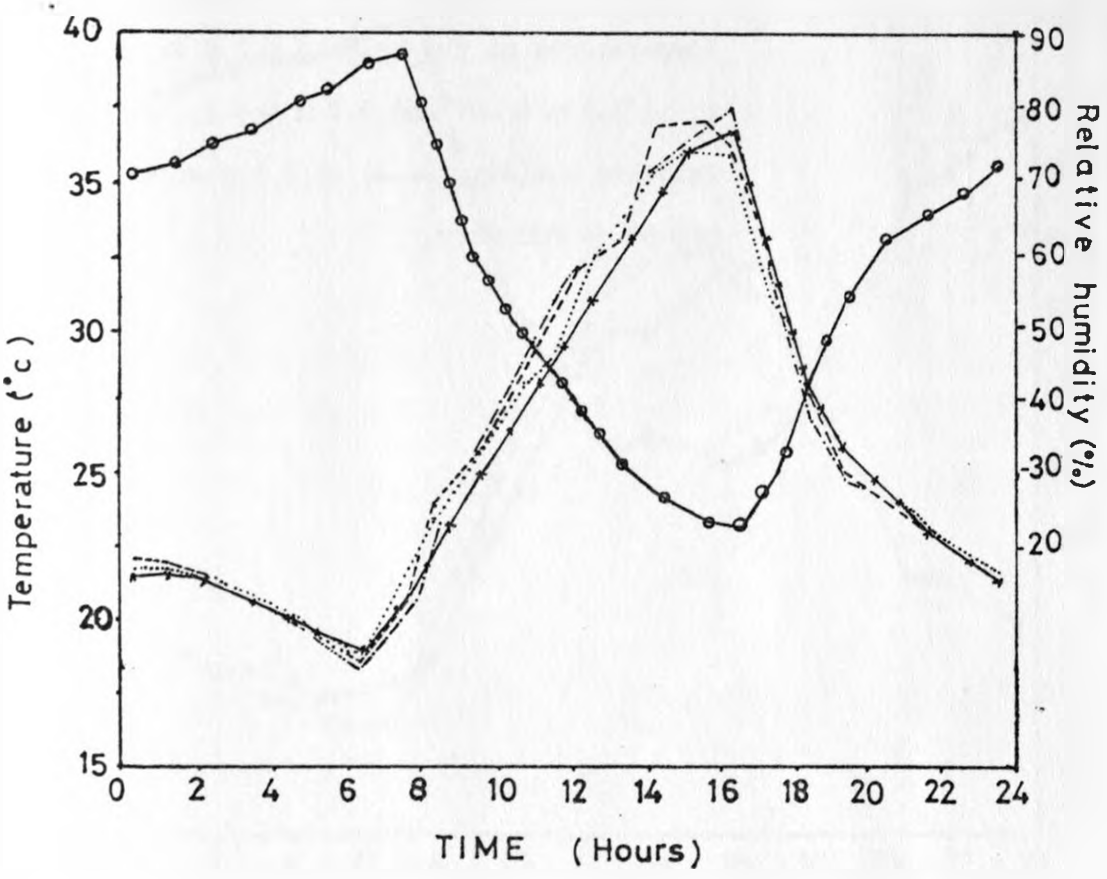

40
35
30
25
20
15
Temperature (°c)
90
80
70
60
50
40
30
20
Relative humidity (%)
0
2
4
6
8
10
12
14
16
18
20
22
24
TIME (Hours)

Fig. 6 Vertical distribution of the mean air temperatures at the heights 0.5 m (×—×) 1.5 (·····) 2.5 m (- - -) and 3.5 m (-·-·), and relative humidity (o—o) at 1.5 m above the ground in February.

Fig 6

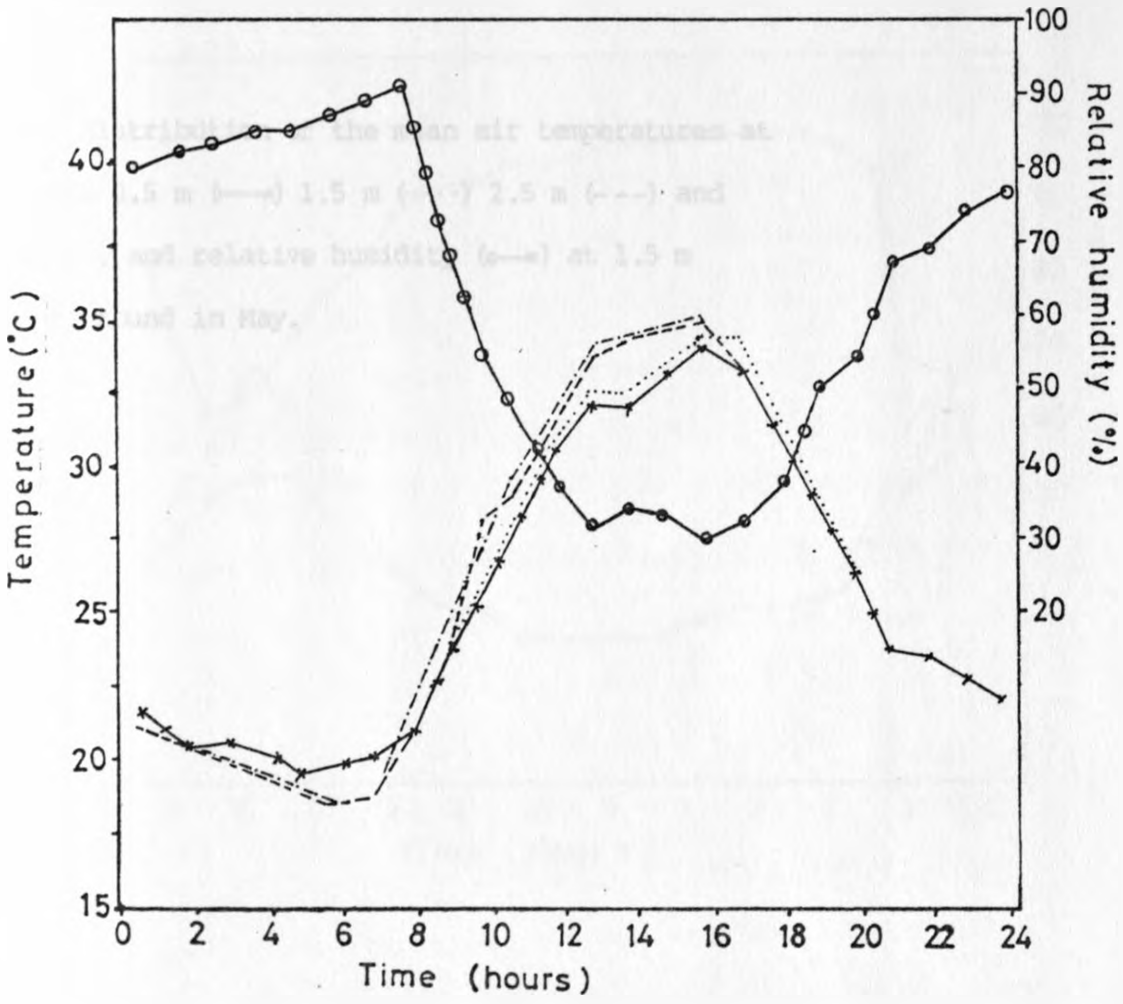
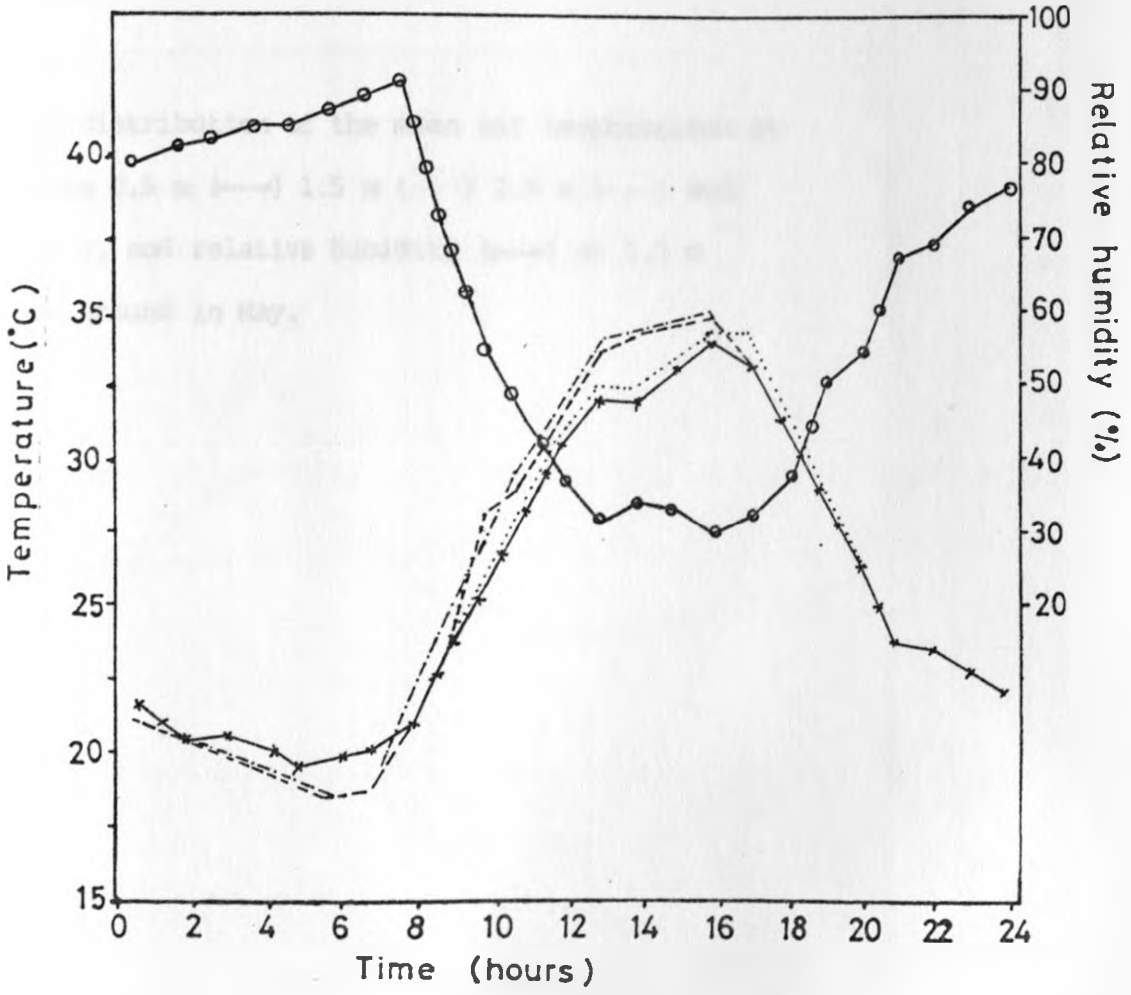

Temperature (°C)
Relative humidity (%)
Time (hours)
15
20
25
30
35
40
20
30
40
50
60
70
80
90
100
0
2
4
6
8
10
12
14
16
18
20
22
24

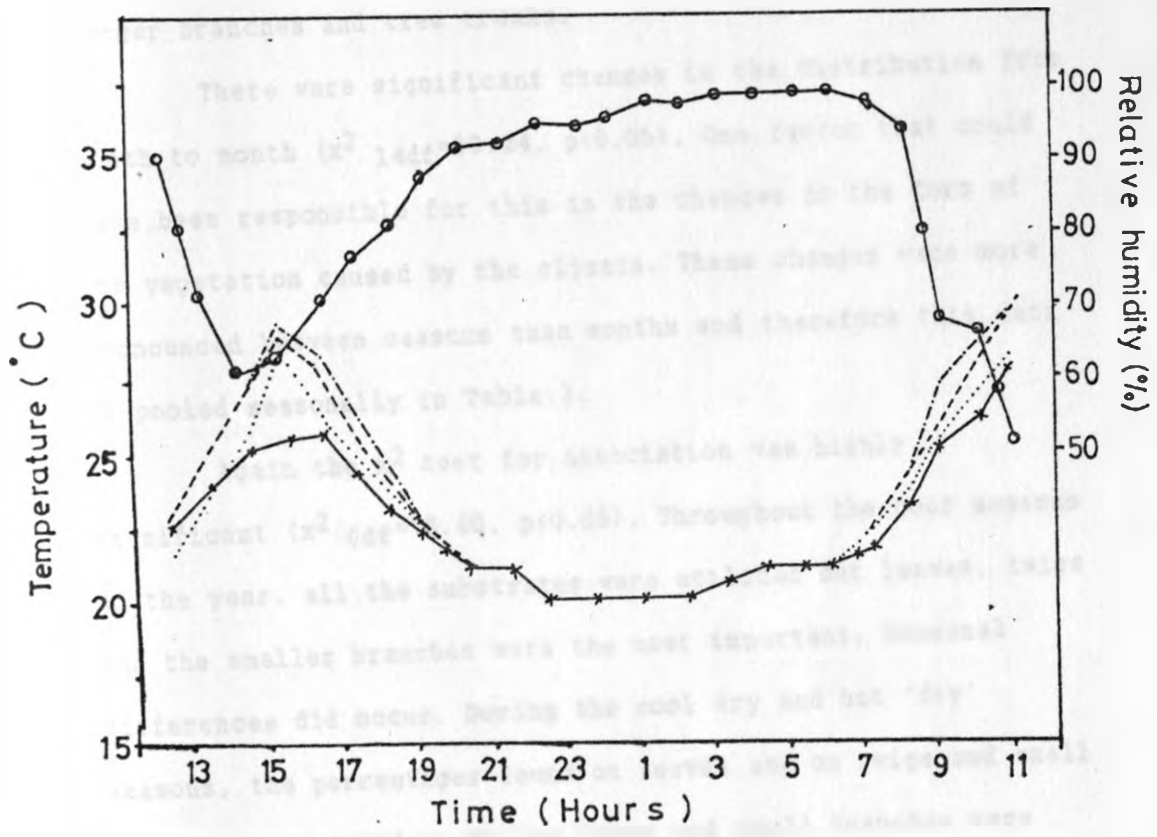
Fig. 6 Vertical distribution of the mean air temperatures at the heights 0.5 m (×—×) 1.5 m (·····) 2.5 m (- - -) and 3.5 m (—·—·), and relative humidity (●—●) at 1.5 m above the ground in February.

Fig 6


Temperature (°C)
Relative humidity (%)
Time (hours)
40
35
30
25
20
15
100
90
80
70
60
50
40
30
20
0
2
4
6
8
10
12
14
16
18
20
22
24

Vertical distribution of the mean air temperatures at the heights 0.5 m (×—×) 1.5 m (····) 2.5 m (- - -) and 3.5 m (—·—·), and relative humidity (●—●) at 1.5 m above the ground in May.

Fig 7


Temperature (°C)
35
30
25
20
15
13
15
17
19
21
23
1
3
5
7
9
11
Time (Hours)
100
90
80
70
60
50
Relative humidity (%)

3.3.2 Nocturnal resting substrates

The monthly distribution of the substrates for nocturnally resting tsetse is shown in Table 2. Due to the comparatively low frequencies involved in some classes, it was necessary to combine together twigs and small branches, and larger branches and tree trunks.

There were significant changes in the distribution from month to month ($x^2_{14df}=80.24$, $p<0.05$). One factor that could have been responsible for this is the changes in the form of the vegetation caused by the climate. These changes were more pronounced between seasons than months and therefore this data is pooled seasonally in Table 3.

Again the x^2 test for association was highly significant ($x^2_{6df}=78.40$, $p<0.05$). Throughout the four seasons of the year, all the substrates were utilized but leaves, twigs and the smaller branches were the most important. Seasonal differences did occur. During the cool dry and hot 'dry' seasons, the percentages found on leaves and on twigs and small branches were similar, whilst twigs and small branches were preferred in the short rains. In the long rains, the position was reversed with over 75% of flies found on the leaves. Large branches and tree trunks were only important during the cool dry season.

Table 2 Monthly distribution (%) of resting tsetse at night on different substrates

Month	Resting substrate: Leaves	Twigs and small branches	Larger branches and tree trunks	Total N
August	57.7	34.6	7.7	26
September	29.4	37.3	3.3	51
October	18.5	55.6	25.9	27
November	33.3	52.2	14.4	90
December	10.5	78.9	10.5	38
January	51.0	38.8	10.2	49
February	30.8	69.2	0	26
May	75.9	21.7	2.4	83

Table 3: Seasonal distribution (%) of resting tsetse at night on different substrates

Season	Resting substrate			Total N
	Leaves	Twigs and small branches	Larger branches and tree trunks	
Cool dry	33.7	41.3	25.0	104
Short rains	26.6	60.1	13.3	128
Hot 'dry'	44.0	49.3	6.6	75
Long rains	75.9	21.7	2.4	83
Overall	42.3	44.9	12.8	390

For the tsetse found resting on the leaves, their distribution among the lower and upper surfaces is shown in Table 4. Two thirds were found on the upper surface, one third on the lower surface and this proportion was maintained in the cool dry, short rainy and hot dry seasons. During the long rains, over three quarters were found on the upper surface accounting for over 60% of the total number found on all sites during that season. Analysis of these frequencies showed that they were not changing seasonally ($x^2\ 3_{df}=3.98\ p>0.05$)

3.3.3 Nocturnal resting heights

Individual records of resting heights ranged from 0.10 m above the ground to slightly over 4 m while monthly mean resting heights ranged from 1.29 (October) to 2.47 m (January). Frequency distributions of resting heights in the different months are shown in Fig. 8. Apart from the month of October, over 85% of flies were found between the ground and 3 m height. An analysis of variance (General Linear Models Procedure) was carried out with respect to month, season, substrate and their interactions; and with height as the dependent variable. Significant differences between mean heights were identified using the Student-Newman-Keuls test. Table 5 shows the results of this analysis by months and substrates. Month and substrate both had a significant effect on resting height, but there was an interaction between the two. The mean monthly and substrate resting heights recorded are summarised in Table 6.

Table 4 Seasonal distribution of tsetse resting on upper and lower surfaces of leaves at night.

Season	Leaf surface Upper (%)	Lower (%)	Total N
Cool dry	65.7	34.3	35
Short rains	67.6	32.4	34
Hot 'dry'	66.7	33.3	33
Long rains	81.0	19.0	63
Overall	72.1	27.9	165

Fig. 8 Monthly frequency distribution of resting heights of G. pallidipes at night.

Fig 8

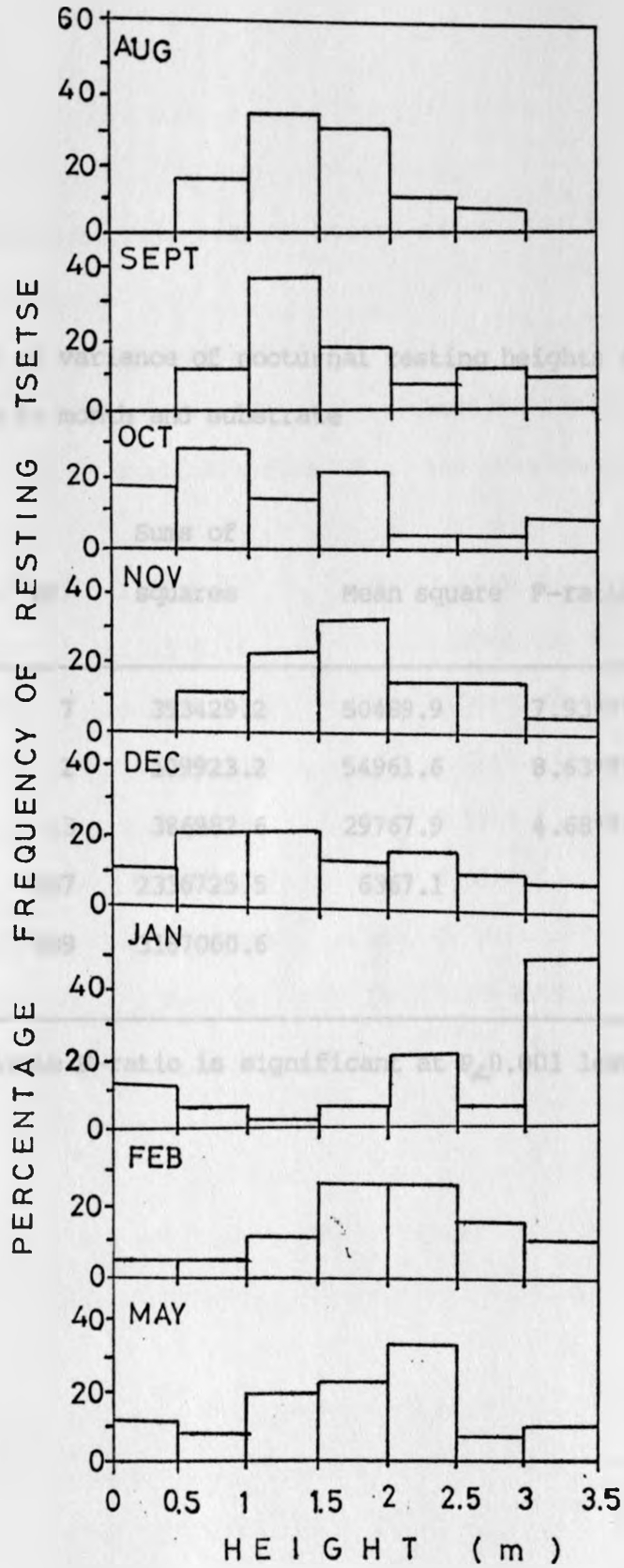

AUG
SEPT
OCT
NOV
DEC
JAN
FEB
MAY
60
40
20
0
PERCENTAGE FREQUENCY OF RESTING TSETSE
0 0.5 1 1.5 2 2.5 3 3.5
HEIGHT (m)

Table 5 Analysis of variance of nocturnal resting heights in relation to month and substrate

Source of variation	DF	Sums of squares	Mean square	F-ratio
Month	7	353429.2	50489.9	7.93***
Substrate	2	109923.2	54961.6	8.63***
Month x Substrate	13	386982.6	29767.9	4.68***
Error	367	2336725.5	6367.1	
Total	389	3187060.6		

*** indicate F-ratio is significant at $P < 0.001$ level

Table 6. Monthly and substrate resting height means (X-S.E) m

Month	Resting substrate: Leaves	N	Twigs and small branches	N	Larger branches and tree trunks	N
August	1.58+0.17	15	1.35+0.17	9	2.15+1.20	2
September	1.52+0.18	15	1.41+0.16	19	1.97+0.19	17
October	2.31+0.56	5	1.15+0.18	15	0.86+0.29	7
November	1.85+0.11	30	1.67+0.11	47	2.01+0.24	13
December	1.33+0.11	4	1.71+0.18	30	0.93+0.11	4
January	2.96+0.18	25	2.36+0.26	19	0.39+0.13	5
February	2.44+0.16	8	1.83+0.19	18	0	0
May	1.86+0.09	63	1.35+0.24	18	1.00+0.60	2

There was no obvious relationship between resting height and resting substrates. For example, in August, September and November, there was a decreasing height with increasing diameter only for the first two substrates but increased on the thickest substrate. This pattern was reversed in the month of December. In October and from January to May, an increase in diameter of resting substrate was associated with a decrease in resting height. This lack of uniformity caused the interaction between the month and resting substrate.

Monthly mean resting heights are given in Table 7. The heights at the two extremes were significantly different from each other. Mean prevailing temperatures and the relative humidities are also shown. These observations were made when temperatures were rapidly and steadily dropping with an associated subsequent rise in humidity. Regression analysis was done on resting heights and the temperatures and relative humidities prevailing at the time of making the observations. A scatter diagram for the relationship between resting height and temperature is shown in Fig. 9 and that for the relationship between resting height and relative humidity is shown in Fig. 10. No influence of these two factors on nocturnal resting height was inferred.

To further investigate the effects of season on resting height, the data for the appropriate months were pooled and reanalysed. Frequency distribution of resting heights in the different seasons is shown in Fig. 11. During the cool dry season over two thirds (i.e. 77%) rested lower than 2 m, the distribution being skewed to the left. During the short rains

Table 7. Monthly mean variation (X+S.E) of nocturnally resting heights and the prevailing mean temperatures and relative humidities.

Month	Mean height (m)	Temp.(°C)	RH (%)
August	1.54+0.12 bc	21.3	54.3
September	1.63+0.11 bc	24.8	41.0
October	1.29+0.18 c	26.5	48.0
November	1.78+0.08 bc	26.5	40.0
December	1.59+0.15 bc	25.5	68.0
January	2.47+0.15 a	25.2	57.0
February	2.01+0.15 b	25.0	55.0
May	1.73+0.09 bc	25.8	79.0

(mean heights followed by the same letter are not significantly different)

Fig. 9. Relationship between nocturnal resting heights and the prevailing temperatures. No obvious relationship was evident

Fig 9

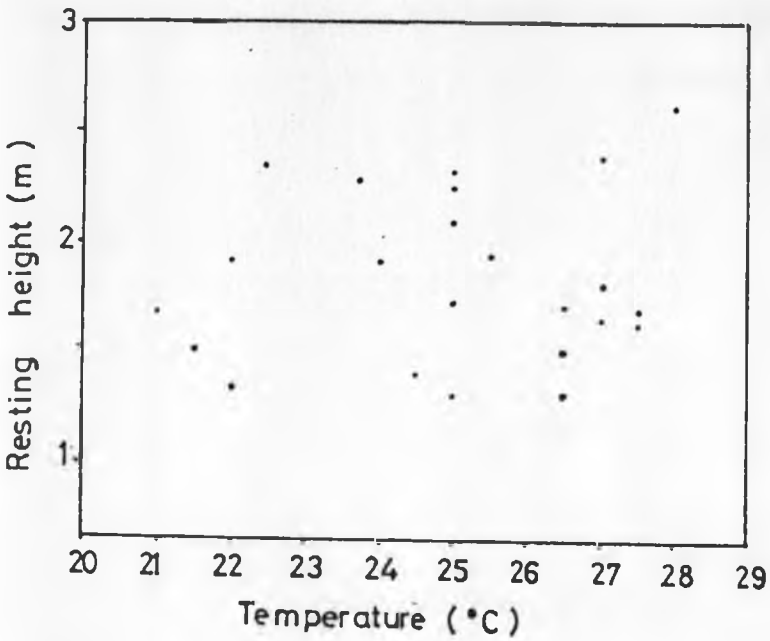


Fig. 10. Relationship between nocturnal resting heights and the prevailing relative humidity. Again no obvious relationship was inferred

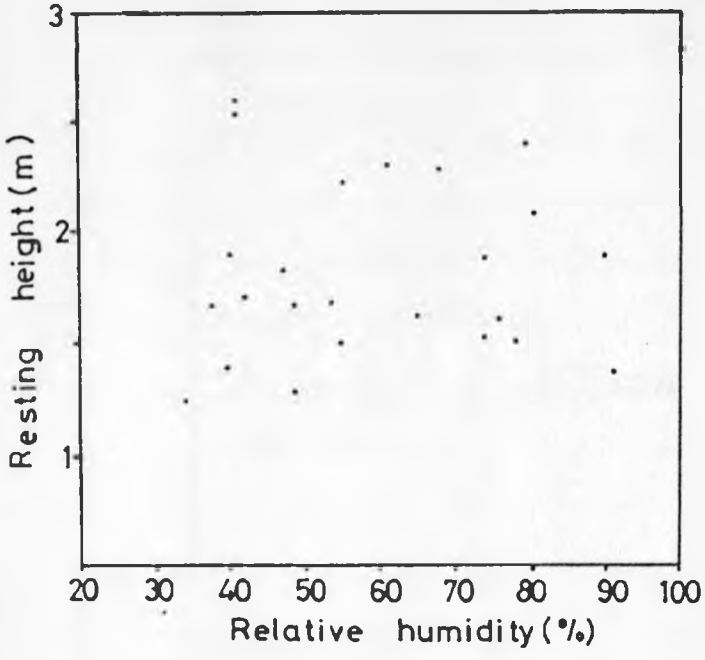
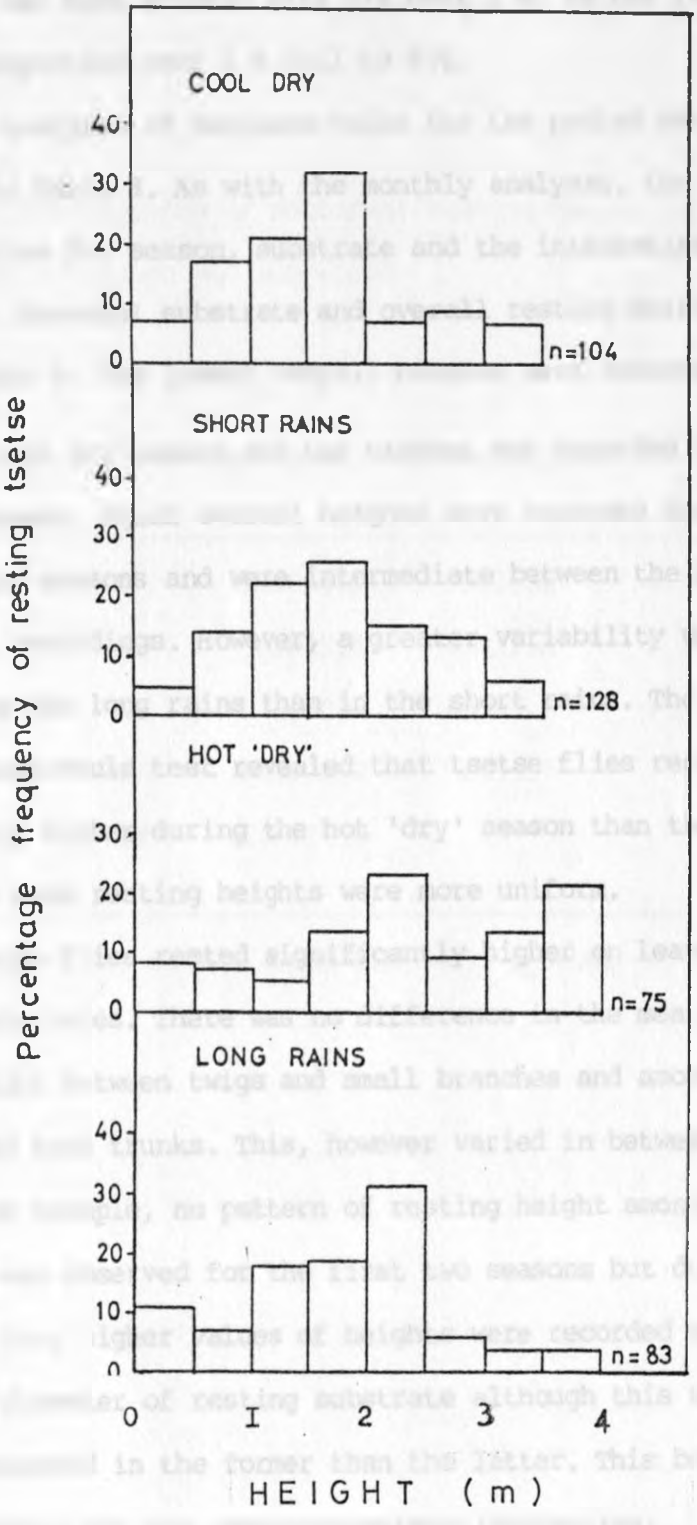

3
2
1
Resting height (m)
20
30
40
50
60
70
80
90
100
Relative humidity (%)

Fig. 11 Seasonal distribution of resting heights of tsetse flies at night.

Fig 11


COOL DRY
40
30
20
10
0
n=104
SHORT RAINS
40
30
20
10
0
n=128
HOT 'DRY'
30
20
10
0
n=75
LONG RAINS
40
30
20
10
0
n=83
0
I
2
3
4
HEIGHT (m)
Percentage frequency of resting tsetse

the distribution was approximately normal while two thirds (i.e. 66%) were below 2 m. During the hot 'dry' season the variability was much greater with 67% over 2 m. In the long rains the proportion over 2 m fell to 45%.

The analysis of variance table for the pooled data is reproduced in Table 8. As with the monthly analysis, the variance ratios for season, substrate and the interaction were significant. Seasonal substrate and overall resting heights are shown in Table 9. The lowest overall heights were recorded during the cool dry season and the highest was recorded in the hot 'dry' season. Equal overall heights were recorded during the two rainy seasons and were intermediate between the lowest and highest recordings. However, a greater variability was shown during the long rains than in the short rains. The Student-Newman-Keuls test revealed that tsetse flies rested significantly higher during the hot 'dry' season than the other three whose mean resting heights were more uniform.

Tsetse flies rested significantly higher on leaves than on other substrates. There was no difference in the mean resting height between twigs and small branches and among large branches and tree trunks. This, however varied in between seasons. For example, no pattern of resting height among substrates was observed for the first two seasons but during the latter two, higher values of heights were recorded with increasing diameter of resting substrate although this was better pronounced in the former than the latter. This behaviour was responsible for the season-substrate interaction.

Table 8 Analysis of variance of nocturnal resting height in relation to season and substrate

Source of variation	DF	Sums of squares	Mean Square	F-ratio
Season	3	287614.2	95871.4	4.36***
Substrate	2	130855.6	65427.8	9.80***
Season x Substrate	6	245190.5	40865.1	9.12***
Error	378	2523400.3	6675.7	
Total	389	3187060.6		

Stars indicate level of significance i.e *** $p < 0.001$

Table 9: Seasonal mean nocturnal resting heights (X + S.E)m

Season	Resting substrate			
	Leaves	Twigs and Small branches	Larger branches and tree trunks	Overall
Cool dry	1.66+0.14	1.31+0.10	1.69+0.18	1.52+0.08
Short rains	1.79+0.10	1.69+0.10	1.76+0.21	1.73+0.07
Hot 'dry'	2.34+0.15	2.10+0.17	0.39+0.13	2.31+0.13
Long rains	1.86+0.09	1.35+0.24	1.00+0.60	1.73+0.19
Overall	2.00+0.07	1.65+0.07	1.56+0.13	1.73+0.05

3.3.4 Diurnal resting substrates

Daytime resting behaviours showed important contrasts between the various times of the day as would be expected given that tsetse are active during this period. The distribution of resting tsetse on different substrates during the hot 'dry' season is shown in Fig. 12.

In the early morning, over 80% were found on leaves, twigs and small branches but by the late morning this had shifted to over 85% being found on woody parts of the vegetation viz. small branches, larger branches and tree trunks. By the early afternoon about 80% were found on the tree trunks and on the ground with 47% on the ground. By the late afternoon 74% were found on these two sites but with 59% of the tsetse on the ground. In the evening over 90% of the flies returned to the leaves, twigs and small branches which are as their nocturnal resting sites. This change through the day in the preference of resting substrate was further shown by a significant association between time and substrate ($x^2_{20df}=187.193$, $p<0.05$). This shows that the choice of resting substrates with time was specifically directed rather than being random. Within the daylight hours, there was a progressive shift to thicker resting substrates.

The distribution of tsetse on different substrates in the long rainy season is shown in Fig. 13. Very strong association was found between time and substrate ($x^2_{16df}=274.792$, $p<0.05$). In the early morning over 60% were found on leaves, and 30% on twigs. Then from late morning to late in the afternoon, over 95% were found on small branches, large

Fig. 12 The distribution of resting tsetse flies at different times of the day among the various substrates (L- Leaves, Tw- Twigs, SB- Small branches, LB- Large branches, Tr- Tree trunks, G- Ground) during the hot 'dry' season.

Fig 12

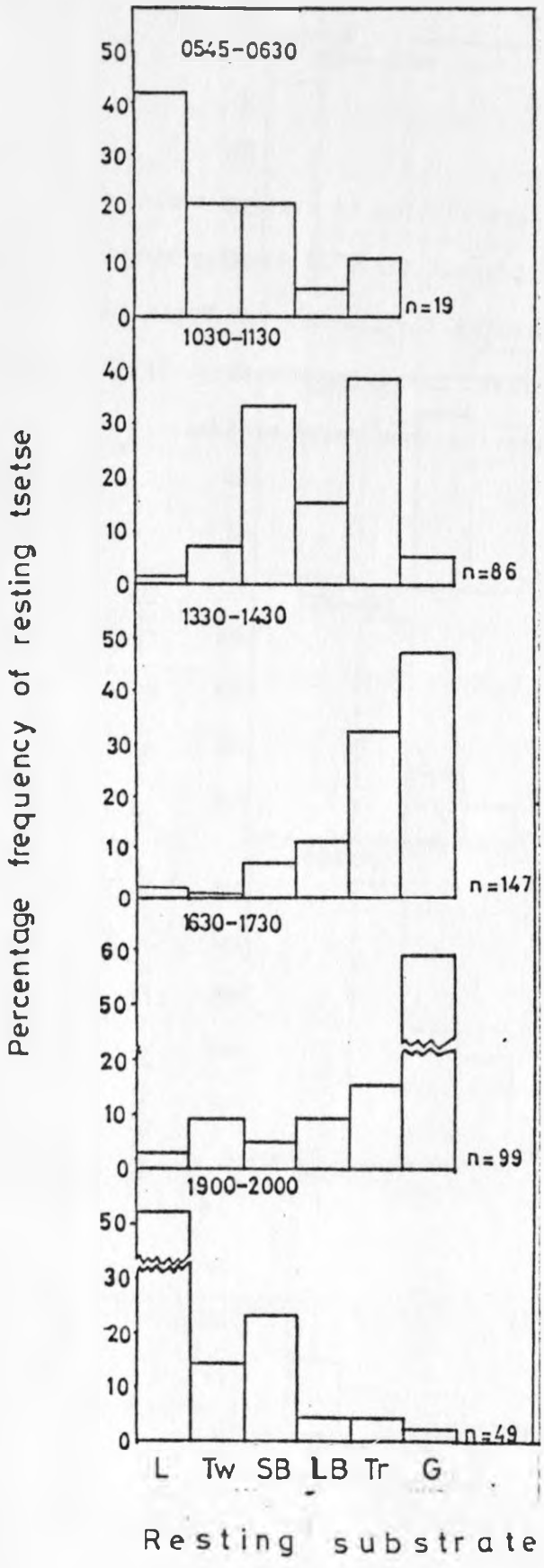
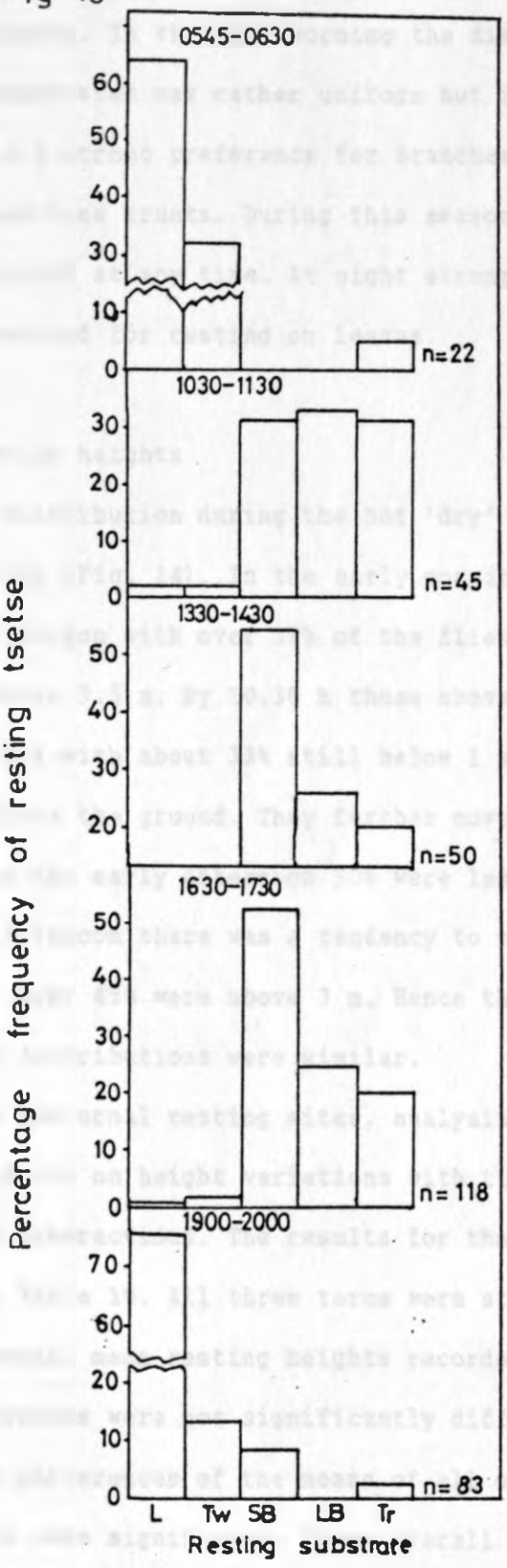

0545-0630
n=19
1030-1130
n=86
1330-1430
n=147
1630-1730
n=99
1900-2000
n=49
Percentage frequency of resting tsetse
L Tw SB LB Tr G
Resting substrate

Fig. 13 The distribution of resting tsetse flies at different times of the day among the various substrates (L- Leaves, Tw- Twigs, SB- Small branches, LB- Large branches, Tr- Tree trunks.) during the long rainy season.

Fig 13


0545-0630
1030-1130
1330-1430
1630-1730
1900-2000
n=22
n=45
n=50
n=118
n=83
Percentage frequency of resting tsetse
L
Tw
SB
LB
Tr
Resting substrate

branches and tree trunks. In the late morning the distribution among these three substrates was rather uniform but in the afternoon, there was a strong preference for branches, followed by large branches and tree trunks. During this season no tsetse were found on the ground at any time. At night strong preferences were observed for resting on leaves.

3.3.5 Diurnal resting heights

The height distribution during the hot 'dry' season varied through the day (Fig. 14). In the early morning, there was a bimodal distribution with over 35% of the flies resting below 1 m and 40% above 3.5 m. By 10.30 h those above 3 m had moved to lower heights with about 33% still below 1 m and 53% between 1 and 2 m above the ground. They further moved lower with time and during the early afternoon 90% were less than 1 m high. By the late afternoon there was a tendency to move higher and by the evening, over 45% were above 3 m. Hence the early morning and evening distributions were similar.

As with the nocturnal resting sites, analysis of variance was carried out on height variations with time, substrate and their interactions. The results for the hot 'dry' season are shown in Table 10. All three terms were strongly significant. The overall mean resting heights recorded in the early and late afternoons were not significantly different from each other, but the differences of the means of all other combinations of time were significant. These overall mean resting heights, together with those at the resting substrates are shown in Table 11.

Fig. 14 The height distribution of resting tsetse flies at different times of the day during the hot 'dry' season.

Fig 14

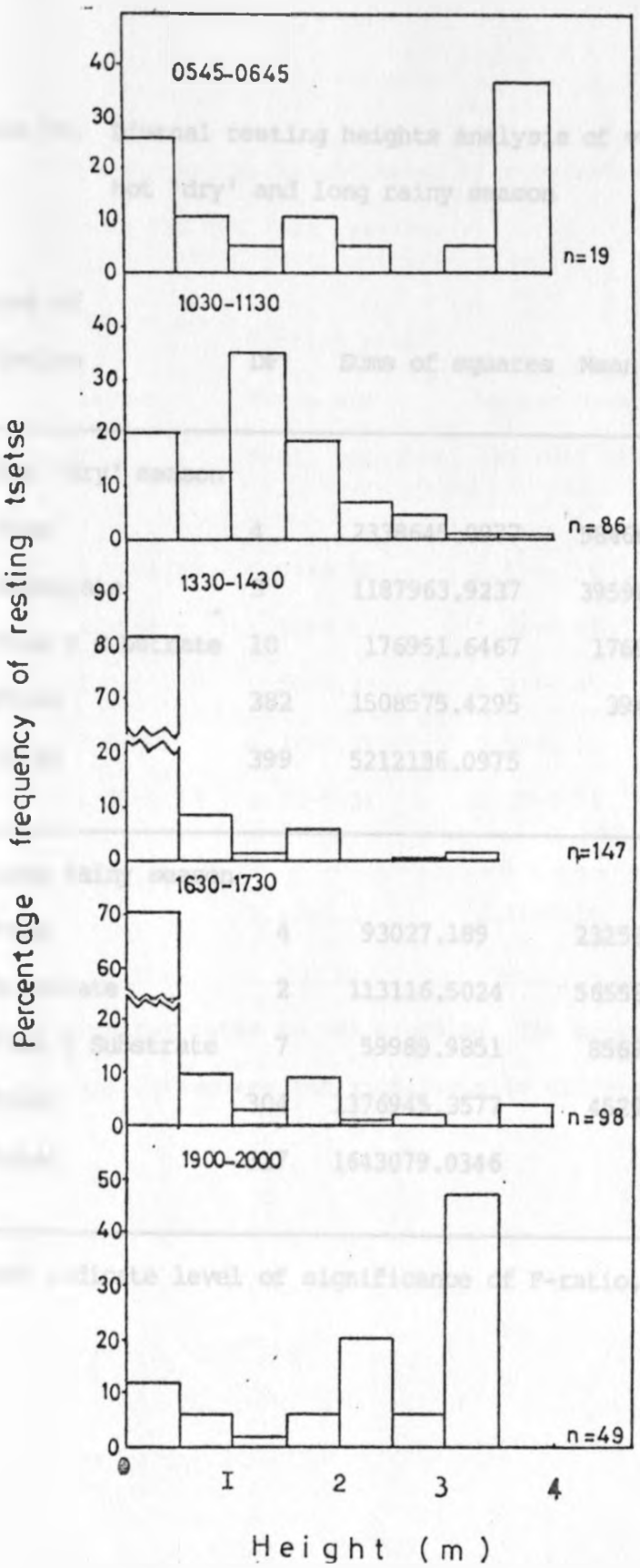

0545-0645
n=19
1030-1130
n=86
1330-1430
n=147
1630-1730
n=98
1900-2000
n=49
Percentage frequency of resting tsetse
Height (m)
I
2
3
4

Table 10. Diurnal resting heights analysis of variance during the hot 'dry' and long rainy season

Source of variation	DF	Sums of squares	Mean square	F-ratio
A. Hot 'dry' season				
Time	4	2338645.0977	584661.2744	148.05***
Substrate	3	1187963.9237	395987.9746	100.27***
Time x Substrate	10	176951.6467	17695.1647	4.48***
Error	382	1508575.4295	3949.1503	
Total	399	5212136.0975		
B. Long rainy season				
Time	4	93027.189	23256.7974	5.13***
Substrate	2	113116.5024	56558.2512	12.12***
Time x Substrate	7	59989.9851	8569.9979	1.89
Error	304	1376945.3577	4529.4255	
Total	317	1643079.0346		

(Stars indicate level of significance of F-ratio, i.e *** $p < 0.001$)

Table 11: Diurnal resting height means by substrates (X+ S.E) m during the hot 'dry' season.

Time (h)	Resting site: Leaves	Twigs and Small branches	Larger branches and tree trunks	Overall means
0545-0630	2.71+0.51	1.64+0.50	1.57+1.15	2.03+0.34(b)
1030-1130	3.94+0	1.50+0.12	1.06+0.09	1.21+0.08(c)
1330-1430	2.14+1.06	1.20+0.23	0.31+0.05	0.28+0.05(d)
1630-1730	3.50+0	1.78+0.21	0.59+0.11	0.50+0.09(d)
1900-2000	2.97+0.18	2.36+0.26	0.39+0.13	2.47+0.15(a)
Overall		2.92+0.17	1.70+0.10	0.64+0.06

(letters in bracket refer to SNK grouping. The overall means followed by the the same letter are not significantly different.)

There was a steady decrease in resting height from very early in the morning to the early afternoon, then a gradual rise towards the late afternoon, followed by a very sharp rise in the evening to get to the nocturnal resting heights. A decrease in resting height associated with an increase in diameter of the resting substrates was observed throughout the day. The overall resting heights at these substrates were also shown to be significantly different from one another.

During the long rains, the resting heights were more stable through the day (Fig. 15). The majority of the flies were found between 1.0 and 2.5 m above the ground. Over 95% were less than 3 m high, but this fell to 86% during the evening, hence showing that some tsetse flies went to rest higher at night than they had done at daytime. The analysis of variance is also shown in Table 11.

The resting heights at various substrates and overall mean resting height during the long rains are shown in Table 12. They ranged from 1.74 m (early morning) to 1.34 m (late afternoon). The value found in the evening of 1.73 m compares very well with the one for the early morning, and were generally significantly higher than those of the rest of the day. Overall resting heights from the late morning to the late afternoon were also similar.

The differences between mean resting heights at the various substrates during this season were however not as great as those found in the hot 'dry' season. Except for the mean resting heights for the flies on twigs and small branches very early in the morning and the lone fly found low on leaves in

Fig. 15 The height distribution of resting tsetse flies at different times of the day during the long rainy season.

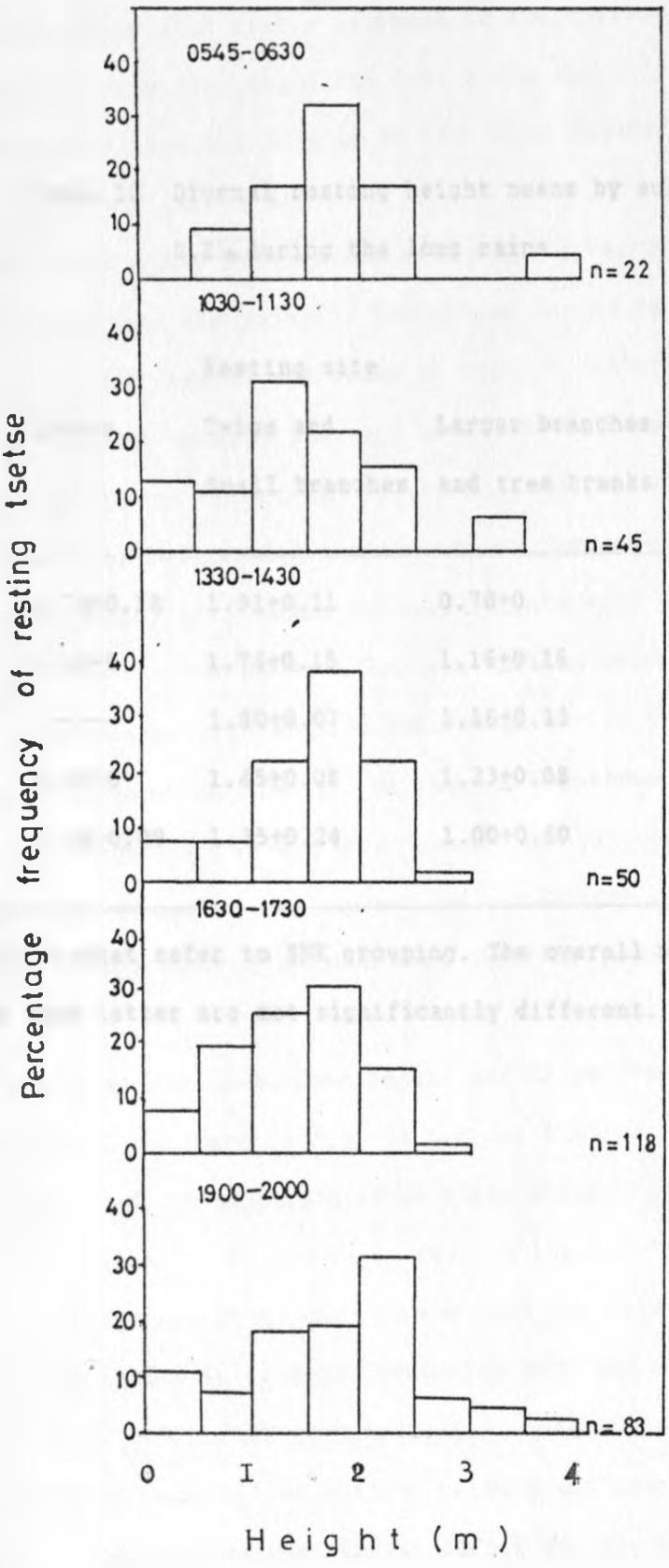

0545-0630
n=22
1030-1130
n=45
1330-1430
n=50
1630-1730
n=118
1900-2000
n=83
40
30
20
10
0
0
1
2
3
4
Percentage frequency of resting tsetse
Height (m)

Table 12 Diurnal resting height means by substrates ($\bar{X}$+ S.E$_m$ during the long rains.

Time (h)	Resting site: Leaves	Twigs and Small branches	Larger branches and tree trunks	Overall means
0545-0630	1.72+0.18	1.91+0.11	0.78+0	1.74+0.13(a)
1030-1130	2.18+0	1.74+0.15	1.16+0.16	1.38+0.12(ab)
1330-1430	------	1.80+0.07	1.16+0.13	1.51+0.08(ab)
1630-1730	0.40+0	1.45+0.08	1.23+0.08	1.34+0.06(b)
1900-2000	1.86+0.09	1.35+0.24	1.00+0.60	1.73+0.12(b)

(letters in bracket refer to SNK grouping. The overall means followed by the the same letter are not significantly different.)

the late afternoon, there was also a progressive increase in resting height associated with a decrease in the thickness of the resting substrate throughout the day. Hence the difference between the overall resting heights at the three substrates were shown as significantly different.

The relationship between the mean resting heights and the mean temperatures and relative humidities in the daytime during the hot 'dry' season are shown in Fig. 16. Afternoons of the hot 'dry' season usually had very high temperatures (up to 37°C) and very dry air (about 20% RH), conditions at which tsetse rested very low. During periods of low temperatures and high relative humidities, higher resting heights were recorded.

The relationship between the mean resting heights and the mean temperatures and relative humidities during the long rainy season is shown in Fig. 17. Maximum temperatures were much lower than during the hot 'dry' season and relative humidities were higher. Under the weather conditions of the long rains, stable resting heights were observed throughout the day.

The relationship between height and temperatures in the hot 'dry' season is shown in Fig. 18 and for the long rains in Fig. 19. The range of temperatures at which observations were made was much narrower in the rains than in the hot 'dry' season. In both dispersions also showed that the heights were randomly distributed at temperatures below 25°C and their variances were much higher than those for temperatures above 25°C. Regression analysis of resting heights and temperatures above 25°C (and relative humidities) during the two seasons were carried out.

Fig. 16 The relationship between the mean resting heights and the mean temperatures and relative humidities at corresponding times during the hot 'dry' season.

Fig 16

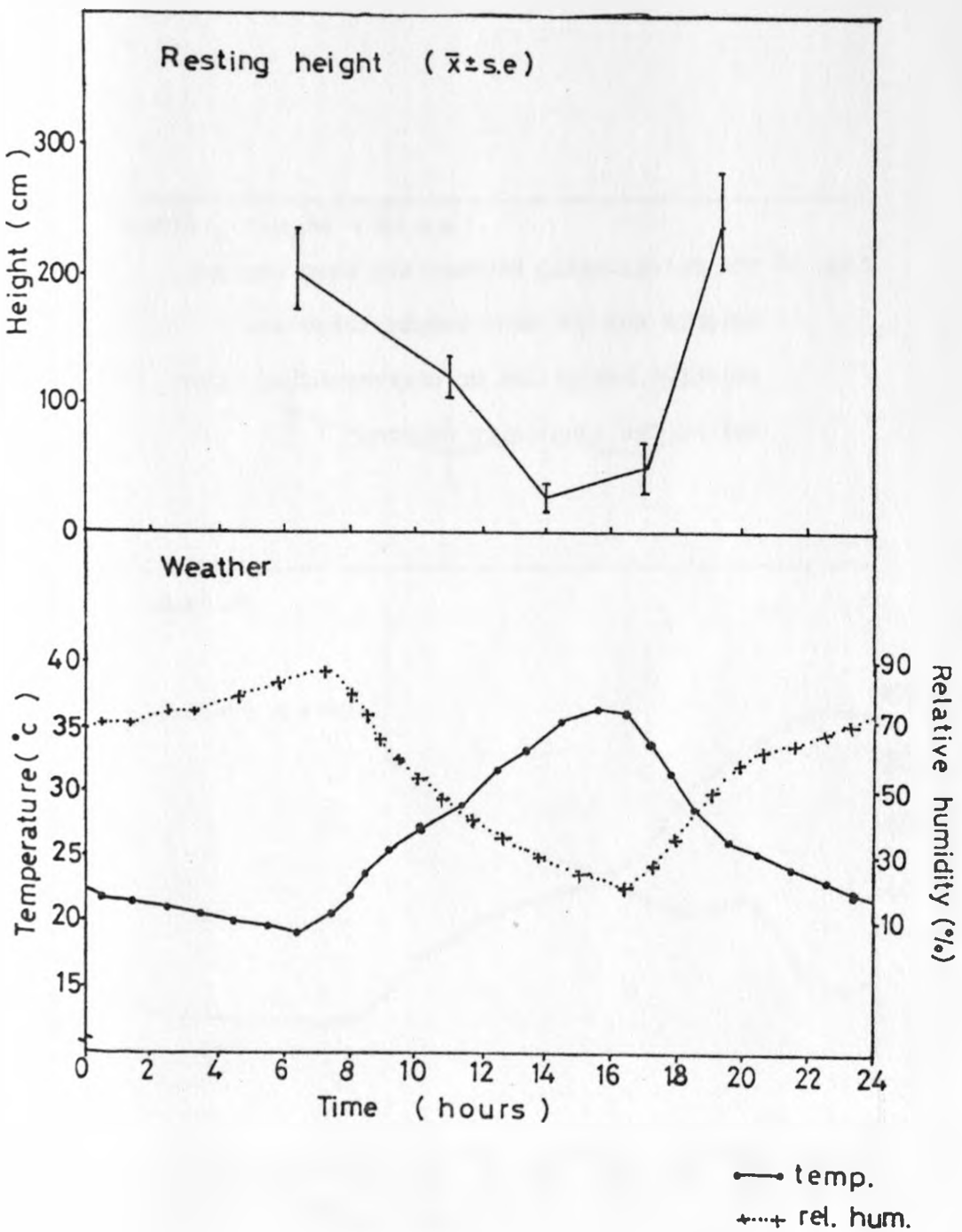

Resting height (x̄±s.e)
Height (cm)
300
200
100
0
Weather
Temperature (°c)
40
35
30
25
20
15
Relative humidity (%)
90
70
50
30
10
0
2
4
6
8
10
12
14
16
18
20
22
24
Time (hours)
temp.
rel. hum.

Fig. 17 The relationship between the mean resting heights and the mean temperatures and relative humidities at corresponding times during the long rainy season.

Fig 17

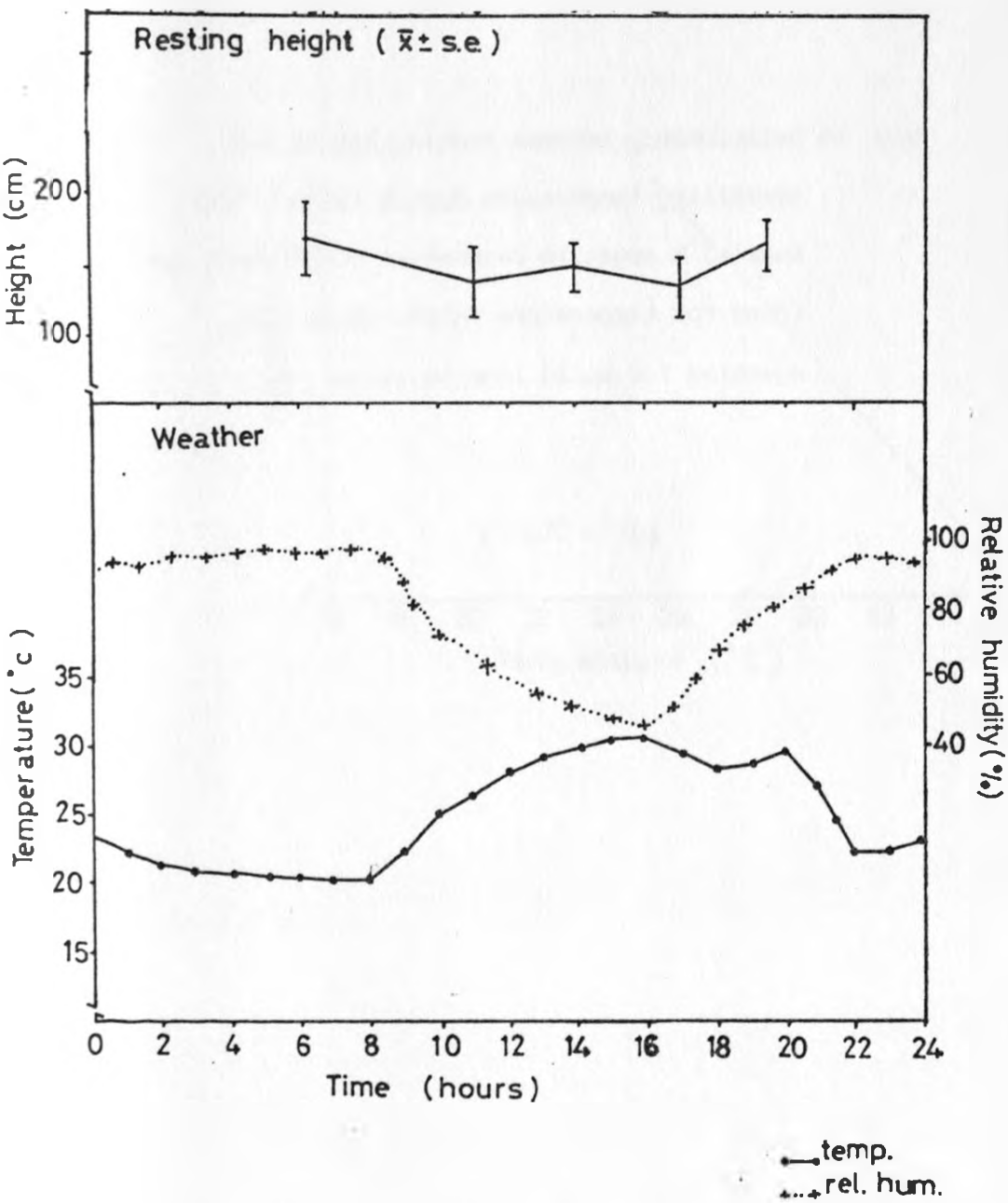

Resting height (x̄ ± s.e.)
Height (cm)
200
100
Weather
Temperature(°c)
35
30
25
20
15
Relative humidity(%)
100
80
60
40
0
2
4
6
8
10
12
14
16
18
20
22
24
Time (hours)
temp.
rel. hum.

Fig. 18 Relationship between resting height and prevailing temperature during the hot 'dry' season. A negative regression coefficient was found for temperature values above 25°C. Equation for solid line is given.

Fig 18

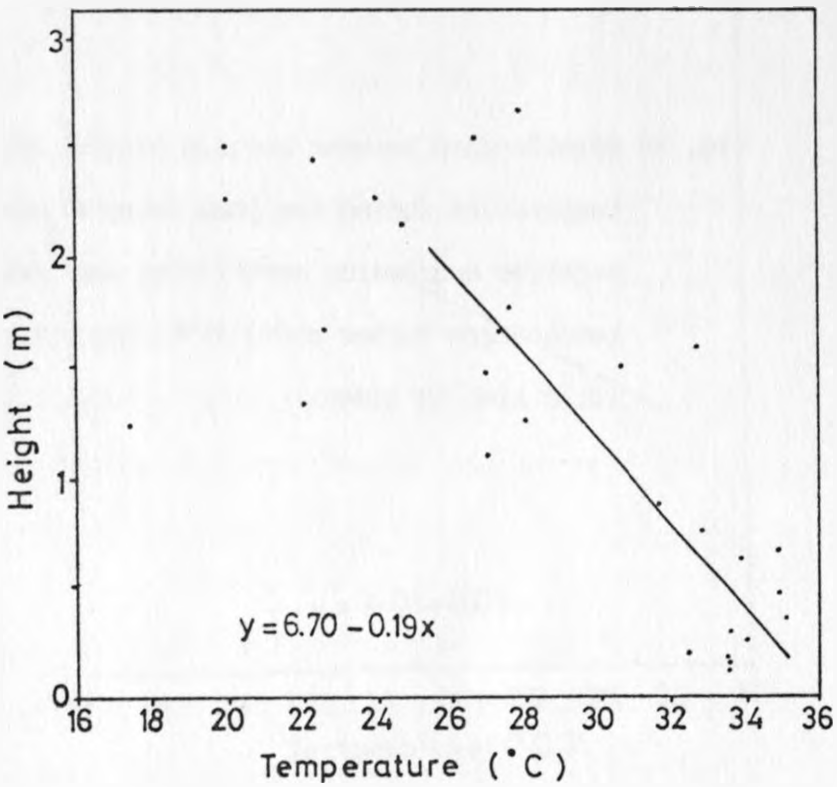
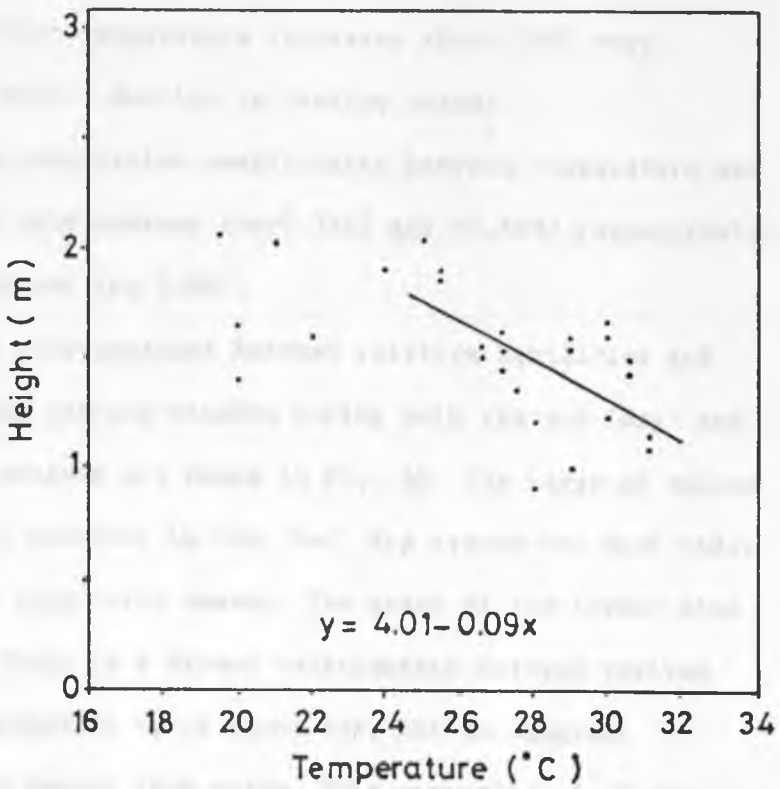

Height (m)
3
2
1
0
16
18
20
22
24
26
28
30
32
34
36
Temperature (°C)
y = 6.70 – 0.19x

Fig. 19 Relationship between resting heights and temperature during the long rainy season. A negative regression coefficient was found for temperature values above 25°C. Equation for solid line is given.

Fig 19


3
2
1
0
Height (m)
y = 4.01 - 0.09x
16
18
20
22
24
26
28
30
32
34
Temperature (°C)

Analysis of variance (Table 13) showed that the regression coefficients for both seasons were significant indicating that temperature increases above 25°C were associated with a decline in resting height.

The correlation coefficients between temperature and heights for both seasons ($r=-0.7515$ and -0.5803 respectively) were significant ($p < 0.05$).

The relationships between relative humidities and corresponding resting heights during both the hot 'dry' and long rainy seasons are shown in Fig. 20. The range of values for relative humidity in the 'hot' dry season was much wider than in the long rainy season. The graph of the former also shows that there is a direct relationship between resting height and humidity up to about 50%, but no apparent relationship beyond this value. This suggestion is further supported by the scatter for the long rainy season for which most of the values are above this thresh hold.

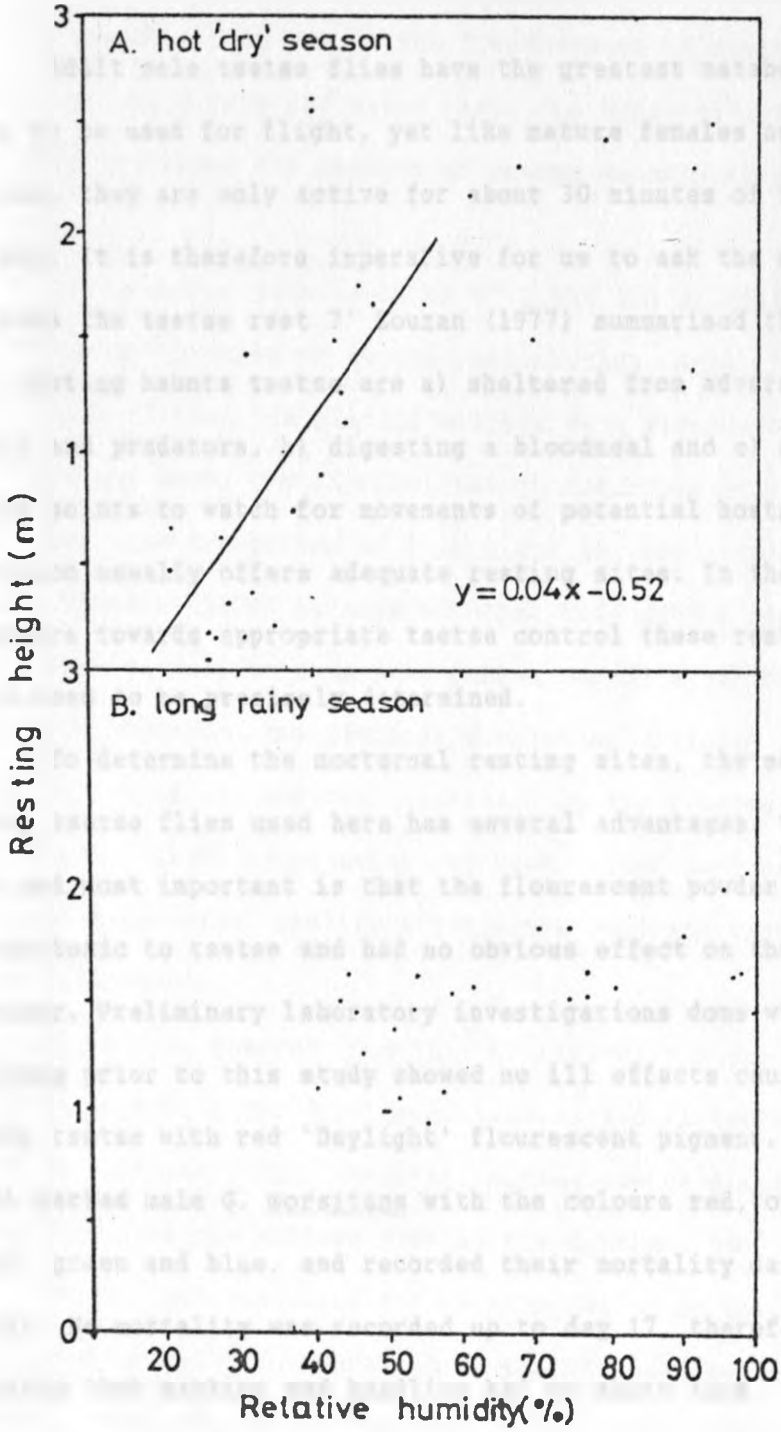
Table 13 Temperature vs height regression analysis of variance during the hot 'dry' and long rainy seasons

Source of variation	DF	Sums of squares	Mean square	F-ratio
A: Hot 'dry' season				
Temperature	1	8.0928	8.0928	33.648***
Error	20	4.8102	0.2405	
Total	21	12.9031		
B: Long rains				
Temperature	1	0.5779	0.5779	9.003**
Error	18	1.1554	0.0642	
Total	19	1.7333		

Stars indicate level of significance of F-ratio i.e ** $p < 0.01$, *** $p < 0.001$

Fig. 20 The relationship between mean resting height and relative humidity in the hot 'dry' (A) and the long rainy (B) seasons. Relative humidity values below 50% had a direct positive correlationship with resting height.

Fig 20


A. hot 'dry' season
y = 0.04x - 0.52
B. long rainy season
Resting height (m)
Relative humidity(%)
0
1
2
3
20
30
40
50
60
70
80
90
100

3.4 DISCUSSION

Adult male tsetse flies have the greatest metabolic excess to be used for flight, yet like mature females and tenerals, they are only active for about 30 minutes of flight each day. It is therefore imperative for us to ask the question 'Why does the tsetse rest ?' Bouzan (1977) summarised that at their resting haunts tsetse are a) sheltered from adverse weather and predators, b) digesting a bloodmeal and c) at vantage points to watch for movements of potential hosts. Vegetation usually offers adequate resting sites. In the endeavours towards appropriate tsetse control these resting haunts need to be precisely determined.

To determine the nocturnal resting sites, the method of marking tsetse flies used here has several advantages. The first and most important is that the flourescent powder used was non-toxic to tsetse and had no obvious effect on their behaviour. Preliminary laboratory investigations done with G. morsitans prior to this study showed no ill effects caused by marking tsetse with red 'Daylight' flourescent pigment. Turner (1980) marked male G. morsitans with the colours red, orange, yellow, green and blue, and recorded their mortality daily for 21 days. No mortality was recorded up to day 17, therefore appearing that marking and handling had no short term detrimental effect.

Tsetse flies marked and released in the field during these studies have been caught after a month. This, together with the fact that those used were not stressed, means that

there is no reason to believe that they did not rest in their natural sites. Secondly, the marked tsetse could be observed from all visual angles due to the fluorescence of their whole bodies, including legs and wings under the ultra-violet light beam. This increased the chances of seeing as many flies as possible.

The combined advantages of UV light and a ladder facilitated observation of tsetse resting high. Scholz et al. (1976) observed that low resting heights were recorded when these were not used. The difficulties of searching at greater heights was also recognized by Pilson and Leggate (1962). Further, Okiwelu (1976) pointed out that this method does not provide for the simultaneous observation on all sides of boles, fallen logs, branches and canopies without an alarming increase in manpower. This is, however, countered by the finding of Scholz et al. (1976) by pointing out that fallen logs were less likely to be nocturnal resting sites since released tsetse flew vertically upwards.

It is not, however, possible to effectively use this marking technique in the daytime because marked tsetse only glow in UV light at night. Moreover, marked tsetse disperse very rapidly from the release site in the daytime. The alternative of just searching for resting tsetse in their natural environment has several problems. The searcher is often faced with the difficulty of deciding whether the tsetse is naturally resting where it is seen, or it temporarily perched there while following him. Rates of finding tsetse are also usually very low in such studies. It was after taking these

considerations in mind that the method of using a large field cage was adopted.

Swynnerton (1936) was the first person to use a cage to study the diurnal resting sites of tsetse. Even with the certainty of finding released tsetse in a cage, their cryptic colouration with the background is usually a drawback and calls for much patience. Pilson and Leggate (1962) appreciated the elegance of using marked flies in the daytime, where marked G. pallidipes resting on woody parts of the vegetation were easily spotted on account of the coloured powder disrupting their camouflage. Combining these two advantages, the recovery rates were greatly improved. This method of using a cage has, however, a few disadvantages.

Firstly, tsetse were restricted to resting only on the substrates available in the cage. These were nevertheless natural because the cage was erected over a site naturally used by tsetse for larviposition. Secondly, this confinement could arouse atypical behaviour, especially when too many tsetse were released into the cage. This unnatural aggregation stimulated more flight activity with tsetse concentrating at the roof top. This was taken care of by first determining the capacity of the cage and thereafter releasing only optimum numbers.

The possibility of arousing other atypical behaviour was reduced in two ways. First, tsetse were fed before release. It has been documented (Pilson and Leggate, 1962) that such flies rested upon release on the immediately available substrate to excrete water and then change to real resting sites. In this study, two hours was considered long enough for

this change to occur. Secondly, tsetse found resting on or near the cage netting and framework were not considered.

It is considered therefore, that these methods have given valuable information on the resting behaviour of G. pallidipes in Nguruman which can be compared with findings from other areas and on different species. In Nguruman, the nocturnal resting sites for Glossina pallidipes throughout the study period mainly comprised of leaves, twigs and small branches. These accounted for slightly under 90% of the resting population. Minter, (1971) found 90% or more of the same species resting on leaves and twigs in Kiboko, Roo and Otuok. Both works demonstrate a preference for leaves and thin woody parts of the vegetation.

Scholz et al. (1976) did not observe any seasonal differences in the preference for leaves as nocturnal resting sites for G. p. palpalis, but Minter (1971) noted a change of nocturnal resting sites for G. pallidipes between the wet and dry seasons, and related this to the effects of seasonal leaf-fall. Leaves were preferred when they were abundant, while twigs were preferred when leaf-fall was considerable. This study has also demonstrated a changing distribution of nocturnally resting tsetse among substrates between seasons, with a preference for leaves when they were abundant in the long rainy season. The predominance of flies resting on the upper surfaces of the leaves recorded by Minter (1971) was also observed in this case.

Minter (1971) found that the range of nocturnal resting heights for the majority of G. pallidipes was between one and

three metres above the ground level. These were stable throughout the wet and dry seasons. Heights found in this study varied monthly and seasonally, as did those obtained for G. p. palpalis reported by Scholz et al. (1976).

From the literature, day and night resting sites are known to be different. Further, diurnal resting sites change with time of day and season. The work of Pilson and Leggate (1962) showed that G. pallidipes in Zimbabwe changed their resting sites through the day only during the late dry season but not during the rainy, cool and early dry seasons. During the late dry season, flies rested in rot holes around mid-day, on boles of larger trees in the afternoon (14.45-15.45) and on branches in the morning (06.45-09.45) and evening (16.45-17.45 h) of the day.

Results from Nguruman show that the shift within the daylight hours is much more evident during the hot 'dry' season than it is during the long rains. This shift is from leaves, twigs and branches in the early morning to branches and tree trunks in the late morning. In the afternoon, there is a shift to tree trunks and the ground, and with the ground predominant late in the afternoon. Rot holes were not available in the cage but flies were found resting on the extremely shaded bases of tree trunks and below the cage flame, suggesting that rot holes may also be used in Nguruman.

During the long rains, the equal preference between branches and tree trunks in the late morning is narrowed down to strong preferences for small branches from the early to the late afternoon. During the seasons in which no shift is

reported by Pilson and Leggate (1962), there was exclusive preference for branches. What is not given is the definition of 'branches' to compare it with its definition in this study.

Seasonal differences in resting heights also occur. Pilson and leggate (1962) noted that the percentage of G. pallidipes seen at three feet and under was very much greater in the late dry season than in any of the other seasons, and that this difference was significant. Comparisons of the diurnal resting heights of G. pallidipes at Nguruman with other species are however not generally valid because other workers have usually pooled the heights of all tsetse found throughout the day. This study has shown that there are considerable variations through the day especially during the hot 'dry' season. Such pooled results are therefore only valid during the long rains.

In the daytime, a decrease in the resting height with an increase in diameter of resting substrate showed only during the hot 'dry' season. There was a shift from leaves in the very early morning, through thick substrates at lower heights and eventually to settle low on ground, before the evening ascent to leaves at higher altitudes as nocturnal resting sites. Similar results were obtained by Pilson and leggate (1962) during a late dry season by recording heights from 0.14 m to 11.5 m on branches, from 0 to 1.7 m on the boles of larger trees and from 0 to 0.2 m under fallen logs.

G. pallidipes appears to rest higher than most other tsetse. Similar results were obtained for the species by Pilson and Leggate (1962) and Minter (1971). It therefore looks like

this is a characteristic of the species. Other high resting heights documented are 3.8 m for G. p. palpalis (Scholz et al., 1976) and a few individuals found slightly over 4 m (Turner, 1980).

If the choice of resting substrate and height by Glossina pallidipes is not random, then what directs it ? Factors that cause this response could broadly be categorised into physical, climatic and biotic. Physical factors are largely those of the vegetation. The important role played by the amount of vegetation available with respect to the resting behaviour of tsetse flies has been noted above. The form of the vegetation, and hence the resting substrate, is largely influenced by the climate.

In Nguruman, there was an increase in the proportion of flies found on leaves during the long rains when there is a pronounced flush of leaves. The amount of rainfall in other seasons was apparently not enough to cause the vegetation to be adequately leafy. By the same argument, the relative importance of the larger branches and tree trunks during the cool dry season was due to the reduced leaf surfaces in this season.

The times of making the night searches in the other months were usually dry. The increased preference for resting on the leaves during the long rainy season could possibly be due to the greater accumulation of water droplets and dew on twigs and small branches than on large leaves as observed by Scholz et al. (1976) and Spielberger and Barwinek (1978). The suggestion by Minter (1971) of the importance of humidity and oxygen tension close to the leaf surfaces could explain the

preference, at the physiological level, for the upper side of the leaves.

The month of August saw the least, and unusually low temperatures at the times of night searches. In the other months, temperatures were uniform and the differences between the highest and lowest value was less than 2°C. The month of May had the highest relative humidity while those of the other months were relatively uniform. These were not, however, the months that showed unusual monthly nocturnal resting heights. Regression analysis showed that these two factors did not affect these resting heights. This is presumably because the weather conditions at night were not adverse for tsetse. Their failure to account for tsetse resting behaviour at night has also been reported by Turner (1980) and Challier (1982).

Vegetation does not show changes during the course of the day. The change of resting substrates and heights with time of day are due to the influence of weather conditions, and possibly biotic factors. How did weather determine these resting sites at Nguruman, and how does this relate to findings by other workers ?

Observations at Nguruman indicate that by mid afternoon, tsetse were always found on the shaded sites perching on the underside of branches, stems and tree trunks. The advantage conferred to tsetse flies resting on these thick substrates are best explained by the phenomenon of substrate-height interaction observed.

This was best pronounced during the hot 'dry' season when weather conditions were harsh for tsetse. Deep shade is at

a premium and would only be provided by branch-type sites, rot holes and the bases of large trees. These substrates are shaded by the leaves that are found towards the outside of the bushes. Lower substrates enjoyed more shade and were therefore cooler than the upper ones. In this study, the ground was the most shaded, and hence coolest substrate. Adabie (1987) showed that at Nguruman, the soil temperature at a depth of 1 cm was more than two degrees below that at the ground surface. THis study showed that air temperatures were low near the ground than higher up.

Thick substrates are also cooler than thin ones and than the surrounding air. Laveissiere et al. (1978) (cited in Challier, 1982) showed that living organs of plants were cooler than dead ones, leaves became hot faster than trunks and small organs were hotter than bigger ones. It further appears that the thicker the substrate, the cooler it is. Tsetse at Nguruman therefore appear to be utilising the advantages of shaded cooler thick substrates that are also low down to rest in a favourable site.

The significant negative regression between resting height and temperatures (and positive correlation with RH) has, however, shown that there is a threshold below which weather has no obvious effect on resting height and above which the effect is direct. This threshold seems to be about 25^{o}C for temperatures and between 40-50% for relative humidity.

These explanations are also supported by results in the long rainy season when factors of temperature and relative humidity were not so harsh for tsetse and branches and more stable resting heights were maintained through the day.

What appears difficult to elucidate is which of the two factors, temperature and relative humidity is actually responsible for resting behaviour in this case. Both factors are important in the physiology of tsetse, and therefore it is important to know whether they interact (if they do) in an additive or a multiplicative manner. This would probably necessitate laboratory analysis. The possibility of a third factor (e.g light intensity) also exists.

Perhaps predator avoidance is also a factor in the choice of resting sites. During the night, Minter (1971) recorded that resting tsetse are warned of approaching invertebrate predators by the vibrations they cause to the thin leaves resting substrates. Tsetse resting on the woody parts of the vegetation at daytime have developed cryptic colouration. The possibility that predation could have offerred selective pressure to their choice of resting sites and the development of homochromy of resting tsetse flies is considered in the next chapter.

CHAPTER 4

PREDATION OF GLOSSINA PALLIDIPES AT RESTING SITES.

4.1 Introduction

The obvious effects of weather on the survival of tsetse flies demonstrated the importance of the effects of abiotic mortalities on their populations (Rogers and Randolph, 1985). The lack of critical experiments to investigate biotic mortalities, coupled with a general reluctance to believe in them (Jackson, 1937) led to the view that climate, in some way, both controlled and regulated population size. It was felt that with such a low reproductive rate and after suffering the vagaries of climate, tsetse would have too little reproductive potential 'left over' for density dependence to be in any way a significant feature of their life cycles. It is now realized, however, that the stability of these populations reflects significant density dependent regulation leading to renewed interest in biotic mortality factors. Understanding of these is required before attempting biological or chemical control (Rogers, 1974)

The level of natural mortality of tsetse flies has been conservatively set at 0.036 per day (Rogers et al, 1984). This is the identified critical level for population replacement beyond which if mortality is consistently raised, tsetse control can be achieved. One way in which the level of the imposed mortality can be raised is through increasing predation pressure.

Predation of adult Glossina can occur at any time during its life-time; e.g after larviposition, emergence, mating, during feeding or in first flight. Tsetse, however, spend most of their adult life resting, and perhaps this is where the largest amount of predation takes place. The cryptic colouration of resting tsetse suggests predation may have been a major selective pressure. This study was therefore restricted to predation of resting tsetse flies.

4.2 Materials and methods

Difficulties of quantifying predation in the field have already been noted. The method described by Rogers (1974) of tethering tsetse flies at their resting sites was adopted. Each tsetse was held between the thumb and first two fingers by the thorax and abdomen. The noose of a short length of light cotton thread was then placed around the neck. Noosed tsetse were then tethered at resting sites in the vegetation. A noose of about 6 to 10 cm was preferred. Shorter nooses were difficult to handle while longer ones resulted in tsetse entangling with the vegetation, eventually hanging instead of resting naturally.

This method enabled comparisons to be made between the different localities, resting substrates, densities and times of day although it is accepted that the overall level of predation may be over-estimated. Several experiments were therefore set to provide data on some of these aspects. In these experiments, the level of predation was defined as the numbers preyed upon as a proportion of the number available. Predation by vertebrates was recorded separately from that by

invertebrates. The distinction was done by making direct observations and by inferring on the type of predator from the impressions left behind on the thread after tsetse is taken away.

4.2.1 Identification of predators

The vertebrate predators of tethered/resting tsetse, mainly birds, were watched from a distance so that they were not disturbed. Their colour, body size, shape of beak and their food searching behaviour were noted. Reptiles, mainly lizards, were observed from a closer range without them being disturbed. Their size, colour, body texture, body stripes and the substrates on which they were found were noted. Some were caught by netting them after which they were preserved in 70% alcohol plus gycerol for identification.

Invertebrate predators were mainly observed by making inspection rounds at those sites where tsetse were tethered. Ants were not interrupted by these inspections but spiders were cautious about any movements in their vicinity and were not easy to catch. Specimens were also collected and preserved as mentioned above.

Basic identification was attempted by the researcher, but species of insect predators was verified by Mr. J. Muhangani, while reptilian predators by Ms D. Rotich, both from the National Museums of Kenya, Nairobi. Spiders were identified at the British Museum of Natural History, London by Dr F. Wanless.

The food searching and predatory behaviour of all these predators i.e, lone or group hunting, and how they devoured their tsetse prey, were noted.

4.2.2 Effects of resting substrate, locality and day/night times on Predation Levels

The predation levels of tsetse on three different resting substrates (leaves, large branches and tree trunks) were compared. Replicate groups of ten tsetse flies were tethered randomly within a 'metre cube' on each of the three substrates. Tsetse flies were always tethered in the shade and at a height of between one and two metres above the ground. Nooses were tacked onto the vegetation using thumb tacks that were blackened to avoid their visibility and hence their probable association with prey by predators.

The experiments described above were replicated in three different localities. Location 1 refers to the junction of the Oloibototo river bed and the regular sampling transect 1 (see Fig. 2). Location 2 is at the junction of Sampu river bed and the cross track linking transects 1 and 3. This is about 2 Km to the west of location 1. Location 3 is about 10 km to the north of the other two. It is at the junction of the Oloibototo river bed and transect 4. Since all localities were near river beds, vegetation was similar although location 3 is less densely wooded than the others.

Predation of resting tsetse has previously been scored after 24 hours (Rogers, 1974; Adabie, 1987). However, different predators are likely to be active at daytime and at night, so

the experiments described above were run both at daytime and night time. Daytime experiments were run from 10.00 to 18.00 hours and night time ones were run from 18.00 to 06.00 hours of the next day. Tsetse were tethered between 1 and 2 m above the ground.

4.2.3 Effects of marks on predation levels of tsetse flies

The importance of the cryptic colouration of tsetse flies was investigated by tethering tsetse marked with conspicuous colours. This experiment was also devised to determine whether the marking technique used in mark-release-recapture studies by other workers at Nguruman were resulting in higher losses of marked flies through predation.

Marks conventionally used for such studies are thought to disrupt this added advantage of resting tsetse by making them easily spotted by predators. The marks consisted of two spots of artists oil paints (approximately 1 mm in diameter) on the notum of the thorax of the tsetse. Marking studies going on at the time of this experiment included applying spots either one above the other along the long axis of the insect or beside each other on its short axis. Colours used on alternate days were green and pink. A simple cross over design was adopted with replicates of marked and unmarked tsetse placed in sites alternating daily.

In the third experiment, distance between experimental positions remained unaffected but the experimental time during the day was reduced to 3 hours to reduce the level of predation (15.00 to 18.00 hours).

In all density experiments, predation was expressed as a percentage of the number eaten of total number of prey available. Data were normalised by the arcsine (square root proportion) transformation. Comparison of means was done using the Duncan's new multiple range test.

4.2.5 Predation of flying tsetse

Some of the predators of flying tsetse flies were also seen at Nguruman. An attempt was made to study their predatory behaviour as well. Asilidae were sweepnetted in the area and transferred singly into cages of mosquito netting. They were then released into the large field cage used for diurnal resting sites described in Chapter 3. Two hours were allowed for them to adapt and resume their usual behaviours as in the natural environment. Tsetse flies were then released therein and any interactions between the tsetse and asiliids were watched from outside the cage.

4.3 RESULTS

4.3.1 Predators of resting tsetse

Birds were important daytime predators. They actively searched for the prey by jumping between branches within the bushes. These most commonly found birds included the little yellow flycatcher (Chloropetella holochlora) and the golden pipit (Tmetothylacus tenellus). These were lone hunters. They grasped their prey by the thorax and abdomen, usually leaving heads still attached to the cotton threads. In a few cases the entire tsetse was eaten, leaving an empty noose.

Lizards were also observed as daytime predators. They were solitary and hunted by sight. The two species identified included the skink Mabuya striata (Sauria, Scincidae) and the yellow headed dwarf gecko Lygodactylus picturatus (Sauria, Gekkonidae). They walked about on the branches and stems of bushes. Upon noticing prey, they stopped at a distance and then suddenly leapt at and held it by the mouth. Lizards were not however, observed to effectively prey on tethered tsetse flies. The dwarf gecko was once observed to put tethered tsetse in its mouth, but they were not swallowed, and were again released alive. This behaviour was mainly studied in the large field cage when lizards fed on tsetse which were being used for resting site studies. The lizards had not been introduced but were present naturally.

Spiders (Araneae) were implicated during the day and night, but were apparently more important at daytime. Both mature and immature spiders were observed. From the total

number of all spider specimens collected for identification, members of the family Salticidae formed over 70% and were therefore the most important. Hyllus brevitarsus Simon was the most common salticid. Other salticids included Stenaelurillus sp. and a Tusitala sp., the latter being a new species. Other spiders included two species of Oxyopes (family Oxyopidae) and a Monaeses sp. (family Thomisidae). All spiders were active and cursorial lone hunters of resting tsetse.

Spiders implicated at night were largely web builders. In two incidences, tsetse dusted with flourescent powder and trapped in spider webs were found being devoured by spiders. In another incident also observed at night, a tsetse trapped in a web was briskly leapt at by a spider and very rapidly wrapped in the spiders silk and preserved for a later meal.This spider was not identified.

Ants (Formicidae) were observed as predators both during the day and at night. Subfamilies included Ponerinae (Platythyrea sp., Odontomachus sp.), Dilichoderinae (Technomyrmex sp.) and Myrmicinae (Crematogaster sp.). The Ponerinae and Dilichoderinae were lone hunters but occasionally two or three could be found devouring the same prey. The Myrmicinae were largely pack hunters, with several of them being found on the same prey.

Ants generally first cut all the legs and wings off the tsetse thus immobilizing it. They then burrowed into the internal organs of the prey, frequently leaving a hollow exoskeleton. Occasionally, they removed all traces of the tsetse, and teased out the individual fibres of the thread.

4.3.2 Predation levels by location, substrate and time

The total, vertebrate and invertebrate predation levels observed in the three localities and substrates at both day and night times are shown in appendix 1. These results were analysed by a 3-way analysis of variance and the analysis is given in Table 14. For total predation, location and time were significant factors, for vertebrates substrate and time were significant whilst for invertebrates, only time was significant. Means for the three variables, namely total, vertebrate and invertebrate predation levels at each of the factors locality, substrate and time are shown in Table 15.

Duncan's multiple range test showed that the mean total predation at location 2 was significantly higher than that of location 1. This apparently resulted from differences in the vertebrate predation among the three localities since the amount of predation by invertebrates was uniform over the study localities. This suggests the existence of localized population of birds and/or their activities whereas invertebrates were randomly distributed in the area.

Table 14 Total, vertebrate and invertebrate predation analysis of variance table.

Source of variation	df	Total ms	F-ratio	Vertebrate ms	F-ratio	Invertebrate ms	F-ratio
Location	2	3086.431	3.854*	1845.493	2.92	68.903	0.16
Substrate	2	1620.811	2.023	3545.554	5.61**	746.967	1.78
Time	1	3247.754	4.055*	34900.347	55.18***	18324.812	43.65
Loc. x sub.	4	508.189	0.634	101.655	0.16	136.783	0.33
Loc. x time	2	-214.350	-0.267	821.442	1.30	136.783	0.33
Sub. x time	4	625.110	0.780	347.771	0.55	33.518	0.08
Loc.xsub.xtime	4	500.424	0.624	232.786	0.37	330.783	0.79
Error	111	800.797		632.464		419.822	

Stars indicate level of significance of F-ratio i.e * $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

NB Uneven number of replicates for the experiment resulted in negative sums of squares for Loc. x time interaction for total predation (type 3SS,SAS)

Table 15 Total, vertebrate and invertebrate mean predation levels as per location, substrate and time (detransformed means($\bar{x} \pm s.e.$).

	Total	Vertebrate	Invertebrate	n
Location 1	43.13±3.52	21.02±3.10	24.86±2.52	660
Location 2	60.61±4.81	35.45±5.13	25.15±4.18	270
Location 3	51.73±4.95	25.96±4.19	27.24±3.41	360
Substrates				
Leaves	44.28±4.32	17.14±4.22	31.05±3.44	430
Branches	47.20±4.50	28.19±4.22	23.25±3.44	430
Trunks	56.08±4.28	37.10±4.22	22.10±3.44	430
Time totals				
Day	53.86±3.80	45.59±3.15	12.63±2.57	
Night	43.81±3.17	9.37±3.72	38.88±3.03	

Total predation between the three resting substrates did not show any significant differences. However, there was an increase in total predation with an increase in diameter of resting substrate. This was largely due to the significantly increased predation by vertebrates with increasing diameter of resting substrates. Vertebrates predation of tsetse resting on branches and tree trunks was similar but significantly higher than that on the leaves. This was probably because of their better visibility on the former compared to the latter resting substrates. Invertebrate predation was equally important on all three substrates. This was possibly because ants mainly hunted by random search of prey, and not by sight as done by the birds. Their lower predation on branches and trunks was probably because most tsetse resting here are eaten by birds.

There was significant differences between total day and night predation levels. Vertebrate predation was five times higher during the day than at night. Invertebrate predation was three times higher at night than at daytime. At daytime predation by vertebrates was about four times higher than that due to invertebrates while at night invertebrate predation was over four times higher than that due to vertebrates. This implies that the relative importance of the two predator groups changed with time. Vertebrates were mostly active during the day while invertebrates were active at night. In conjunction with the above, it appears that these two groups can probably only be fully compared if we assume that vertebrate predation occurs first, and the the level of invertebrate predation is expressed as a percentage of what is left.

4.3.3 Effects of marking

Results on the levels of predation of marked and unmarked tsetse during the day and night periods by vertebrates, invertebrate, and the total predation were subjected to analysis of variance as shown in Table 16. Their mean predation levels are given in Table 17.

The significance of the difference between day and night predation is in agreement with prior findings reported here. Overall predation levels of marked and unmarked flies were not significantly different. However, since the crypsis is probably only important with respect to daytime vertebrate predators, it is interesting to compare only the amount of predation of marked and unmarked flies due to vertebrates in the daytime. Analysis shows that although predation of marked flies (39%) was higher than that of unmarked flies (31%), the difference was again not significant (t (13df)=0.698, $p>0.05$). More replicates might produce a significant difference, but the marks used clearly had little effect on predation.

Table 16 Analysis of variance table for total predation

Source of variation	df	ss	ms	F-ratio
Treatments	1	237.123	237.123	0.394
Time	1	2916.967	2916.967	4.850*
Marking x time	1	439.903	439.903	0.730
Residual	52	31274.503	601.433	
Total	55	34868.496		

Star indicates level of significance of F-ratio i.e * $p < 0.05$

Table 17 Predation of marked and unmarked tsetse at daytime (X+SE)

Predator group	Day	n	Night	n
A. Marked				
Vertebrates	38.832±9.266	140	13.593±3.742	140
Invertebrates	13.350±4.070	140	20.341±5.544	140
Total	48.858±8.505	140	28.818±5.630	140
B. Unmarked				
Vertebrates	30.657±7.151	140	13.593±3.742	140
Invertebrates	12.445±3.712	140	22.974±4.985	140
Total	39.137±6.330	140	30.308±5.266	140

4.3.4 Effects of prey density on predation levels

4.3.4.1 Predation with positions close together (density experiment 1)

Total percentage predation in the first density experiment over the various experimental positions and densities is given in Appendix 2. Vertebrate and invertebrate predation are given in Appendices 3 and 4 respectively. Inspection of these data show that there were very high levels of predation. The results of their analysis of variance are shown in Table 18. For total predation no factor was a significant source of variation but for vertebrate and invertebrate separately, time and position were significant. For all the three variables, no significant effects of density or the interaction between time and position, and between time and density were noted.

The mean predation levels at the various positions at both day and night times are shown in Table 19. Vertebrate predation in the daytime was significantly higher than at night while mean invertebrate predation was significantly higher at night than in the daytime. Relatively high vertebrate predation was realized at night because 'night' here includes some daylight hours. Both vertebrate and invertebrates showed significant differences in their predation level between the five positions. However, it was generally observed that experimental positions with high vertebrate predation had low invertebrate predation and vice versa.

The efects of density on predation is shown in Fig. 21. No clear trends are evident, and density did not appear to be affecting the level of predation.

Table 18 Analysis of variance table for the total, vertebrate and invertebrate predation levels in experiment 1.

Source of variation	df	Total		Vertebrate		Invertebrate	
		ms	F-ratio	ms	F-ratio	ms	F-ratio
Time (day/night)	1	80.75	0.85	200.69	5.90*	2802.05	8.64*
Days W/ time	8	95.20		339.00		324.23	
Positions	4	153.67	2.47	1820.72	5.78*	1569.64	5.40*
Density	4	32.72	0.53	470.89	1.49	691.65	2.38
Position x time	4	34.64	0.56	651.88	2.07	528.68	1.82
Density x time	4	46.53	0.75	416.86	1.32	227.02	0.78
Residual	24	62.24		315.18		290.75	

Stars indicate level of significance of F-ratio i.e * $p \leq 0.05$

Table 18 Analysis of variance table for the total, vertebrate a
invertebrate predation levels in experiment 1.

Source of variation	df	Total		Vertebrate		Invertebrate	
		ms	F-ratio	ms	F-ratio	ms	F-r
Time (day/night)	1	80.75	0.85	200.69	5.90*	2802.05	8.6
Days W/ time	8	95.20		339.00		324.23	
Positions	4	153.67	2.47	1820.72	5.78*	1569.64	5.4
Density	4	32.72	0.53	470.89	1.49	691.65	2.
Position x time	4	34.64	0.56	651.88	2.07	528.68	1.
Density x time	4	46.53	0.75	416.86	1.32	227.02	0.
Residual	24	62.24		315.18		290.75	

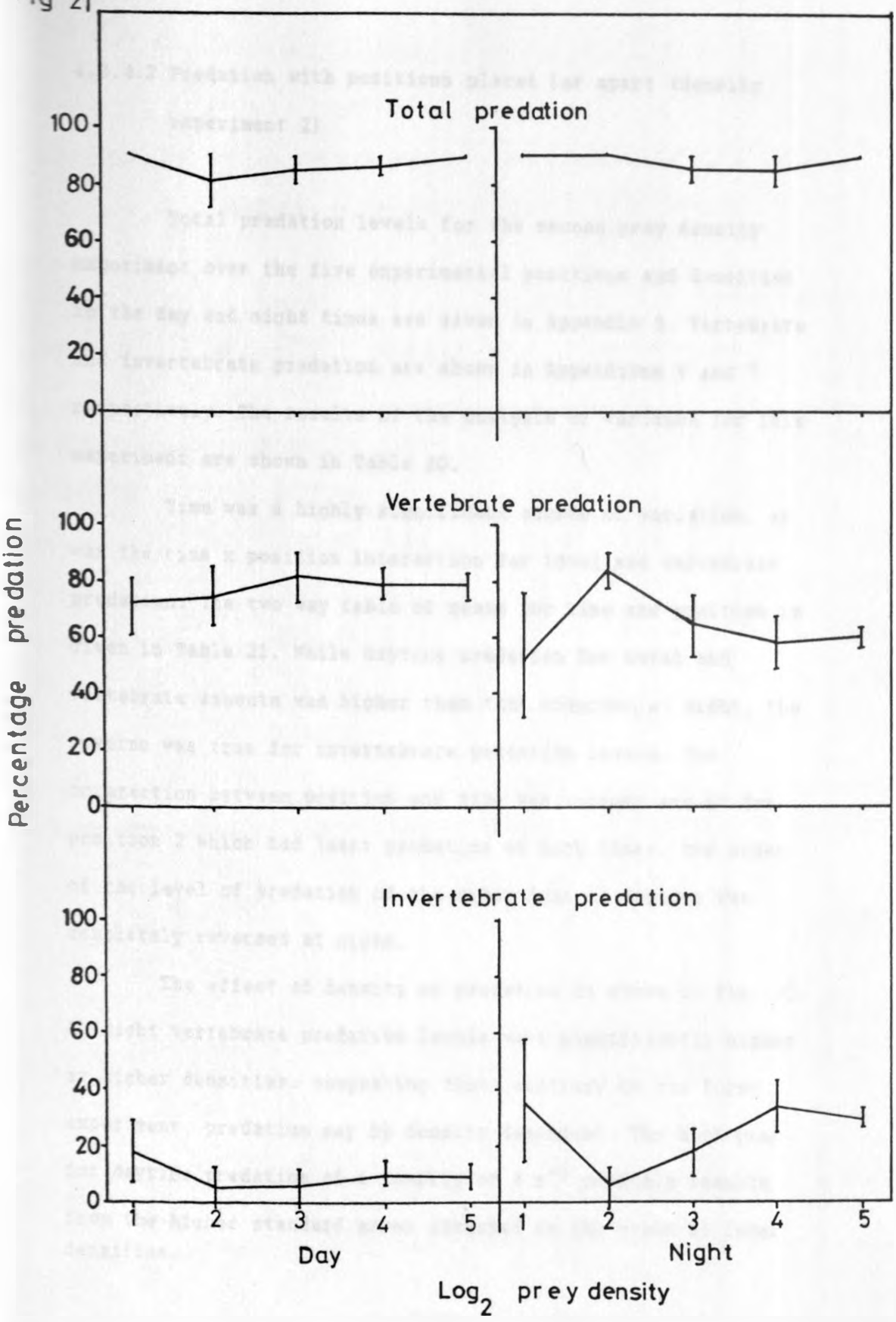
Stars indicate level of significance of F-ratio i.e * $p \leq 0.05$

Table 19 Mean predation levels (%) at experimental positions at day and night times.

		Positions					
		1	2	3	4	5	Mean
Day	Total	90.0	81.0	90.0	80.07	87.96	85.81
	Vert.	87.96	69.96	87.10	56.74	85.07	77.37
	Invert.	2.04	11.04	2.90	29.80	2.90	9.74
Night	Total	90.0	90.0	90.0	81.72	90.0	88.34
	Vert.	48.26	71.06	85.34	44.63	74.28	64.72
	Invert.	41.74	18.94	4.66	42.47	15.72	24.70
Mean	Total	90.0	85.50	90.0	80.90	88.98	87.08
	Vert	68.11	70.51	86.22	50.69	79.68	71.05
	Invert.	21.89	14.99	3.78	36.13	9.31	17.22

Fig. 21 Total, vertebrate and invertebrate predation levels at the five densities during both day and night times under close experimental positions

Fig 21


Total predation
Vertebrate predation
Invertebrate predation
Percentage predation
100
80
60
40
20
0
1
2
3
4
5
Day
Night
Log2 prey density

4.3.4.2 Predation with positions placed far apart (density experiment 2)

Total predation levels for the second prey density experiment over the five experimental positions and densities in the day and night times are given in Appendix 5. Vertebrate and invertebrate predation are shown in Appendices 6 and 7 respectively. The results of the analysis of variance for this experiment are shown in Table 20.

Time was a highly significant source of variation, as was the time x position interaction for total and vertebrate predation. The two way table of means for time and position is given in Table 21. While daytime predation for total and vertebrate amounts was higher than that observed at night, the reverse was true for invertebrate predation levels. The interaction between position and time was because except for position 2 which had least predation at both times, the order of the level of predation of the other four at daytime was completely reversed at night.

The effect of density on predation is shown in Fig. 20. At night vertebrate predation levels were significantly higher at higher densities, suggesting that, contrary to the first experiment, predation may be density dependent. The high peak for daytime predation of a density of 4 m^{-3} probably results from the higher standard error attached to the means at lower densities.

Table 20 Total, vertebrate and invertebrate predation levels analysis of variance table for experiment 2

ource of		Total		vertebrate		Invertebrate	
ariation	df	ms	F-ratio	ms	F-ratio	ms	F-ratio
me (day/night)	1	11150.37	9.93*	50700.18	66.66***	18212.23	68.79***
ays W/ time	8	1122.70		760.59		264.79	
ositions	4	170.56	0.41	577.84	2.72	737.83	2.18
ensity	4	1031.31	2.50	713.23	3.36*	234.96	0.70
osition x time	4	1964.44	4.75*	766.84	3.61*	767.98	2.27
ensity x time	4	465.19	1.13	433.69	2.04	514.23	1.52
esidual	24	413.31		212.54		337.87	

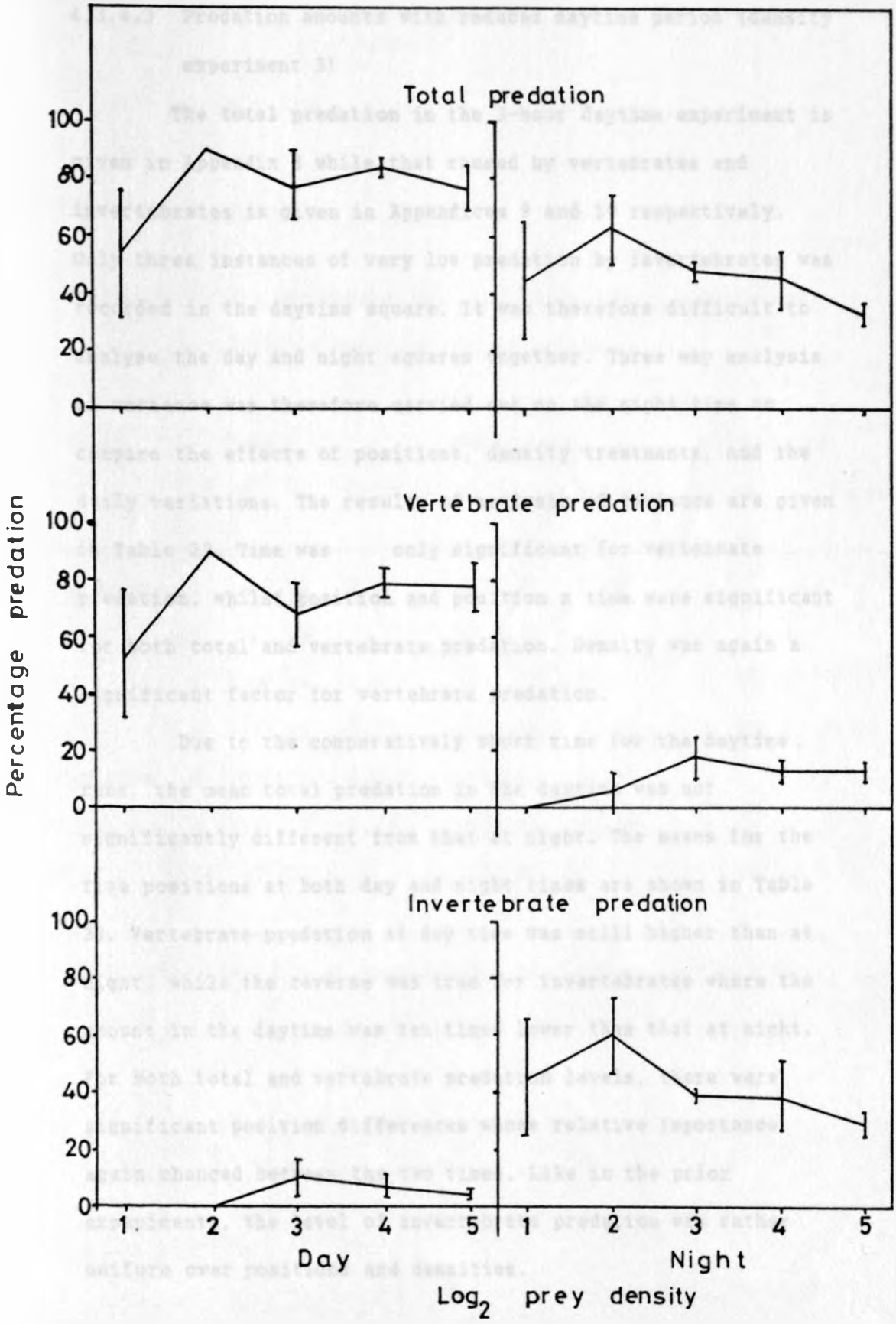
tars indicate level of significance of F-ratio i.e * $p < 0.05$, *** $p < 0.001$

Table 21 Day and night mean predation levels (%) at the five positions.

		Positions					
		1	2	3	4	5	Mean
Day	Total	83.54	64.08	90.0	60.0	87.10	76.94
	Vert.	76.96	56.68	90.0	60.0	84.87	73.70
	Invert.	8.04	9.07	0.0	0.0	4.14	4.25
Night	Total	22.77	62.52	36.68	61.86	46.55	46.08
	Vert.	15.27	2.90	5.79	18.48	7.04	9.89
	Invert.	18.21	61.66	34.82	53.06	44.35	42.42
Mean	Total	53.16	63.30	63.34	60.93	66.83	61.51
	Vert.	46.12	29.79	47.90	39.24	45.96	41.80
	Invert.	13.12	35.36	17.41	26.53	24.25.	23.34

Fig. 22 Total, vertebrate and invertebrate predation levels at the five densities during both day and night times with experimental positions far apart

Fig 22


Total predation
Vertebrate predation
Invertebrate predation
Percentage predation
100
80
60
40
20
0
1
2
3
4
5
Day
Night
Log2 prey density

4.3.4.3 Predation amounts with reduced daytime period (density experiment 3)

The total predation in the 3-hour daytime experiment is given in Appendix 8 while that caused by vertebrates and invertebrates is given in Appendices 9 and 10 respectively. Only three instances of very low predation by invertebrates was recorded in the daytime square. It was therefore difficult to analyse the day and night squares together. Three way analysis of variance was therefore carried out on the night time to compare the effects of positions, density treatments, and the daily variations. The results of analysis of variance are given in Table 22. Time was only significant for vertebrate predation, whilst position and position x time were significant for both total and vertebrate predation. Density was again a significant factor for vertebrate predation.

Due to the comparatively short time for the daytime runs, the mean total predation in the daytime was not significantly different from that at night. The means for the five positions at both day and night times are shown in Table 23. Vertebrate predation at day time was still higher than at night, while the reverse was true for invertebrates where the amount in the daytime was ten times lower than that at night. For both total and vertebrate predation levels, there were significant position differences whose relative importance again changed between the two times. Like in the prior experiments, the level of invertebrate predation was rather uniform over positions and densities.

Table 22 Total, vertebrate and invertebrate predation levels analysis of variance for experiment 3

Source of variation	Total df	ms	F-ratio	Vertebrate ms	F-ratio	Invertebrate df	ms	F-ratio
Time (day/night)	1	450.52	0.45	6575.36	5.42*			
Days W/ time	8	983.95		1212.97				
Positions	4	2007.96	4.61*	2752.77	8.58*	4	401.50	1.19
Density	4	1187.85	2.73	1363.34	4.25*	4	194.63	0.56
Position x time	4	2006.21	4.61*	1420.44	4.43*			
Density x time	4	1187.72	2.73	957.58	2.98*			
Residual	24	435.62		320.92		12	337.64	

Star indicates level of significance of F-ratio i.e * $p \leq 0.05$

Table 23 Mean predation (%) at different positions at day and night times.

		Positions					
		1	2	3	4	5	Mean
Day	Total	36.21	64.96	28.14	2.90	63.63	39.17
	Vert	34.96	64.96	24.00	0.0	63.63	37.51
	Invert	2.90	0.0	4.14	2.90	0.0	1.99
Night	Total	52.02	30.61	21.94	31.14	30.10	33.16
	Vert	26.90	18.69	8.28	4.66	14.35	14.58
	Invert	35.13	18.0	13.66	29.0	17.9	22.74
Mean	Total	44.12	47.79	25.04	17.02	46.87	36.17
	Vert	30.93	41.83	16.14	2.33	38.99	26.05
	Invert	19.02	9.0	8.90	15.95	8.95	12.36

Fig. 23 shows the mean predation at each prey density at both day and night times observed in experiment 3. Again, results in the daytime were erratic at low densities but if results for densities 2 and 4 m^{-3} are pooled, predation seems to increase with density.

4.3.5 Results on predation of flying tsetse

The asilids are well known predators of flying tsetse. The most common and abundant genera at Nguruman were Promachus, and Ommatius. 16 asilids released into the cage flew to the roof top that prevented their escape.

These asiliids did not appear to be aroused by the flight of the introduced tsetse flies. Thus no predator-prey interactions were seen despite providing for the asiliids suitable hunting vantage points. From observations outside the cage, they always went for tips of isolated twigs and small branches. The use of a cage with minimal leafy cover may be a feasible alternative.

Fig 23

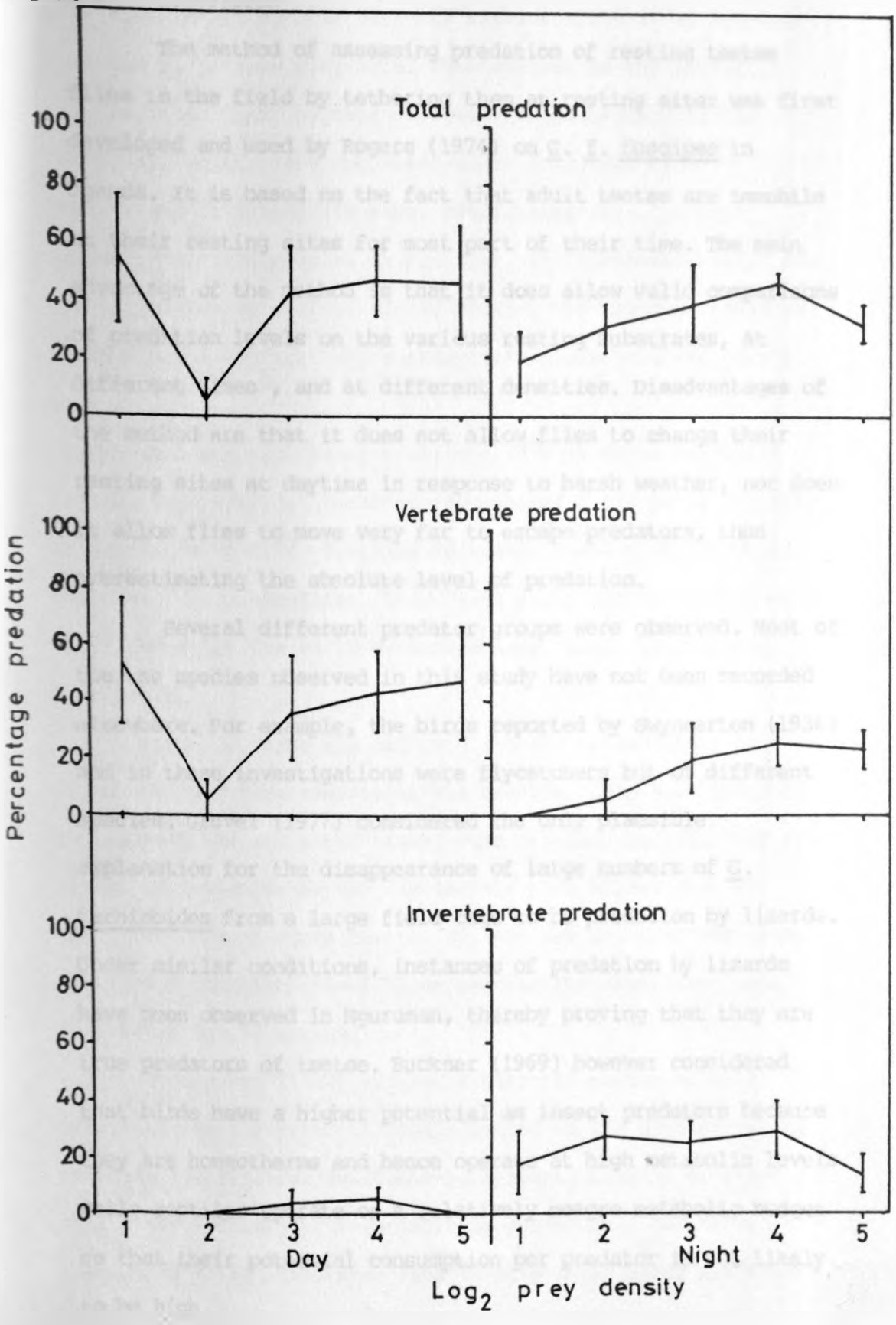
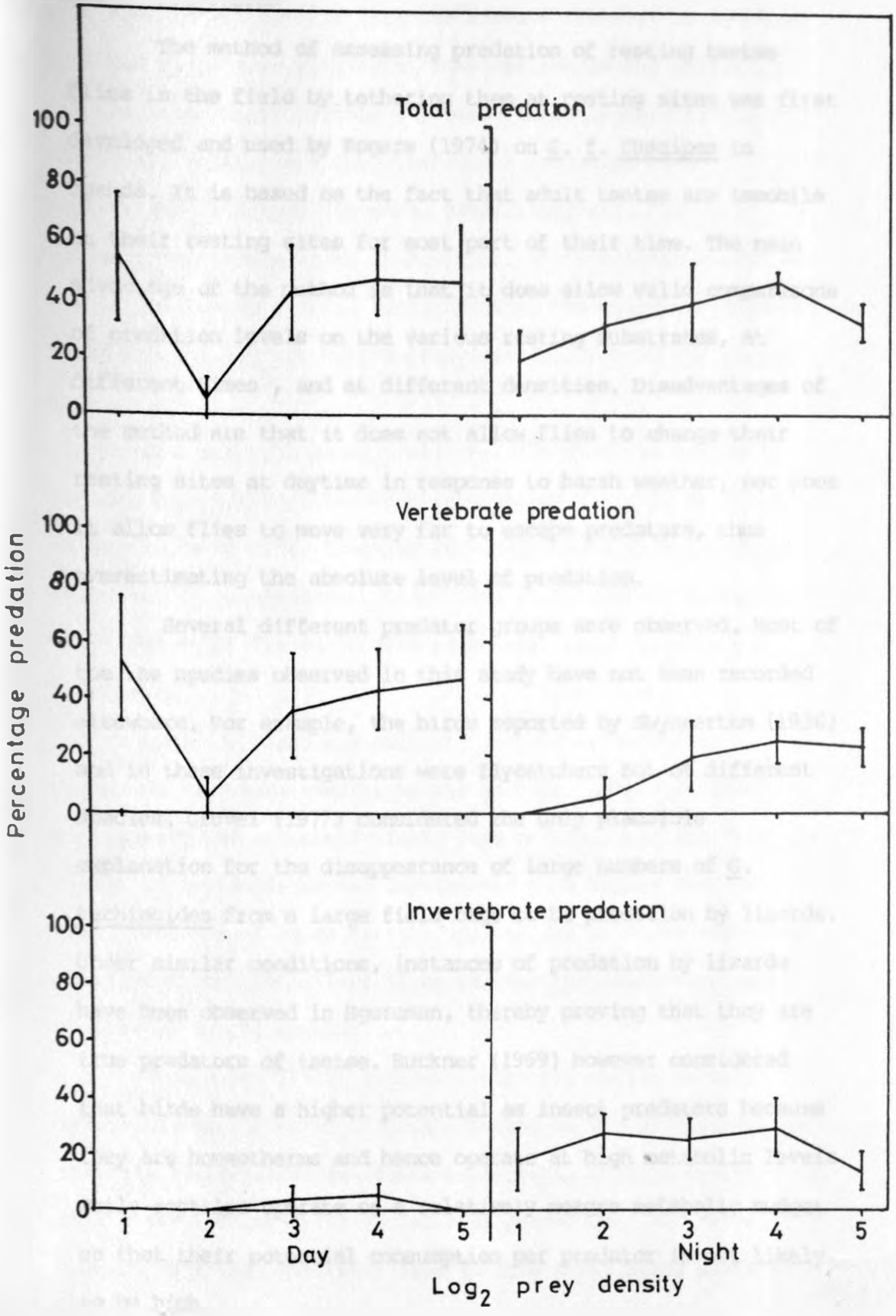

Total predation
Vertebrate predation
Invertebrate predation
Percentage predation
100
80
60
40
20
0
1
2
3
4
5
Day
Night
Log2 prey density

Fig. 23 Total, vertebrate and invertebrate predation levels at the five densities during both day and night times but with reduced daylength

Fig 23


Total predation
Vertebrate predation
Invertebrate predation
Percentage predation
100
80
60
40
20
0
1
2
3
4
5
Day
Night
Log2 prey density

4.4 DISCUSSION

The method of assessing predation of resting tsetse flies in the field by tethering them at resting sites was first developed and used by Rogers (1974) on G. f. fuscipes in Uganda. It is based on the fact that adult tsetse are immobile at their resting sites for most part of their time. The main advantage of the method is that it does allow valid comparisons of predation levels on the various resting substrates, at different times , and at different densities. Disadvantages of the method are that it does not allow flies to change their resting sites at daytime in response to harsh weather, nor does it allow flies to move very far to escape predators, thus overestimating the absolute level of predation.

Several different predator groups were observed. Most of the the species observed in this study have not been recorded elsewhere. For example, the birds reported by Swynnerton (1936) and in these investigations were flycatchers but of different species. Gruvel (1977) considered the only plausible explanation for the disappearance of large numbers of G. tachinoides from a large field cage to be predation by lizards. Under similar conditions, instances of predation by lizards have been observed in Nguruman, thereby proving that they are true predators of tsetse. Buckner (1969) however considered that birds have a higher potential as insect predators because they are homeotherms and hence operate at high metabolic levels while reptiles operate on a relatively meagre metabolic budget so that their potential consumption per predator is not likely to be high.

Spiders are well documented tsetse predators, but it is also of interest to note that the species observed at Nguruman have not been found elsewhere. This applies to the salticids and the other families here reported. While members of the family Salticidae were not observed as predators of G. swynnertoni in Uganda (Southon, 1958), they were the most commonly observed species at Nguruman. All specimens caught for identification were found either sinking the venomous fangs of their chelicerae into, and sucking out juices from the prey's body.

Ants are well known predators of both pupae and adult tsetse. Rogers (1974) recorded only those of the genus Pheidole as predators of G. f. fuscipes in Uganda while this study has revealed more subfamilies. Large ants could capture tsetse on their own while for small Myrmicine ants, group hunting was inevitable.

Birds, lizards and salticid jumping spiders hunt by sight and therefore operate in the daytime. Ants were observed during both day and night times. This probably explains why the amount of predation in the daytime was much higher than at night. The amount shown for the vertebrates at night must have occurred at twilight, just after setting the experiment, and very early in the morning.

Swynnerton (1936) suggested that the choice of tree trunks as resting sites of female tsetse in the daytime was in response to predation avoidance by spiders. Results obtained in this study indicate that vertebrates preyed more on tsetse resting on thick substrates than on thin ones. Birds searched

for their prey while hopping from within and between the branches and tree trunks in the bushes and hence encountered more tsetse resting on these substrates. Tsetse resting on leaves are less visible to them. Predation by invertebrates was indifferent of the substrates. Whereas ants were found patrolling equally on all substrates in the bushes (and their encounter with the tsetse prey appeared to be random), all spiders in Nguruman were collected from leaves and thin branches and not on tree trunks.

No previous records in literature refer to predation in localities within the same tsetse habitat. This study has shown the existence of pockets of high amounts of predation and others with low amounts. This difference is attributed to local aggregations of vertebrate predators.

Cryptic colouration of resting tsetse has been thought of as providing protection against predation. Marks applied on the thorax of tsetse for ecological studies make them visible and hence more vulnerable to attack by predators. Gruvel (1977) for example noted that tsetse marked with coloured spots formed the major percentage of those captured by Hersiliid spiders. Results obtained from these studies however, show no significant differences between predation rates on marked and unmarked flies. This suggests that either the colours of these marks are not perceived by the predators, or they are, in general, not associated with the presence of prey. Perhaps then it is the general body outline or the shape of the tsetse that is associated with the presence of food, and which is mapped out against the cryptic resting substrate by the searching

vertebrate predator. It is however possible that more replicates of this experiment would have shown a significant difference for vertebrate predation in the daytime.

From the data given, it is possible to assess the relative importance of the two predator groups. Vertebrate predation was always higher than invertebrate predation, and when vertebrate predation was highest, invertebrate predation was lowest. This suggests that interference occurred because one group of predator reduced the amount of mortality caused by the other.

In the density experiments there were often significant position effects and differences between days. Factors that affect the behaviour of these predators may therefore come into play. Weather had a significant effect on the activity of predators. The movement and vocalising of the birds was minimal when it was very hot as opposed to a cooler day. This probably caused the large amount of variability observed by casual inspection of the field data between the days.

In two of the experiments there was evidence of density dependent predation by vertebrates resulting from either aggregation or development of a search image. The localisation of the activity of birds observed is evidence of aggregation of predators. This is generally known to occur (Hassel and May, 1973; 1974). In addition, predators are known to enhance their food searching behaviours like other searching animals, and hence usually spend more time where their requisites are more plentiful (Hassel and May, 1974). Moreover, Tinbergen (1949, 1955) (cited in Holling, 1961) proposed that birds preying upon

a variety of insects developed this 'searching image' of the prey when the prey became dense enough to make this profitable. Why then was there no evidence of density dependence in the first experiment performed ? This was probably because experimental positions were quite close and the densities used behaved as one huge density at one position.

The third density (8 m^{-3}) considered in these experiments was the highest among those considered by Rogers (1974) where direct density dependence was strongly recorded for vertebrates. In these experiments a density of eight appeared to be the threshold for this to occur.

Several other factors were not investigated and might have had some effects on these results. Prime among them is the predator densities of their populations. Also, their searching efficiencies need to be better assessed, as well as their functional and numerical responses. This information can help to better understand the probability by which a predator would encounter and capture prey in the natural environment. Such an index, together with a knowledge of the food preferences of the predators in that specific tsetse habitat can then be used to adjust the results got from tethering experiments. But because experimental positions here were choosen with a knowledge of the resting sites of this tsetse, then these results are valid.

CHAPTER 5

GENERAL DISCUSSION

The many years of trying to eliminate tsetse flies from the African continent have been without much overall success. Rogers and Randolph (1984) suggested this was a result of placing too much emphasis on the technological aspect of how to do it, at the expense of the biological aspect of when and where to apply this technology. There is now, however, a revolution in the approach towards tsetse control, with empasis on the latter through the acquisition of a more comprehensive understanding of the ecology of tsetse flies. To quote from Rogers (1974), 'at present we can teach the tsetse fly virtually nothing, we can only learn from it.' Knowledge on the population ecology of the target species is therefore a priority.

Population ecology has unfortunately been a neglected field of tsetse research until Rogers (1974) explained the need for understanding natural population regulation before attempting chemical or biological control. Factors implicated can then be incorporated into a mathematical model to describe both the average level of abundance and the observed changes about that level. This regulation is due to density dependent factors that need to be adequately determined and quantified. Mortality due to biotic factors contribute to this regulation.

Allsopp (1984) acknowledged the fact that resting behaviour still needs to be studied. With specific reference to Glossina pallidipes Glover (1967) considered it an elusive fly, difficult to study and whose resting habits are little known. However, some effort has now been made in this respect. The previous rationale for resting site studies was to maximise contact between resting tsetse and the insecticides used in their control. Earliest among these was the selective and discriminative ground spraying of residual insecticides in their diurnal resting sites. More recent interests centered on aerial spraying of low dosages of insecticides in the night resting sites when temperature inversion conditions are optimal.

Several instances are reported where insecticides have played a major role in tsetse and trypanosomiasis control. However, owing to the serious economic problems and the disastrous environmental impacts, there is now an apparent reluctance to accept and expand their use. Perhaps they may be used for emergency action to break disease transmission as in Busoga, Uganda, but their continued use on a wide scale may even make the problem more difficult.

Insecticides used in pest control may have detrimental effects on other non-target organisms. Such non-target organisms usually include the natural enemies of the pest that help to regulate the pest population. This problem is particularly serious with tsetse control because unlike the agricultural pests that are seasonal and spread over small areas, tsetse infestations occur throughout the year and over large areas. Hence the natural enemies of tsetse flies

surviving outside the sprayed area may take a long time not only to re-invade again, but also to exert any appreciable amount of population regulation. Rogers and Randolph (1984) recognised that due to the absence of these normal density dependent constraints, tsetse may show unexpected demographic vigour. The case of Lambwe Valley is a classic example where Opiyo et al. (1988) for example reported that ants were affected after two sprays of natural pyrethroid. This may have been responsible for the rapid resurgence of the tsetse population to levels higher than the previous ones.

With this in mind, non-pesticidal methods are receiving increased priority and with emphasis on alternative more appropriate and less polluting methods of control. Trapping-out or the use of targets are thus favoured because they offer additional mortality without killing the natural enemies of the pest. Targets made of screens of cloth do not in themselves kill tsetse, but this is brought about by the insecticide with which they are impregnated. The amounts of insecticide used on targets is much lower than that used in sprays but some problems remain. There is a possibility that doses acquired by tsetse from the targets are sublethal. This may therefore promote the development of resistance to insecticides in tsetse.

Traps therefore emerge as the most convenient means of tsetse control. Caught tsetse die due to hunger or stress inside the traps cages. These traps also enhance the activity of the predators because the aggregation of tsetse around them also cause the predators to localize their food searching there. While birds concentrate their searches in bushes around

the trap. Asilidae poise at vantage points ready to attack tsetse circumnavigating the trap and ants climb up the trap to prey on those that land on it without entering.

Control of any pest species is adding more mortality to the already existing natural mortality. How relevant therefore is the knowledge of resting sites to the understanding of the ecology of, and the eventual control of G. pallidipes at Nguruman by removal trapping? The study of resting sites today is relevant in relation to the predator-prey interactions and hence evaluate the levels of predation of resting flies that represent the majority of the adult population. This study is the first, albeit preliminary attempt, to link the two together and to compare predation levels on different substrates and at different times.

Predation ofcourse may also play a part in determining the resting sites of tsetse flies and the circadian changes observed. However, the resting sites of tsetse flies seem to be primarily determined by climate, rather than predators. This is because harsh weather conditions in the day cause them to go lower and onto thick substrates where it is cooler. On these branches and woody substratates, their protection by cryptic colouration is especially important given the predation pressure by birds. Such harsh conditions are also adverse for these predators and because they require shade, they also move lower and continue their search for food. This will tend to increase tsetse-predator interactions.

How then does this predation of adult tsetse compare with overall mortality rates? Until the fundamental work of

Southon (1958), unfortunately no attempt had been made to consider mortality of adult tsetse quantitatively. The biggest problem was that of methodology. However, it was suggested that 30% of the total daily mortality of G. swynnertoni was due to predation by a spider of the genus Hersilia. The tethering technique undoubtedly overestimates the level of predation but even so, these results suggest that a subsstantial compcnent of adult mortality is caused by predation. What the technique does allow us to do is investigate the mode of action of adult predation, specifically whether it is density dependent.

Rogers (1974) found that ants are a major cause of density dependent pupal mortality, while invertebrate (ants and spiders) action on adult tsetse was density independent. In both his work and this, vertebrate predation stands out as the most important density dependent mortality factor affecting adult tsetse flies. Thus these regulatory factors supplement one another to maintain populations at their equilibrium levels. But are these predators prey-specific ?

It seems most likely that tsetse predators are polyphagus and only concentrate their search on the most readily available prey for food. The food preference of the different predator groups and the role of alternate prey (also called buffer species) was not investigated in this study. However, Buckner (1966) considered that if they are preferred to the pest species, their abundance can cause a reduction in predation and thus reduce the effectiveness on their impact of the pest.

At Nguruman during the dry season there are relatively few other insects around. Musca domestica is the closest relative of tsetse flies there but it is only abundant in the rainy seasons. Tsetse, being depedent on vertebrate hosts are present all year round. Thus in the dry season some predators occupying the same biotope as tsetse in Nguruman may be relatively tsetse specific.

An adequate study of predation needs much more data than covered here which should be collected in the same localities for several years and under widespread ecological conditions. Results given here can only form a background to such a study, but nevertheless indicate a level of mortality sufficient to be adequately contributing to the natural population regulation. Hence this must be borne in mind in any strategies adopted for control. Widespread application of insecticide may clearly be counterproductive leading to rapid resurgence of tsetse populations to above pre-control levels. Traps and targets would on this basis offer the best prospects for future control. But even here, studies should be carried out to quantify any mortality caused to tsetse natural enemies.

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Appendix 1 Total, vertebrate and invertebrate predation levels at locations 1, 2 and 3 on leaves, branches and tree trunks in the day and night times($\bar{x}$ ± SE)

		Day time	Night time
Location 1	Total	45.70±5.58	40.57±4.33
	Vertebrate	34.40±5.52	7.64±1.86
	Invertebrate	13.33±2.65	36.40±4.00
Location 2	Total	65.56±5.25	50.71±9.48
	Vertebrate	57.94±5.05	12.95±5.61
	Invertebrate	9.68±3.60	40.61±6.20
Location 3	Total	51.17±8.38	46.30±5.25
	Vertebrate	44.43±9.86	7.50±4.24
	Invertebrate	14.87±5.84	39.62±5.46
Substrate			
Leaves	Total	45.38±6.45	43.04±5.75
	Vertebrate	29.60±5.84	1.84±1.27
	Invertebrate	18.55±4.78	41.78±5.45
Branches	Total	51.95±7.21	41.74±4.87
	Vertebrate	44.04±7.37	9.00±2.60
	Invertebrate	9.62±2.92	36.65±5.25
Trunks	Total	64.28±5.63	46.65±6.01
	Vertebrate	55.84±6.82	14.35±4.25
	Invertebrate	10.17±3.17	35.55±4.21

Appendix 2 Total percentage predation at day and at night in experiment 1

Densities	Experimental positions 1	2	3	4	5
a) Daytime					
2	90.00	90.00	90.00	90.00	90.00
4	90.00	45.00	90.00	90.00	90.00
8	90.00	90.00	90.00	69.30	90.00
16	90.00	90.00	90.00	75.52	90.00
32	90.00	90.00	90.00	75.52	79.82
b) Night time					
2	90.00	90.00	90.00	90.00	90.00
4	90.00	90.00	90.00	90.00	90.00
8	90.00	90.00	90.00	69.30	90.00
16	90.00	90.00	90.00	69.30	90.00
32	90.00	90.00	90.00	90.00	90.00

Appendix 2 Total percentage predation at day and at night in experiment 1

Densities	Experimental positions 1	2	3	4	5
a) Daytime					
2	90.00	90.00	90.00	90.00	90.00
4	90.00	45.00	90.00	90.00	90.00
8	90.00	90.00	90.00	69.30	90.00
16	90.00	90.00	90.00	75.52	90.00
32	90.00	90.00	90.00	75.52	79.82
b) Night time					
2	90.00	90.00	90.00	90.00	90.00
4	90.00	90.00	90.00	90.00	90.00
8	90.00	90.00	90.00	69.30	90.00
16	90.00	90.00	90.00	69.30	90.00
32	90.00	90.00	90.00	90.00	90.00

Appendix 3 Day and night vertebrate percentage predation in experiment 1.

Densities	Experimental positions 1	2	3	4	5
a) Daytime					
2	90.00	45.00	90.00	45.00	90.00
4	90.00	45.00	90.00	60.00	90.00
8	90.00	90.00	90.00	52.24	90.00
16	90.00	90.00	75.52	64.34	75.52
32	79.82	79.82	90.00	62.11	79.82
b) Night time					
2	0.00	90.00	90.00	0.00	90.00
4	60.00	90.00	90.00	90.00	90.00
8	69.30	60.00	90.00	45.00	90.00
16	56.01	48.59	90.00	37.76	41.41
32	56.01	66.72	66.72	50.40	60.00

Appendix 4 Invertebrate predation (%) levels in experiment 1

Densities	Experimental positions 1	2	3	4	5
a) Daytime					
2	0.00	45.00	0.00	45.00	0.00
4	0.00	0.00	0.00	30.00	0.00
8	0.00	0.00	0.00	30.00	0.00
16	0.00	0.00	14.48	20.70	14.48
32	10.18	10.18	0.00	23.28	0.00
b) Night time					
2	90.00	0.00	0.00	90.00	0.00
4	30.00	0.00	0.00	0.00	0.00
8	20.70	30.00	0.00	37.76	0.00
16	33.99	41.41	0.00	45.00	48.59
32	33.99	23.28	23.28	39.60	30.00

Appendix 4 Invertebrate predation (%) levels in experiment 1

Densities	Experimental positions 1	2	3	4	5
a) Daytime					
2	0.00	45.00	0.00	45.00	0.00
4	0.00	0.00	0.00	30.00	0.00
8	0.00	0.00	0.00	30.00	0.00
16	0.00	0.00	14.48	20.70	14.48
32	10.18	10.18	0.00	23.28	0.00
b) Night time					
2	90.00	0.00	0.00	90.00	0.00
4	30.00	0.00	0.00	0.00	0.00
8	20.70	30.00	0.00	37.76	0.00
16	33.99	41.41	0.00	45.00	48.59
32	33.99	23.28	23.28	39.60	30.00

Appendix 5 Total percentage predation in experiment 2

Densities	Experimental positions 1	2	3	4	5
a) Daytime					
2	90.00	00.00	90.00	00.00	90.00
4	90.00	90.00	90.00	90.00	90.00
8	90.00	90.00	90.00	30.00	90.00
16	75.52	90.00	90.00	90.00	75.52
32	72.17	50.40	90.00	90.00	90.00
b) Night time					
2	0.00	90.00	0.00	90.00	45.00
4	30.00	90.00	90.00	45.00	60.00
8	52.24	45.00	37.76	60.00	45.00
16	20.70	64.34	30.00	69.30	45.00
32	35.90	23.28	25.66	45.00	37.76

Appendix 6 Vertebrate predation (%) at the five positions at day and night times.

Densities	Experimental positions 1	2	3	4	5
a) Daytime					
2	90.00	0.00	90.00	0.00	90.00
4	90.00	90.00	90.00	90.00	90.00
8	60.00	69.30	90.00	30.00	90.00
16	75.52	75.52	90.00	90.00	64.34
32	69.30	48.59	90.00	90.00	90.00
b) Night time					
2	0.00	0.00	0.00	0.00	0.00
4	0.00	0.00	0.00	30.00	0.00
8	30.00	0.00	0.00	37.76	20.70
16	20.70	14.48	14.48	14.48	0.00
32	25.66	0.00	14.48	10.18	14.48

Appendix 7 Invertebrate predation (%) levels in experiment 2

Densities	Experimental positions 1	2	3	4	5
a) Daytime					
2	0.00	0.00	0.00	0.00	0.00
4	0.00	0.00	0.00	0.00	0.00
8	30.00	20.70	0.00	0.00	0.00
16	0.00	14.48	0.00	0.00	20.70
32	10.18	10.18	0.00	0.00	0.00
b) Night time					
2	0.00	90.00	0.00	90.00	45.00
4	30.00	90.00	90.00	30.00	60.00
8	37.76	45.00	37.76	37.76	37.76
16	0.00	60.00	25.66	64.34	45.00
32	23.28	23.28	20.70	43.21	33.99

Appendix 8 Total predation levels (%) for experiment 3 at day and Night.

Densities	Experimental positions 1	2	3	4	5
a) Daytime					
2	0.00	90.00	90.00	0.00	90.00
4	0.00	0.00	0.00	0.00	30.00
8	30.00	69.30	20.71	0.00	90.00
16	75.52	75.52	30.00	14.48	41.41
32	75.52	90.00	0.00	0.00	66.72
b) Night time					
2	45.00	0.00	45.00	0.00	0.00
4	45.00	30.00	0.00	45.00	30.00
8	69.30	60.00	0.00	20.71	45.00
16	48.59	48.59	41.41	56.01	37.76
32	52.24	14.48	23.28	33.99	37.76

Appendix 9 Vertebrate predation (%) levels for experiment 3

Densities	Experimental positions 1	2	3	4	5
a) Daytime					
2	0.00	90.00	90.00	0.00	90.00
4	0.00	0.00	0.00	0.00	30.00
8	30.00	69.30	0.00	0.00	90.00
16	69.30	75.52	30.00	0.00	41.41
32	75.52	90.00	0.00	0.00	66.72
b) Night time					
2	0.00	0.00	0.00	0.00	0.00
4	30.00	0.00	0.00	0.00	0.00
8	52.24	45.00	0.00	0.00	0.00
16	14.48	33.99	41.41	0.00	33.99
32	37.76	14.48	0.00	23.28	37.76

Appendix 10 Invertebrate predation levels (%) in experiment 3

Densities	Experimental positions 1	2	3	4	5
a) Daytime					
2	0.00	0.00	0.00	0.00	0.00
4	0.00	0.00	0.00	0.00	0.00
8	0.00	0.00	20.71	0.00	0.00
16	14.48	0.00	0.00	14.48	0.00
32	0.00	0.00	0.00	0.00	0.00
b) Night time					
2	45.00	0.00	45.00	0.00	0.00
4	30.00	30.00	0.00	45.00	30.00
8	30.00	30.00	0.00	20.71	45.00
16	45.00	30.00	0.00	56.01	14.48
32	25.66	0.00	23.28	23.28	0.00