MOVEMENT AND DISTRIBUTION OF TSETSE FLIES IN NGURUMAN, SOUTH-WESTERN KENYA

BY

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The nature of the fight against trypanosomiasis requires organisation, luck and speed:

> "To those who have participated in
> the Danse Macabre with trypanosomiasis,
> or will do so in the future: good luck,
> good will and Godspeed."
>
> Lorne E. Stephen (1986)

DECLARATION

I, the undersigned declare that this thesis is my own original work which has not been submitted for any degree in any university and all sources of material and help have been duly acknowledged.

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APPROVAL CERTIFICATE

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DEDICATION

To the memory of

Peter Kapelwa Siziya

father

who first introduced me to numbers

ACKNOWLEDGEMENTS

When the decision was made that I undertake Ph.D. studies in entomology, I knew that I was going to face many problems during the compulsory course work due to lack of a strong biological foundation. Dr M.E. Smalley, former academic coordinator of the African Regional Postgraduate Programme in Insect Science (ARPPIS), and Prof A.A. Siwela, Deputy Vice-Chancellor of the University of Zambia (UNZA), are due for special thanks for their encouragement.

Data collection was painful, but the assistance of the Nguruman team under the direction of Dr R.D. Dransfield made work a lot more bearable during the period of the study. I also thank the Permanent Secretary/Secretary to the Cabinet, Office of the President, Department of Defence for granting me permission to purchase East Africa 1:50,000 (Kenya) maps reference GM/A/24/XIX/31 dated June 14, 1990: without which it would have been impossible to produce tsetse distribution maps.

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part in watching over deadly game animals and for undertaking long walks on cage collections, at times when the temperature was 41°C, at other times in the pouring rain.

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Last, but not least, sincere thanks are due to the Research and Higher Degrees Committee of the University of Zambia for approving this project.

LIST OF ABBREVIATIONS

Periodicals		Page*
Amer. Sci.	American Scientist	339
Ann. Rev. Entomol.	Annual Review of Entomology	322
Ann. Soc. Belge Méd. trop.	Annales de la Société Belge de Médecine tropicale	326
Ann. trop. Med. Parasit.	Annals of Tropical Medicine and Parasitology	326
Austr. J. Zool.	Australian Journal of Zoology	322
Bull. ent. Res.	Bulletin of Entomological Research	318
Bull. Wld. Hlth. Org.	Bulletin of the World Health Organisation	316

* page number on which first used

Cah. ORSTOM, Sér. Ent. méd. Parasitol.	Cahiers ORSTOM, Série Entomologie médicale et Parasitologie	318
Ecol. Entomol.	Ecological Entomology	331
Entomol. exp. applic.	Entomologia experimentalis et applicata	326
Insect Sci. Applic.	Insect Science and its Application	322
Int. J. appl. Radiat. Isotopes	International Journal of Applied Radiation and Isotopes	331
J. Anim. Ecol.	Journal of Animal Ecology	329
J. appl. Ecol.	Journal of Applied Ecology	327
J. Econ. Entomol.	Journal of Economic Entomology	347
J. Entomol.	Journal of Entomology	319
J. Insect Physiol.	Journal of Insect Physiology	319

J. med. Entomol.	Journal of Medical Entomology	328
J. trop. Med. Hyg.	Journal of Tropical Medicine and Hygiene	337
Med. vet. Entomol.	Medical and Veterinary Entomology	319
Parasitol. Today	Parasitology Today	332
Parasitol.	Parasitology	338
Phil. Trans. R. Soc.	Philosophical Transactions of the Royal Society	320
Physiol. Entomol.	Physiological Entomology	318
Proc. R. ent. Soc. Lond.	Proceedings of the Royal Entomological Society of London	318
Proc. Zool. soc. Lond.	Proceedings of the Zoological Society of London	334
Res. Popul. Ecol.	Research on Population Ecology	347

Revue Élev. Méd. vét. Pays trop.	Revue d'Élevage et de Médicine vétérinaire des Pays tropicaux	323
Trans. R. ent. Soc. Lond.	Transactions of the Royal Entomological Society of London	320
Trans. R. Soc. trop. Med. Hyg.	Transactions of the Royal Society of Tropical Medicine and Hygiene	325
Trop. anim. Hlth. Prod.	Tropical Animal Health and Production	355
Trop. Dis. Bull.	Tropical Diseases Bulletin	342
Trop. Pest Manage.	Tropical Pest Management	319
Z. angew. Entomol.	Zeitschrift für Angewandte Entomologie	330

Marks

DBA	Double Blue Across	359
DBD	Double Blue Diagonal	163
DBR	Double Blue Right	359

DBRD	Double Blue Right Diagonal	359
DGA	Double Green Across	359
DGC	Double Green Centre	359
DGD	Double Green Diagonal	163
DGRD	Double Green Right Diagonal	359
DOA	Double Orange Across	359
DOD	Double Orange Diagonal	163
DOUA	Double Orange Upper Across	359
DPA	Double Pink Across	359
DPL	Double Pink Left	359
DPR	Double Pink Right	359
DRA	Double Red Across	359
DRD	Double Red Diagonal	163
DYRD	Double Yellow Right Diagonal	359

Organisations

DITH	Directorat Internationale Technische Hulpverlenig	38
FAO	Food and Agriculture Organisation of the United Nations	323
IAEA	International Atomic Energy Agency	323
ICIPE	International Centre of Insect Physiology and Ecology	vii
IDRC	International Development Research Centre	7

ISCTR(C)	International Scientific Council for Trypanosomiasis Research (and Control)	317
IRLCO-CA	International Red Locust Control Organisation for Central and Southern Africa	ix
KEMRI	Kenya Medical Research Institute	343
KETRI	Kenya Trypanosomiasis Research Institute	343
OCCGE	Organisation de Coopération et de Coordination pour la Lutte contre les Grandes Endémies	322
ORSTOM	Institut Francais de Recherche Scientifique pour le Développement en Coopération	318
TDRC	Tropical Diseases Research Centre	ix
UNZA	University of Zambia	vi

Month

Jan	January	25
Feb	February	25
Mar	March	25
Apr	April	25
Jun	June	25

Jul	July	25
Aug	August	25
Sep	September	25
Oct	October	25
Nov	November	25
Dec	Dcember	25

Statistics

CI	Confidence Interval	233
d.f.	degrees of freedom	116
LOG10	Logarithm to base 10	122
MS	Mean square	298
p	probability	119
r	correlation coefficient	194
s.e.	standard error	239
*	$p<0.05$	117
**	$p<0.01$	116
***	$p<0.001$	116

Units

cm	centimetre	95
h	hour	24
Hz	Hertz	64
m	metre	xxii

mg	milligramme	93
ml	millilitre	55
mm	millimetre	38
mmHg	millimetres of mercury	55

Other abbreviations

%	percentage	xxii
km	kilometre	xxi
km^2	kilometre squared	21
kw/m^2	kilowatt per metre squared	27
lx	lux	69
m/s	metre per second	27
mg/h	milligramme per hour	106
^oC	Degrees Centigrade	xxii
r.h.	relative humidity	27
Min.	minimum	26
Max.	maximum	26

ABSTRACT

The aim of the study was to obtain coordinated information on fly movement and distribution with a view to modelling the dispersal of tsetse flies and providing a sound basis for this aspect of tsetse fly control in Nguruman, south-western Kenya.

The following topics concerning tsetse flies are reviewed: importance of the flies; their systematics and identification; sampling in space and time, host preference; distribution, activity and dispersal of flies and models of these; and mark-release-recapture (MRR) studies.

MRR studies were conducted to study the dispersal rate and movement patterns of the flies. Biconical and Nguruman traps baited with cow urine, acetone and octenol were used to capture flies and to monitor their movement and relative densities. The Nguruman trap was also used in a series of experiments to determine its range of attraction. The flies were marked individually with artist's oil paint by placing two dots of the paint on the thorax. Climatic conditions were monitored using both the automated Delta-T weather station, and maximum and

minimum, and wet and dry bulb thermometers kept in a Stevenson screen.

There were two valleys, Sampu and Oloibortoto, running down the escarpment into the control zone, and one of the objectives of the work was to study the movement of flies between these two valleys.

The flies were concentrated along the Sampu valley. There was better predictability for G. pallidipes than for G. longipennis. All the main factors (Month, Day, Trap and Sex) were significant except for Sex for G. longipennis in both valleys. In the Oloibortoto valley, all the two-way interactions were significant except for Day*Sex for G. pallidipes, and Month*Sex, Day*Sex and Trap*Sex for G. longipennis. Meanwhile in the Sampu valley, the Day*Sex and Trap*Sex interactions were not significant for G. pallidipes nor was the Month*Day, Month*Sex and Trap*Sex interactions for G. longipennis. The G. pallidipes population was at its peak at the beginning of the long rains probably due to reinvasion of the flies from neighbouring uncontrolled areas; it decreased during the wet period probably due to increased pupal mortality because of flooding of the larviposition sites.

During the rainy season, there was more movement of female G. pallidipes into the Sampu valley from the Oloibortoto valley than the reverse, while no marked male was observed to have moved between the two valleys. Female G. pallidipes caught and released at the edge of the escarpment in the Sampu valley may have been moving at a rate of between 1.2 and 1.4 km per day, and dispersing about twice as far as males. Females caught and released in the Oloibortoto valley dispersed about 1.5 times further than those caught and released in the Sampu valley. The movement of the flies in a linear habitat along the Oloibortoto valley was not by random diffusion, but male G. pallidipes may have been moving at random in a relatively wider homogeneous habitat.

G. pallidipes preferred woodland vegetation to more open areas, while G. longipennis preferred more open environments to thickets. Tsetse flies spread out into the more open areas during the wet period when marginal vegetation refoliates. With a rise in the maximum temperature, G. pallidipes appeared to have moved from the edge of the woodland to the inner woodland, and a drop in maximum temperature resulted in the flies making the reverse journey. A threshold

temperature for female G. pallidipes above which it was active and below which it was inactive was 20.4°C. A temperature of 32°C (range 30-34°C) and a relative humidity of 32% (range 28-38%) appeared to be optimum for both sexes of G. pallidipes' activity. During the dry period, about 9 out of 1000 marked females but only 2 out of 1000 males crossed the barrier into the suppression zone. Significantly more females flew upwind than downwind. It appears that Nguruman traps baited with cow urine, acetone and octenol may provide an effective trap barrier for G. pallidipes and G. longipennis if the traps are spaced at about 25m apart.

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CHAPTER 1

GENERAL INTRODUCTION

The work covered in this thesis was carried out between March 1988 and March 1991 in Kenya. The first 8 months of this 3-year study period was spent on compulsory course work and developing a research proposal under the African Regional Postgraduate Programme in Insect Science at the International Centre of Insect Physiology and Ecology. Field work commenced in November 1988 with a training on mark-release-recapture experiments.

The study area is in the Rift Valley province of Kenya. It lies east of the Nguruman escarpment which runs down into woodland opening out into plains. Seasonal rivers run down the escarpment. The area north of the waterpipe line, hereafter called free or northern or uncontrolled zone, is the statistical control area; while the area in which flies are being continuously trapped, hereafter called suppression or controlled or southern zone, lies south of the waterpipe line.

The project was aimed at studying the reinvasion of tsetse flies into a suppression zone in Nguruman, south-western Kenya. It was originally planned that the study should cover two suspected sources of reinvasion: the top of the escarpment and the northern area. The track leading to the top of the escarpment was almost impassable and we succeeded in reaching the top of the escarpment on only three occasions. Therefore, observations on reinvasion of tsetse flies into the suppression zone are mainly those on fly movement from the northern zone.

Though detailed ecological studies were started for both Glossina pallidipes and G. longipennis with a view to modelling the movement and distribution of these two species at Nguruman, we have more confidence in the results for G. pallidipes than for G. longipennis, because catches of G. longipennis were generally very low. Partly the density of G. longipennis was low and partly the traps were inefficient for G. longipennis.

The automated Delta-T weather station was only installed in July 1989. Climatic data for the period January 1989 to June 1989 was taken from the wet and

dry, minimum and maximum thermometers and thermo-hydrograph kept in a Stevenson screen.

Data entry, analysis and report writing was done on an IBM compatible personal computer using Lotus 123, dBase III, StatGraphics, SAS, CRIES and Microsoft Word.

Should the reader wish to re-analyse the data, raw data of small data sets are presented in the appendix, and the rest of the data is available on request.

CHAPTER 2

INTRODUCTION

2.1 IMPORTANCE OF TSETSE FLIES

Trypanosomiasis, a wasting disease called human trypanosomiasis, or sleeping sickness in people, and animal trypanosomiasis, or nagana in livestock, is one of the major diseases of developing countries in Africa (Cunningham, 1979). Various species of trypanosomes transmitted by the various species of the tsetse fly play a major role in public health, in human settlement and in land development.

Only certain species of Glossina are vectors of Trypanosoma gambiense and Trypanosoma rhodesiense, the two species of trypanosomes that affect people (Challier, 1973b). Laveissière (1988) lists the following vectors of Trypanosoma gambiense: Glossina palpalis palpalis, G. p. gambiensis, Glossina fuscipes fuscipes, G. f. martini, G. f. quanzensis, Glossina tachinoides and Glossina caliginea; and those of Trypanosoma rhodesiense as being Glossina morsitans morsitans, G. m. submorsitans, G. m. centralis, Glossina pallidipes, Glossina swynnertoni, G. f. fuscipes, G. f. martini and G. f. quanzensis.

The three species of trypanosomes that affect livestock are Trypanosoma vivax, T. congolense and T. brucei. In the coastal region of Kenya (East Africa), T. congolense is transmitted primarily by G. austeni and near the shores of lake Victoria (Kenya) it is transmitted by G. pallidipes (Majiwa et al., 1989). It has been reported that G. m. morsitans transmits T. congolense (Roberts, 1981) and all three species of trypanosomes that affect livestock (Moloo, 1983) and that G. morsitans transmits T. b. rhodesiense (Girgrich et al., 1982) and T. brucei (Bailey, 1966).

A tsetse fly may become infected with trypanosomes when it feeds on a person or an animal already infected with trypanosomes. It has been observed that not all infected blood meals give rise to infection in tsetse (Fairbairn and Watson, 1955; Elce, 1971; Tarimo, Snow et al., 1985). Harmsen (1973) showed that there is a physical and chemical barrier in the gut of G. pallidipes which affects its capacity to become infected. He suggested that in the young fly, the peritrophic membrane is still too short to immediately contain all the ingested blood stored in the crop. As a result, the trypanosomes

remain in the crop for 1-3 hours undergoing the enzymatic transformation necessary to protect themselves from the hostile intestinal environment. He further suggested that, unlike in the young flies, the peritrophic membrane in the older flies can immediately contain the entire meal leading to the destruction of trypanosomes. These results indicate that only the young flies can become infected but Gingrich et al. (1982) have shown, although only in the laboratory, that older male G. morsitans (21-25 days old) starved for 3-4 days can become infected in the same proportions as the young males (8-12%). Once infected with trypanosomes, a tsetse fly generally remains infected for the rest of its life (which can, exceptionally, be for up to six months) and may in turn infect any animal on which it feeds (Cunningham, 1979). The number of trypanosomes injected into the host determines whether or not a host will become infected. It is estimated that between 300 and 500 trypanosomes are required to induce infection in man, and it is assumed that an infected tsetse fly does not always inject this necessary "dose" at each meal (Laveissière, 1988).

Until recently, it was believed that the only mode of transmission of trypanosomes was so-called

"cyclical transmission". Gingrich et al. (1983), however, have shown that G. morsitans can transmit T. b. rhodesiense mechanically. In their laboratory experiment, nearly 51% of the flies fed intermittently on infected mice transmitted trypanosomes to other mice. The results of this work confirms earlier speculations on mechanical transmission of sleeping sickness by the tsetse fly (Bruce et al., 1910) and Bailey's (1966) finding that T. brucei can be transmitted mechanically by G. morsitans. The importance of mechanical transmission in the epidemiology of nagana should not be overlooked (Wells, 1972).

Trypanosomiasis has had a tremendous impact on the economic and social development of Africa. About 40% of the tropical Africa is infected by the tsetse, Glossina (Rogers et al., 1985). The affected area lies between approximately latitude 15°N and 20°S, but extending to about 30°S along the eastern coastal area of Africa (Service, 1980), covering an area of about 11 million square kilometres in total (Cunningham, 1979). Earlier on, IDRC (1974) had estimated the area occupied by tsetse species to be about 10 million square kilometers in tropical Africa, representing one-third of the continent and

one-half of its inhabited area. To put it in another way in 1986, about 35 million people and 25 million domestic animals were at risk from trypanosomiasis in Africa (WHO, 1986). At the present time 50 million people are at risk from African sleeping sickness (Laitman, 1990).

Human trypanosomiasis can be fatal and causes much ill health (Kershaw, 1970). Mc Kelvey (1973) discusses the symptoms of the disease. In its early stages the symptoms are malaise, insomnia, drowsiness, headache, muscular cramps, neurological pains and swollen glands, and these symptoms, coupled with others occurring in the right progression, indicate sleeping sickness as a disease and death to the victim. As the disease progresses, fear develops, the pulse rate increases accompanied by rigor, severe sweating, drowsiness and insomnia, and at this stage of the disease malnutrition develops. Patients eventually do not take food unless aroused. In the final stages of the disease, patients grow irritable, emotional and depressed; their memory fades until they finally become comatose and die.

Human trypanosomiasis does not occur throughout the so-called "tsetse-belt" of Africa but is

restricted to isolated areas where it has, nevertheless, been the cause of millions of deaths. Human trypanosomiasis is endemic in Africa. In recent years, about 10,000 new cases have been detected annually (Service, 1986). Currently, about 25,000 people are reported to be suffering from the African sleeping sickness (Laitman, 1990). A total of 87,062 cases were reported between 1976 and 1983 but this figure is an underestimate due to lack of comprehensive case-finding (Laveissière, 1988). Severe epidemics of the disease have occurred in the past and between 1902 and 1905 some 200,000 people died of the disease in the Busoga province of Uganda alone (Cunningham, 1979).

In economic terms, nagana is a much more important disease than human trypanosomiasis. Cattle are economically the most important hosts affected by trypanosomiasis. Stephen (1986) states that among the three species of Trypanosoma: T. vivax, T. congolense and T. brucei affecting cattle in eastern and some central areas of Africa, T. vivax infections in cattle are the most common. He also reports that T. vivax infections are usually regarded as being relatively mild in nature compared with those due to T. congolense, and that cattle in all regions of

tropical Africa exhibit a high degree of resistance to T. brucei. He goes on to list clinical manifestations of T. vivax as follows: In acute forms of the disease, the animal usually has reduced appetite, high body temperatures of about 40oC, increased respiratory rate, watery or even haemorrhagic diarrhoea which result in weight loss in the early stages of the infection. In less severe cases, the animal has swollen and prominent superficial lymph nodes, nasal and lacrimal discharge, oedema and ocular lesions. He also states that abortions and still-births may be seen in pregnant cows and milk production is depressed. Stephen (1986) also lists clinical manifestations of T. congolense infections which are very similar to those of T. vivax but develop more slowly and less dramatically. When infected by T. congolense, the appetite is usually good except during periods of pyrexia when the animal appears dull, inactive and depressed, but as the disease progresses, the infections become more marked and severe anaemia sets in. Death may occur in a few weeks but usually takes several months to a year.

Nagana kills large numbers of cattle but, perhaps more importantly, it severely constrains

rural development, excluding livestock, especially cattle, from large areas of Africa (Griffiths, 1986; Willett, 1970; Nash, 1969; 1960; Buxton, 1955; Hornby, 1952) thus contributing to the widespread malnutrition in Africa (Kershaw, 1970). Nagana is a zoonosis (game animals serve as reservoir of infection) and tsetse flies may acquire their infections when feeding on game animals and then pass the infections on to domestic animals, and in certain cases to people as well (Cunningham, 1979).

Tsetse flies still thrive, although they have been the target of one of the broadest and most intensive eradication campaigns in history. Despite many years of intensive more or less continuous research during most of this century, the problem of effective control, let alone eradication of tsetse flies as vectors of trypanosomiasis, has not been resolved (World Bank, 1986) and the distribution of tsetse flies in Africa has not changed significantly in the last 30 years (Rogers et al., 1985). A significant factor in the failure of efforts to control the fly has been the lack of knowledge of the environmental factors affecting the fly density and in particular the low level of understanding of fly movement which determines the flies' ability to re-

invade areas within which control has been attempted. Lack of appropriate and cost effective technology had also contributed to the failure to control the fly density. In the past people have tried to eradicate tsetse flies by means of aerial spraying and bush clearing but this has failed. More recently, efforts have been directed towards the control of the tsetse flies by use of traps and targets. This has revolutionized the way of thinking about the technology, relevant biology, sociology and economics concerning the tsetse flies.

2.2 IMPORTANCE OF MODELS

Models have been used to study complex biological systems. All models, whether verbal, diagrammatic or mathematical are abstractions of the real world (Wiegert, 1979) and hence will never contain all the features of the real system, because, then it would be as complicated as the real system itself (Jorgensen, 1988). But it is important that the model contains the main features that are essential to the problem being tackled.

General reviews and extensive literature describing population models are found in Pielou (1969), May (1973) and Maynard-Smith (1974). Models have been characterized according to their degree of generality, realism and accuracy (Southwood, 1978). Levin (1966) characterized models as: (1) those that sacrificed generality for the advantages of reality and precision, (2) those that emphasized generality and reality but sacrificed precision, and (3) those that were unrealistic but very general and precise. According to Royama (1971), classical models of population dynamics developed before 1935 all share the quality of generality coupled with precision. In all these models, a single variable represents population size; and its relationship with the rate

of growth of the population and the environmental carrying capacity are expressed in terms of differential equations (Wiegert, 1979).

Berryman and Rogers (1986) argue that the optimal model lies between two extreme types of models (high-resolution and low-resolution). High-resolution models mimic real life situations and are thus very detailed, while low-resolution models are simple and do not depend on precise details. Whatever approach is finally adopted, the following features are desirable: (1) realism or ability to mimic real life situations (detailed models are generally more realistic), (2) transparency or the ability for the user to see and understand what is going on (simple models are more transparent), (3) tractability or easy of solution (simple models are usually easier to solve), and (4) precision or accuracy. The fourth feature depends on the degree of knowledge and skill of the modeler; detailed models often being more precise when a skillful modeler has a high level of knowledge. Otherwise, when data and knowledge are incomplete simple models are usually more precise (Berryman and Rogers, 1986).

Wiegert (1979) categorised models as those that are deterministic and those that are stochastic. He pointed out that deterministic models have certain advantages of simplicity but assume large population sizes to reduce the effects of variability in the bahaviour of individuals. On the other hand Maynard-Smith (1974) pointed out that stochastic models make the more plausible assumption that in a short time interval an individual will produce one offspring with a certain probability. The use of deterministic rather than stochastic models can only be justified by mathematical convenience and the underlying biology (Maynard-Smith, 1974), but at the end of the day, only the biology matters.

In the process of creating models, data are organized in an efficient and logical manner revealing gaps in the data on which future research can be concentrated (Berryman and Rogers, 1986). Thus, good models should reveal the weak links in our knowledge and can be used to identify research priorities. In particular, work with mathematical models has exposed many deficiencies in present ecological knowledge and subsequent empirical work to fill these gaps has led to more refined theories (Watt, 1962). Models permit prediction of outbreaks

of diseases so that efficient ways of reducing populations of harmful organisms can be designed and the productivity of tropical agriculture systems can be increased (Williams, 1988). Model creation should enable us to develop our intuition and increase our understanding of the ecosystem.

CHAPTER 3

STATEMENT OF THE PROBLEM AND OBJECTIVES

3.1 STATEMENT OF THE PROBLEM

Two of the thirty species and subspecies of Glossina, G. pallidipes and G. longipennis are found at Nguruman. Tarimo, Golder et al. (1985), working at the Nguruman escarpment on a Maasai group ranch, have reported that Trypanosoma congolense infection rates are much lower than those of T. vivax in G. pallidipes and that overall trypanosomiasis infection rates were 4.6% in G. pallidipes and 1.6% in G. longipennis. Both T. vivax and T. congolense infect livestock owned by the Maasai farmers (Ochieng and Gray, 1989; Stevenson et al., 1989), and about 30% of the cattle have trypanosomes in their blood (Tarimo et al., 1985). Otieno and Dransfield (1990) have recently reported that in the dry season, when animals are moved from the open plains to the woodland, trypanosome infection rates in the Maasai cattle reach 50%. In order to find ways to reduce this enormous trypanosomiasis challenge to Maasai pastoralist cattle, a multi-displinary project commenced in early 1983.

Monitoring of tsetse flies (G. longipennis and G. pallidipes) was started in May 1983. In February 1987 a suppression programme was started, and by October of that year the fly population had been reduced to about 1% of its precontrol level. In November 1987 and subsequently, large invasions of the fly were observed in the study area with numbers increasing by as much as 10 times in one week. This could not have been due to fly reproduction as increases were 6 times the possible reproduction rate and it must have been related to fly movement. The question pertaining to my study was to find out whether fluctuations in tsetse fly density at Nguruman result from fly movement between the suppression and free zones. Thus, for the control project at Nguruman to be effective, a clear understanding of fly movement and distribution is vital. In addition, Nguruman has five distinct types of vegetation communities (these are open flood plains, Acacia woodland, riverine thicket, low-land woodland, wooded bushland and dense valley woodland) and this provides a rare opportunity to study the movement of flies in relation to vegetation types.

3.2 OBJECTIVES

The aim of the study was to obtain coordinated information on fly movement and distribution with a view to modelling the dispersal of tsetse flies and providing a sound basis for this aspect of tsetse fly control.

The following objectives were set out for the project:

1. To identify those climatic factors that are associated with the distribution and movement of *G. pallidipes* and *G. longipennis*, the two *Glossina* species present in Nguruman.

2. To determine the distribution of *G. pallidipes* and *G. longipennis* in Nguruman.

3. To determine activity patterns of *G. pallidipes* and *G. longipennis* in the study area.

4. To establish the pattern of fly movement between suppression and free zones.

5. To apply predictive (computer) models to the movement, distribution and activity of the fly.

6. To evaluate the potential for the use of such models in the control of tsetse flies.

CHAPTER 4

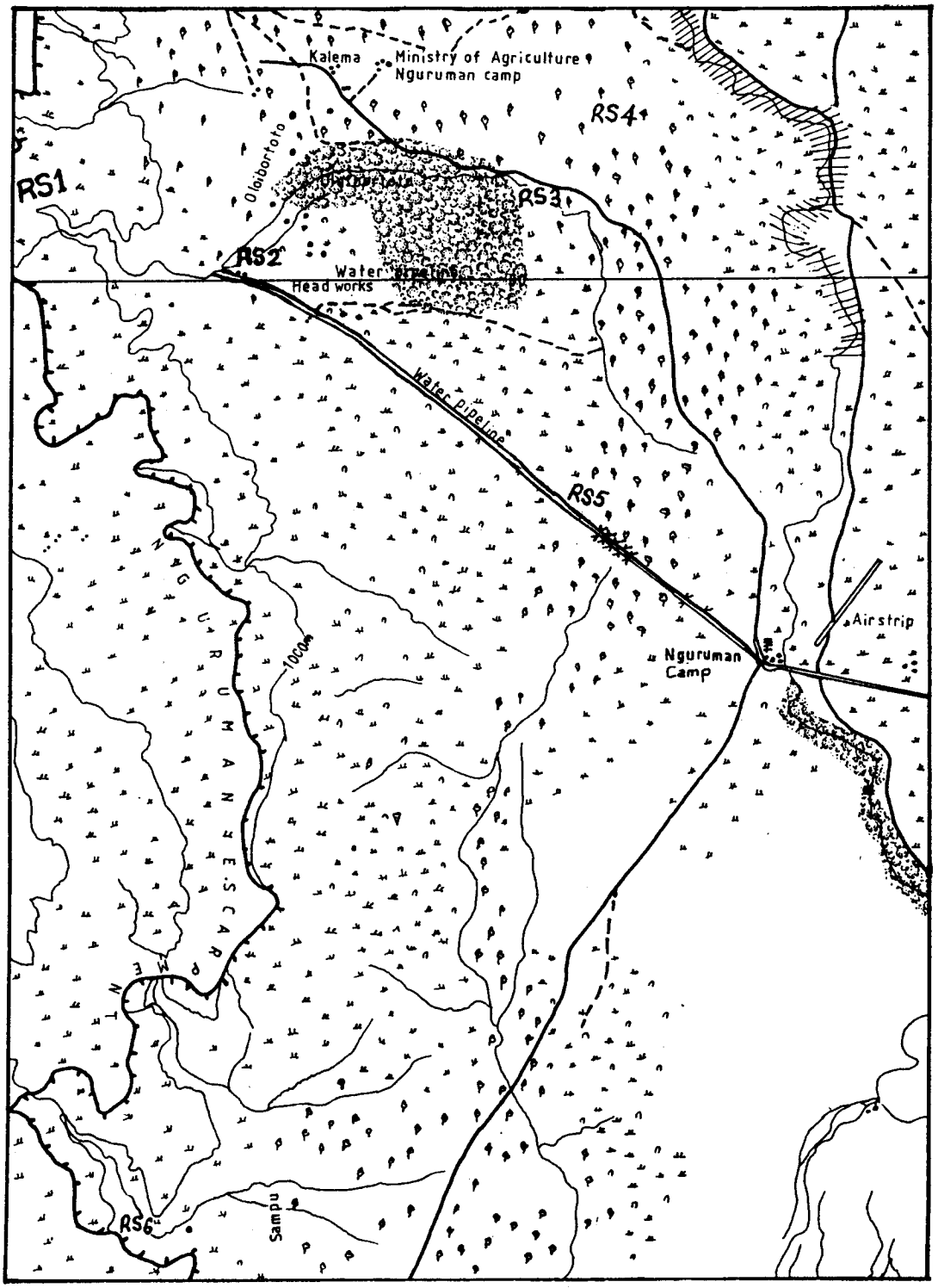
STUDY AREA

4.1 INTRODUCTION

The Nguruman study area (Figure 4.1) which covers about 260 km^2 has great potential for livestock development for the Maasai inhabitants of the Olkeramatian group ranch who maintain over 6000 zebu cattle (Otieno *et al.*, 1990; Dransfield *et al.*, 1990). In order to realize this potential, the ICIPE Tsetse Research Programme has been working in the area since 1983 in order to reclaim the land infested by tsetse flies. Of the two species *G. pallidipes* and *G. longipennis*, *G. pallidipes* is the major vector contributing to trypanosomiasis at Nguruman (Tarimo *et al.*, 1985). The *Trypanosome* species transmitted by the tsetse flies present at Nguruman are *T. vivax* and *T. congolense* (Ochieng and Gray, 1989; Stevenson *et al.*, 1989; Tarimo *et al.*, 1985). Only few instances of occurrence of *T. b. brucei* have been observed, but no human sleeping sickness has ever been observed in the area (Adabie, 1987).

FIGURE 4.1

General map of the study area



4.2 GEOGRAPHY

The study area is located at the foot of the Nguruman escarpment in south-western Kenya, lying between latitudes 36° 00′ and 36° 07′ East and between longitudes 1° 45′ and 1° 56′ South. The study area can be divided into four regions. The first region is the Olkeramatian plain which lies at an altitude between 650m and 680m above sea level to the east of the Ewaso-Ngiro river. The second region lies up against the base of the escarpment to the west of the Ewaso-Ngiro river. It is watered seasonally by the Oloibortoto and Sampu rivers. The third region is at the top of the escarpment at an altitude between 1100m and 1500m above sea level. Finally, further back from the edge of the escarpment are the Olosha hills rising to 2524m which must be well below the low temperature survival limit for tsetse flies.

4.3 CLIMATE

Nguruman is in the semi-arid zone, with a mean annual rainfall of between 255 and 510 mm (National Atlas of Kenya, 1970) and a marked seasonal variation. The two rainy seasons are from March to May and from October to December, with maximum precipitation in April and November.

During the study period from July 1989 to June 1990, an unusually high total rainfall of about 843 mm of rain was recorded. Maximum precipitation occurred in March when 232 mm fell during the main rains and in December when 143 mm fell during the short rains. A small amount of rain was also recorded in each of the "dry" months except June. Distribution of the rainfall for the year beginning July 1989 is shown in Figure 4.2a.

Annual mean maximum and minimum temperatures vary from 30° to 34° and 18° to 22°C, respectively (National Atlas of Kenya, 1970). During the period of this study, maximum temperatures ranged from about 31°C in July to about 35°C in October and February, while minimum temperatures ranged from about 17°C in July to about 21°C in February, October and December. Average monthly maximum, minimum and mean temperatures during the study period were about 33°, 20° and 26°C, respectively. Temperature readings taken at 8:00 and 15:00h averaged 23° and 33°C per month, respectively. Figure 4.2b shows temperature profiles for the year beginning July 1989.

FIGURE 4.2a

Total monthly rainfall for Nguruman from July 1989 to June 1990

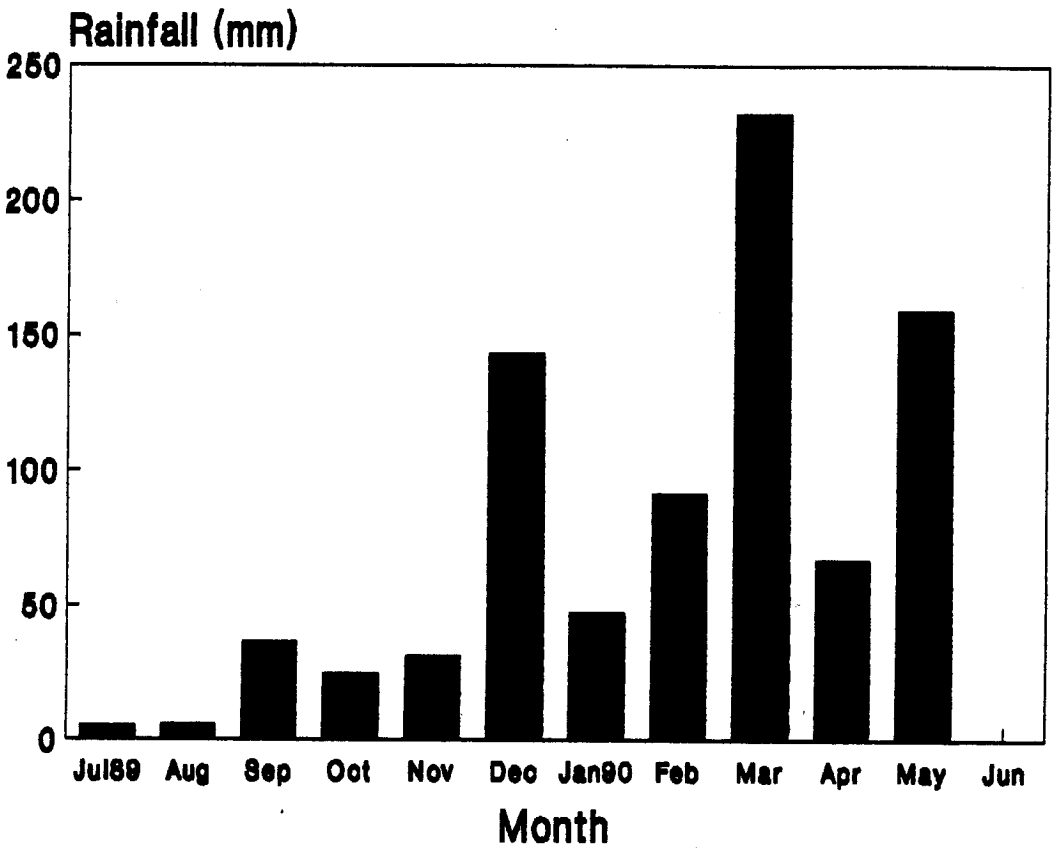
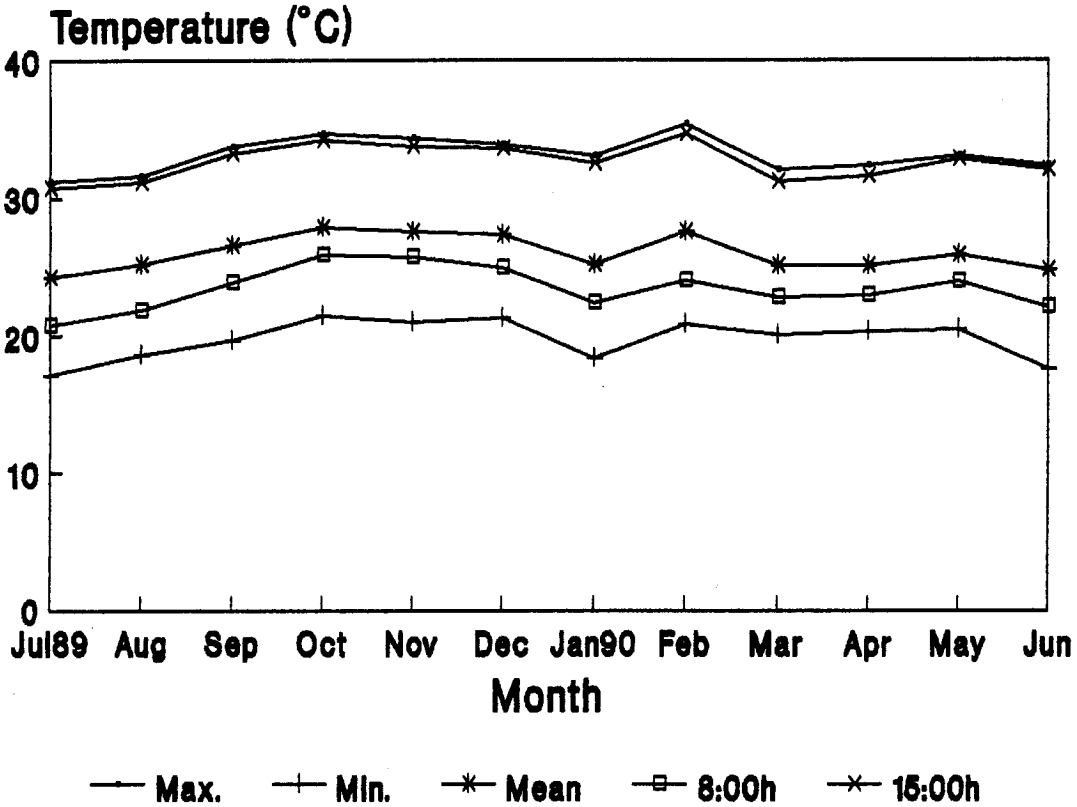


FIGURE 4.2b

Mean monthly temperature for Nguruman from July 1989 to June 1990



Mean monthly wind speeds during the study period were less than 1 m/s. They peaked between October and December at about 0.9 m/s (Figure 4.2c). Maximum wind speeds were rarely more than 2 m/s throughout the study period.

Due to the non-functioning of the solar radiation sensor at the beginning of the study, readings from this sensor are not available for the period July to October 1989. Mean monthly solar radiation for the period November 1989 to June 1990 averaged 0.284 kw/m^2 with the highest mean reading of about 0.317 kw/m^2 in January (Figure 4.2d). Maximum solar radiation never exceeded 1.3 kw/m^2.

The lowest relative humidity reading was observed in October, while the highest readings were recorded between March and May. Mean relative humidity increased from October to January, and decreased from April to October. Minimum and maximum ranges were 32% to 55% and 71% to 100% r.h., respectively. The minimum relative humidity readings were about the same as of those taken at 15.00h, while 8.00h readings were higher than average

FIGURE 4.2c

Mean monthly wind speed for Nguruman from July 1989 to June 1990

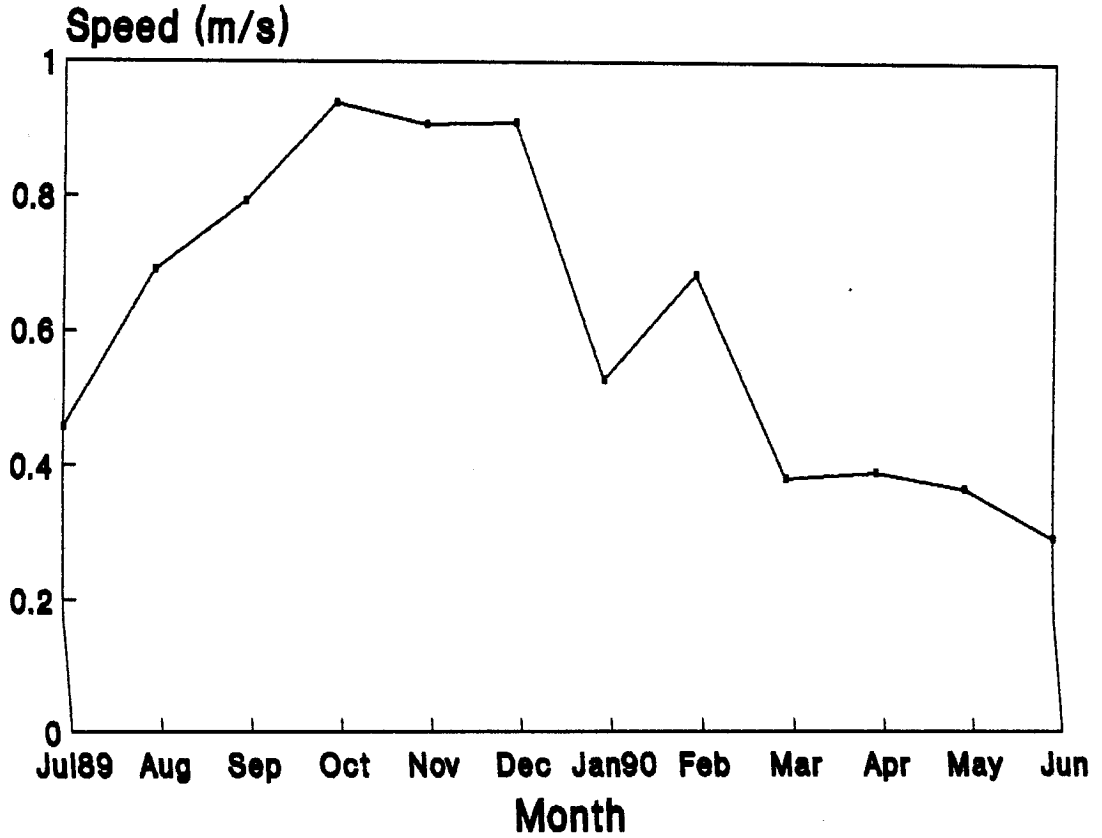
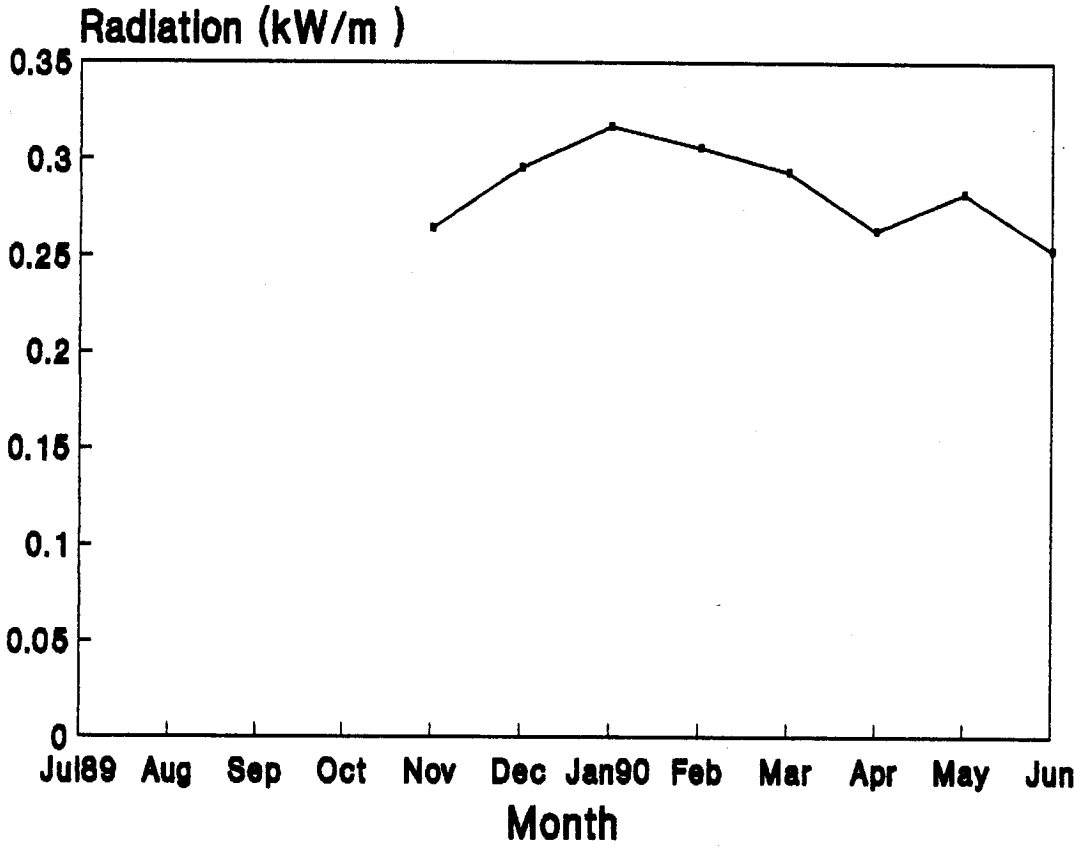


FIGURE 4.2d

Mean monthly solar radiation for Nguruman from July 1989 to June 1990



readings and lower than the maximum readings. Relative humidity profiles are shown in Figure 4.2e.

4.4 SOIL

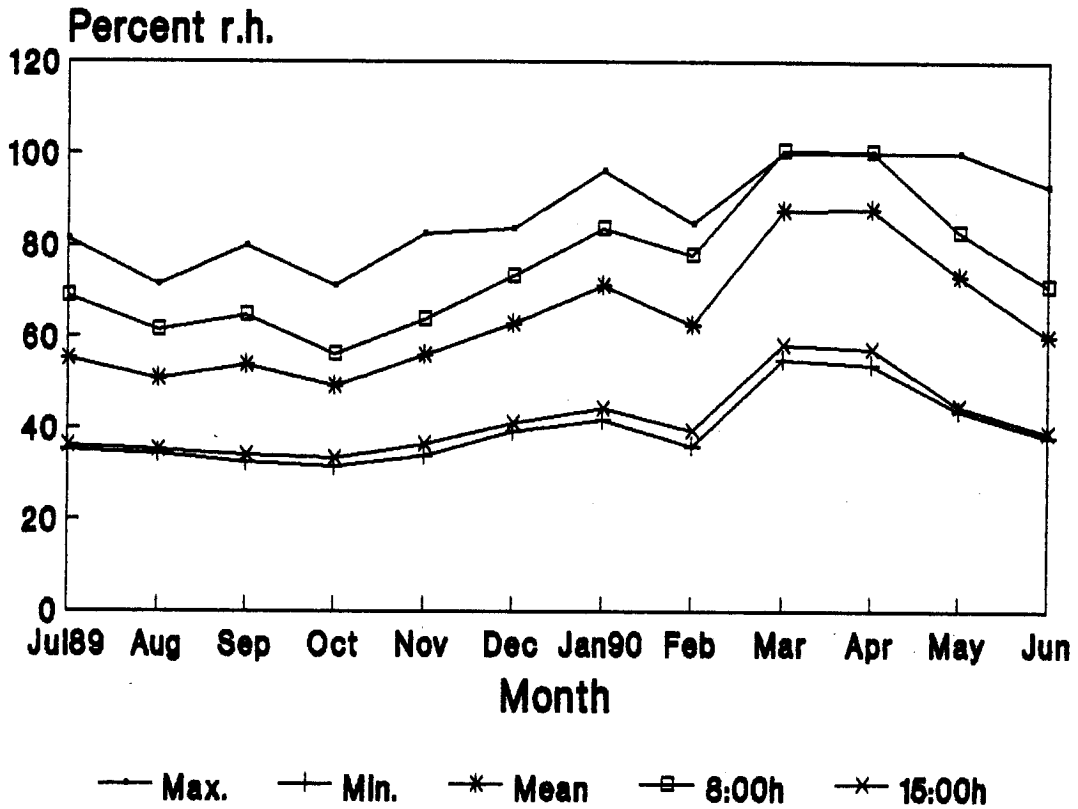
The soil of the Nguruman escarpment is derived from volcanic ash. It is pale brown to brown calcareous loam called chestnut soil (National Atlas of Kenya, 1970). The soil is very fine and in the dry season dust storms frequently occur.

4.5 POPULATION AND LAND USE

The land in the study area is classified as a County Council Trust land. It has a low and sparsely distributed population of 1 to 4 persons per square kilometre (National Atlas of Kenya, 1970). The area is populated by peoples of the Maasai tribal group who are Nilotic pastoralists. The Maasai live in small dispersed family settlements called manyattas. Other tribes found in the study area include: Luhya, Kikuyu, Kamba and a group of Tanzanian origin. The area is used basically as a grazing ground for the Maasai pastoralists who keep cows (Bos taurus), goats (Capra hircus), sheep (a member of Ovis, family Bovidae) and donkeys (Equus asinus). Cows are kept mainly for milk and goats for meat.

FIGURE 4-2e

Mean monthly relative humidity for Nguruman from July 1989 to June 1990



During the drought, the Maasai move from the plain lying east of the Ewaso-Ngiro river to the west of the Ewaso-Ngiro river in search of pasture for their animals. This is the time when domesticated animals, driven into the riverine thicket, are subjected to severe trypanosomiasis challenge. At the foot of the escarpment, in the Oloibortoto valley and the area adjacent to it, small scale farming is carried out. Cultivation of maize as well as fruit and vegetable gardening is done mostly by non-Maasai. Due to the availability of game in the study area, tour operators sometimes bring tourists for game watching but this does not benefit the local people directly.

4.6 VEGETATION

The vegetation of the area is described in detail by Sayad and Sayad (1980) and van Etten (1981) and include the following: (1) open flood plain characterized by isolated stands of Acacia seyel fistula and A. sieberana, (2) savannah woodland dominated by fairly dense stands of Acacia species, notably A. albida, A. s. fistula and A. tortilis, (3) riverine thicket low-land woodland dominated by Euphorbia candelabrum, A. pennata and Cassine

aethiopica with undergrowth of shrubs comprising mainly Santia myrtina, (4) wooded bushland consisting of acacias and rather scattered trees of many types growing among grasses, and (5) dense valley woodland which is dominated by trees, Ficus capensis, shrubs, Salvadora persica and Cordia sinensis, and grasses, Sporobolis consimulis, Setaria spacelata, Themeda triandra and Cynodon dactyolon. A short summary of the Nguruman vegetation types can be found in Dransfield et al. (1985).

4.7 WILD LIFE

Game is abundant in the study area. The most common being buffalo (Syncerus caffer), impala (Aepyceros melampus), Grant's gazelle (Gazella granti), giraffe (Giraffa camelopardis), wildebeest (Cannochaetes sp.), baboon (Papio anubis), zebra (Equus burchelli), warthog (Phacochoerus aethiopicus) and dikdik (Rhyncotragus kirkii). Generally, there is an increase of game during the rainy season due to an increasingly abundance of pasture.

The preference of G. pallidipes at Nguruman for different species of game is shown in Table 4.1. Although G. pallidipes feeds on bushpig, elephant and eland at Nguruman (Tarimo et al., 1985), none of them

TABLE 4.1

Occurrence of preferred hosts of *G. pallidipes* between February and April 1989.

Game	Frequency
eland, elephant, bushpig	-
bushbuck, rabbitidae, warthog waterbuck	+
buffalo, impala, wildbeest gazelle, giraffe	++

\- absent

\+ rare

++ common

were seen between February and April 1989. The most frequent game observed were buffalo, impala, and wildebeest.

CHAPTER 5

LITERATURE REVIEW

5.1 SYSTEMATICS

G. pallidipes described by Austen (1903) and *G. longipennis*, described by Corti (1895) are members of the class Insecta, order Diptera and recently placed in the family Glossinidae (Haeselbarth *et al.*, 1966; Davies, 1988). They used to be included in the family Muscidae (Newstead *et al.*, 1924; Imms, 1957). The family Glossinidae includes only one genus, *Glossina* (Ross *et al.*, 1982) which was founded by Wiedemann (1830).

A total of 30 species and subspecies of the genus, *Glossina* are recognized (Jordan, 1974; Laid, 1977) and are classified into three groups: the *fusca* group which has 10 species and 4 subspecies and includes *G. longipennis* Corti, the *palpalis* group which has 2 species and 7 subspecies, and the *morsitans* group which has 4 species and 3 subspecies and includes *G. pallidipes* Austen. This classification was proposed by Newstead (1911) and is based on the taxonomic characters of the genital armature.

5.2 IDENTIFICATION

The identification of species of tsetse flies, and determination of their age and sex is important because the species' age groups and sexes behave differently with respect to their movement and distribution.

Resting tsetse flies can easily be distinguished from other flies by the way their wings lie flat over one another down the back when closed, like the blades of a pair of scissors, while the proboscis projects horizontally in front of the head (Austen, 1911). The sexes of these flies can be easily distinguished by examining the lower end of the abdomen. In the males the external genitalia form a knob-like protuberance called the hypopygium, which is absent in the female (Austen, 1903).

Teneral flies can be distinguished from non-teneral flies by two methods proposed by Pollock (1982). The first method involves gently squeezing the thorax between the finger and the thumb. In the teneral fly the thorax feels soft, while in the non-teneral fly the thorax feels firmer. The other method involves pushing out the ptilinum. In the

teneral fly the ptilinum is easily pushed out when the sides of the head are squeezed, while in the non-teneral fly the ptilinum is not so easily pushed out.

G. pallidipes and G. longipennis can be easily distinguished from each other by their size and colour. G. longipennis measures about 11 mm, while G. pallidipes measures about 9 mm excluding the proboscis and wings (Austen, 1903; 1911). The upper surface of G. longipennis is pale yellow while the abdominal upper surface of G. pallidipes has interrupted brownish or blackish bands down the median line, on a yellowish to orange-coloured background (Nash, 1969).

5.3 SAMPLING IN SPACE AND TIME

Tsetse flies usually have an aggregated pattern of distribution among different vegetation types. An appropriate sampling technique would then be to cut transects through the different vegetation types and take samples at set distances along the transects (DITH, 1986).

Numerous methods of sampling adult tsetse populations have been used in the past. These include fly-rounds (Ford et al., 1959; Buxton, 1955;

Davies, 1967), bait-ox rounds (Vanderplank, 1944), tethered ox (Pilson and Pilson, 1967), motor vehicle patrols (Jack, 1939; 1941; Chapman, 1960), bicycle patrols with sticky screens (Glasgow, 1970; Lambrecht, 1973) and traps (Harris, 1930; Morris, 1949; Smith and Rennison, 1961a; Challier and Laveissière, 1973; Moloo, 1973; Langridge, 1977; Hargrove, 1977; Rogers and Smith, 1977). Of the above sampling devices, traps are nowadays widely used as research tools (Glasgow, 1970b).

Trap catches have been found to give good indications of changes in population sizes. Glasgow and Duffy (1961) have shown that trap catches provide a less biased sample than catches relying on human effort like fly-rounds, though they found both site effects and day to day variability to be large with traps, so that reproducible results were difficult to obtain. One way to reduce the site effect is to use odour attractants on the assumption that flies are then attracted from a greater distance. Several studies have shown that both natural and synthetic odours can be used to increase catch size of Glossina (Vale, 1980; Owaga, 1985; Vale et al., 1986; Dransfield, et al., 1986). In Nguruman, south-western Kenya, Dransfield et al. (1990) have shown

that Nguruman (NG2B) trap catches are linearly related to absolute population estimates with coefficient of determination of 96 and 80% for male and female G. pallidipes, respectively.

For details of early devices used to catch Glossina, one may consult Swynnerton (1936) and Buxton (1955). More information on comparisons of traps with other methods of catching G. pallidipes can be found in Smith and Rennison (1961a; b; c) and in Harley (1967).

5.4 HOST PREFERENCE

A number of authors have reported different feeding habits of the tsetse Glossina from different areas, at different times of the year, under varying climatic conditions and in the presence of variable host populations (see for example Weitz and Jackson, 1955; Weitz and Glasgow, 1956; Weitz et al., 1960; Jordan et al., 1961; 1962; Glover, 1967; Weitz, 1970; Allsopp et al., 1972; Moloo, 1980).

Feeding habits of tsetse flies have been found to be characteristic for each species. Here we review feeding habits for G. pallidipes and G. longipennis, the two tsetse species found in

Nguruman. Weitz (1963) made observations on the feeding habits of G. longipennis. Excluding all blood meals on man or his domestic animals, he observed from blood-meal analyses that in about 70 out of 100 meals G. longipennis fed on elephant, rhinoceros, hippopotamus and buffalo. Meanwhile, G. longipennis fed on bushpig in about 20 out of 100 meals.

Let us consider studies done in Kenya to illustrate varying feeding habits that have been reported for the G. pallidipes. Glover (1967) and Tarimo et al. (1984) working in the coastal part of Kenya reported that G. pallidipes feeds mainly on suids. Allsopp et al. (1972) working in the Labwe valley reported that G. pallidipes feeds mostly on the bushbuck and buffalo, and Tarimo, Snow et al. (1985) in Nguruman found that suids were the preferred hosts during the drought period from May to December 1983.

The distribution of the hosts may affect the distribution of the tsetse flies. Therefore, it is important that the distribution of preferred hosts be considered in the determination of the distribution of tsetse flies.

5.5 DISTRIBUTION

Bearing in mind that views on the evolution of tsetse are largely speculative and deduced from distribution, morphology and so on, a review of these ideas may shed some light on the distribution of the species of the tsetse flies; as Evens (1953) remarked, one could not study the distribution of tsetse flies in the Congo without having the mind directed towards the problem of the historical evolution of the Glossinidae.

5.5.1 EVOLUTION OF THE GLOSSINA GENUS

It is generally believed that the ancestors of Glossina are those whose fossils have been found at Florissant in Colorado, United States of America. These Florissant fossils belong to the Oligocene epoch, Tertiary period (Machado, 1959) and are thus 23 to 38 million years old (Nyamweru, 1980). Nevertheless, no such fossils have been found in Africa (Glasgow, 1967; Ford, 1971). Ford (1970), however, rejects the belief that the ancestors of Glossina are those that have been found in Florissant. Ford suggests that by this time tsetse flies must have been well established in Africa, and it is wrong to think of the Colorado tsetse as

primitive. Ford argues that the genus probably dispersed sometime during the Permian period (Ford, 1970), 225 to 280 million years ago (Nyamweru, 1980; New Scientist DIARY, 1988), leading to its separation into a number of phylogenetic groups. The fusca group, to which G. longipennis belongs, the morsitans group, to which G. pallidipes belongs and the palpalis group are the result of this process (Ford, 1971). Insects probably appeared on the planet some 345 million years ago (Kumar, lecture notes, 1988), and it seems unlikely that tsetse flies could have appeared and established themselves as soon as the date suggested by Ford (1970).

Three views on the phylogeny of Glossina have been proposed. The first was proposed by Evens (1953). Evens' scheme takes into account the 'present day' geography as well as the Florissant fossils. He proposes that when the equator which then passed through the area in which the Mediterranean sea was later to appear started to move southwards it caused shifts in climates that were followed by movements in the flora and fauna associated with them (Potts, 1970). Henceforth, this movement southward carried with it the tsetse flies which had originally appeared in the Eurasian

landmass. By this time the Atlantic trough had not yet formed (Ford, 1971) and the future continents were still united (Potts, 1970), enabling some of the flies to move towards the American tropics and west Africa. Evens (1953) further proposes that another group of flies invaded present day East Africa and spread westwards. This group of flies was then further divided due to the formation of the Rift Valley and the volcanic mountain ranges. The formation of a lake that later became the basin of the Congo river led to further speciation of the western section of the genus.

The invasion of Africa, formerly part of Gondwana, by the genus led to the appearance of the dispersal centres for the three extant groups: the fusca group around the bay of Biafra, the morsitans group in the east of the Rift Valley and the palpalis group also around the bay of Biafra (Potts, 1970; Ford, 1971).

The second view on the phylogenetic diversification of Glossina is that of Machado (1954; 1959). He agrees with Evens (1953) in some essentials, but he also takes into account the orogenies and climatic fluctuations to explain the

phylogeny of the genus. The differences between these two authors will be shortly outlined.

The third view on the phylogenetic pattern of Glossina is that of Bursell (1958) and Glasgow (1963). They argue that the evolution of the subgenera was connected with the development of water-proofing mechanisms. Further review is deferred to section 5.5.3 on the evolution of G. pallidipes.

5.5.2 EVOLUTION OF GLOSSINA LONGIPENNIS

The dispersal centre for the fusca group was in the Congo basin (Ford, 1971), from where the flies spread eastwards and southwards due to the appearance of very dry conditions at the centre of the basin during the Miocene epoch in the Tertiary period, 5 to 23 million years ago (Nyamweru, 1980). The spread southward resulted in the isolation and formation of new species now found around the edge of the Congo basin, while the spread eastwards resulted in the isolation of G. longipennis. Ford (1971) proposes that a reduction of an east African forest that had extensive links with the Congo forest provided a means of isolation of G. longipennis. But Evens (1953) believes that the Rift Valley was the

principal isolating agent in the origin of G. longipennis, which later adapted itself to a dry climate. Nevertheless, Machado (1959) supposes that G. longipennis is morphologically the most primitive and simple species of all modern tsetse. He quotes floristic evidence to show that the Florissant fossils lived under semi-arid conditions. He further points out that the Florissant climate was probably very close to the cold climatic limit of modern tsetse distribution. However, Ford (1971) disagrees and argues that the Florissant climate was warm or sub-tropical. This is in agreement with Bursell's (1959) supposition that G. longipennis has undergone specialized adaptations to a dry climate.

5.5.3 EVOLUTION OF GLOSSINA PALLIDIPES

Bursell (1958) suggested that the evolution of Glossina pallidipes was a result of drought avoidance behaviour patterns. It is often assumed that the evolution of G. pallidipes was a process in which an ancestral line of fusca-like species, inhabiting a wet environment, branched off from the parent stock and adapted itself to drier conditions (Ford, 1971).

5.5.4 SUMMARY ON EVOLUTION

Though Evens regards the Rift Valley as the major isolating agent in the origin of *G. longipennis*, it seems that speciation could have been influenced by the pattern of drier climates and associated biota surrounding the African rainforests (Ford, 1971). It is true that puparial water-proofing efficiency is related to the climatic stresses the puparium must endure, but Bursell's hypothetical phylogenetic scheme cannot be wholly accepted since it has been observed that *G. brevipalpis* and *G. longipennis*, the wet and dry extremes of Bursell's phylogenetic tree, both inhabit the Tsavo game park of Kenya (Ford, 1971). In spite of these various hypotheses, the speculations on the phylogenetic scheme provide starting points for discussion of the zoogeographical distribution of tsetse flies.

5.6 BIOTIC FACTORS AFFECTING DISTRIBUTION

Vegetation plays a major role in the distribution of tsetse flies. It offers the flies protection when climatic conditions are so severe that they adversely affect their behaviour (Nash, 1937; 1969; Sousa, 1960; Ford, 1960). It also provides them with breeding grounds (Nash, 1937).

Vegetation has been principally studied in relation to high critical temperatures but Goodier (1960) has suggested that vegetation near the southern climatic limit or at high altitudes nearer the equator also provides protection from cold.

There is evidence from a large number of data sets relating the various tsetse species to various types of vegetation (Austen and Hegh, 1922; Swynnerton, 1936; Buxton, 1955; Nash, 1969; Mulligan, 1970; Glasgow, 1970; Jordan, 1974; Challier, 1982) but there is no sound theoretical explanation for such relations (Glasgow, 1970).

Laveissière and Challier (1981) working in Ivory Coast with 9 species and subspecies of the subgenera palpalis, morsitans and fusca found that their distribution which was related to the natural environment altered steadily with the changes in vegetation. They have observed that in the northern zones of Ivory Coast the tsetse distribution is contracting while in the southern zones it is expanding.

5.6.1 USUAL HABITATS

It has long been known that tsetse is not found everywhere in those regions in which it occurs, but that is confined to areas known as 'fly belts', whose limits are determined by the physical character of the locality (Austen, 1911). Several countries have published atlases to show the distribution of their tsetse belts (Ford, 1963; 1971).

G. pallidipes inhabits diverse vegetation types. Swynnerton (1936) stated that country without much thicket cannot be used by G. pallidipes, unless good bases especially good riverine thicket, exist close by. He observed that G. pallidipes was found in East Africa in a great part of the country inhabited by G. longipennis and that G. pallidipes occurred within almost all general types of vegetation from the drier Nyika to a light form of rainforest and the margins of true rainforest. He postulated that, when the thicket is really dense and continuous, G. pallidipes seems likely to frequent its outskirts and that in the dry season, tsetse flies are based on riverine thicket and may even penetrate into the dense thicket (Harris, 1930; Burtt, quoted by Swynnerton, 1936; Nash, 1937; McLennan, 1967). Nash (1969) has reported that G. pallidipes inhabits country ranging

from the light rainforest to dry thickets in arid savannah. Glover (1967) has also reported that G. pallidipes inhabits the thicket and savannah country.

The vegetation communities that have commonly been reported to harbour G. pallidipes include Acacia, Acacia/Commiphora, Combretum and Lantana camara woodland (Lambrecht, 1980; Snow, 1981; Matechi and Muangirwa, 1981).

The habitat of G. longipennis is characterized by a range of vegetation types from riverine thicket to thorn bushes in drier savannah or semi-desert (Neave, 1912; Swynnerton, 1936; Buxton, 1955; Nash, 1969). Since G. longipennis and G. pallidipes co-inhabit many areas of East Africa, the vegetation types inhabited by G. longipennis include those that harbour G. pallidipes, of which Acacia/Commiphora thicket is one (Power, 1964).

5.6.2 UNUSUAL HABITATS

There are indications that some species of Glossina can adapt to atypical habitats. For example, G. pallidipes has adapted itself to a commercial crop plantation of coniferous forest in Kenya (Turner, 1981). Finelle (1980) has also

reported tsetse adaptation to commercial coffee and cocoa plantations in West and Central Africa.

5.6.3 SUMMARY ON HABITATS

Both G. longipennis and G. pallidipes live in habitats ranging from riverine thickets to thorn bush in the driest savannah or semi-desert and from light rainforests to dry thickets in arid savannah, respectively (Nash, 1969). Cases of tsetse flies inhabiting atypical habitats such as coffee plantations are rare.

5.6.4 GAME

The distribution of tsetse flies is affected by the distribution of the wild game, in particular that of the most preferred hosts. Sousa (1960) and Ford (1960) suggest that when tsetse flies have established themselves in a suitable area, they depend on the smaller game which feed at night and rest during the day when the flies are active, rather than on the large animals. Hence, it can be postulated that the distribution of tsetse flies should coincide with that of the resting sites for the smaller game. Jackson (1894) suggested that in East Africa, where the `fly belts' were almost devoid of game they relied on smaller animals but in South

Africa, where game was in plenty they relied on larger animals. Austen (1911), on the other hand, assumed that tsetse flies only existed where big game was most plentiful, and that the flies almost disappeared as the game was killed. Ford (1970) argued that the primary factor determining the distribution of G. pallidipes is its attachment to its host (bushbuck) and to a few other animals in the habitat. He further suggested that the disappearance of G. m. submorsitans from the salient of savanna vegetation which stretches north-east into the centre of the Sudanese Republic was a result of extermination of the warthog, kudu, buffalo and giraffe by rinderpest in 1889-1890.

5.6.5 HUMAN ACTIVITIES

Human settlement and agricultural development may affect the distribution of tsetse flies. Sousa (1960) and Ford (1960) have reported that removal of human population from one area to another was followed by extensive regeneration of the abandoned riverine vegetation which then formed a suitable habitat for tsetse flies. Wilson (1958) observed the extension of the distribution of tsetse flies following movements of human populations and their cattle. He noted that the herds of cattle grazing

near the limits of fly-belts were a source of food for tsetse flies. Nash (1969) reports that an increasing human population is continuously encroaching into the forest belt and removing the bush, thereby reducing the populations of the tsetse.

Scheuer (1987) observed that the completion of the Gbarnga-Koindu road in the Foya area, Monrovia led to intensified land use, including small coffee and cocoa plantations and the Foya rice project, all of which could have helped to reduce the tsetse habitat and thus influence the flies' distribution.

Lancien and Gouteux (1984) have reported that after the epidemic of swine fever, the flies showed a reduction in density and a changed distribution. Madubunyi (1988) also found that the reduction in the size of the pig population triggered the collapse of the tsetse population. Earlier on, Kuzoe et al. (1985) had observed that the greatest concentrations of G. tachinoides were found in villages and settlements where domestic pigs were kept.

Takken (1988) reports that after the rinderpest panzootic that wiped out all the cattle, southern Mozambique appeared to have become free of G.

morsitans and G. pallidipes. Evison and Kathuria (1983) maintain that tsetse was wiped out in the river Kwando basin fly belt in Zambia during the 1890s rinderpest epidemic and a tsetse distribution map produced in the 1920s showed the area to be fly-free. They have also noted that the main tsetse advances and problem areas in Zambia are generally associated with free range cattle which provide a predictable food source and thus turn marginal fly areas into ideal habitats.

5.7 ABIOTIC FACTORS AFFECTING DISTRIBUTION

The distribution of tsetse flies may be affected not only by biotic factors but also by abiotic factors such as humidity, temperature and light. In the life of a tsetse fly, water conservation is the prime physiological problem of its survival (Cloudsley-Thompson, 1962). The effects of various abiotic factors on the distribution of tsetse flies have been studied both in the laboratory (see for example Bursell, 1960a; 1963) and in the field (see for example Nash, 1942; 1937; Jackson, 1948).

5.7.1 HUMIDITY

It is believed that humidity is one of the important factors limiting the distribution of tsetse

flies. Glasgow (1970) points out that the early stages of a tsetse's life are more susceptible to dryness than the adult stage when water reserves are replenished at every feed. Below 40% r.h. transpiration becomes so high that the water content of the G. pallidipes pupae becomes lower than normal (Bursell, 1958) and if the flies emerge into air at zero relative humidity they die of desiccation, although G. longipennis is able to complete its puparial development in completely dry air at 0% r.h. (Glasgow, 1970).

Field results suggest that the optimum conditions for tsetse are a mean monthly saturation deficit of 5 to 6 millibars and a mean evaporation of 20 to 25 ml per day (Nash, 1937). Rogers and Randolph (1986) found the southern limit of G. palpalis and G. fuscipes to be set by the limit of 6 to 7 mmHg saturation deficit. Jackson (1948) reports a positive correlation between saturation deficit and death rate of G. m. morsitans.

5.7.2 TEMPERATURE

Climatic studies with tsetse flies have mainly used temperature to identify the limits of the flies' distribution. Laboratory studies show that tsetse

flies appear to thrive at temperatures about 25°C and die rapidly at around 46°C and at sub-zero temperatures (Glasgow, 1970). Bursell (1960a) found that G. pallidipes puparia incubated at 30°C produced pale adults. Bursell (1960b) and Rajagopal and Bursell (1965) have reported a lower limit for successful completion of development of about 14°C for G. pallidipes puparia.

In the field, Glasgow (1970) has suggested that the limits of distribution of the genus are set by temperature: lethal high temperatures on the edges of the Sahara and Kalahari deserts, lethal low temperatures in Natal and the tropical highlands. In Nigeria, high temperatures appear to be the critical factor preventing northward expansion and in Zimbabwe, low temperatures probably prevent further spread southward (Ford, 1971). It has also been suggested that critical temperatures control the limits of tsetse population distributions indirectly by limiting the suitable habitat (Ford, 1968).

5.7.3 RAINFALL

Rainfall can also be an important factor limiting the survival of tsetse pupae. Too much rain would flood larviposition sites, and under conditions

of little or no rainfall, the pupae would die due to desiccation. In addition, female tsetse flies will not larviposit on already flooded ground or ground that is hard and dry. Matechi and Muangirwa (1981) have reported that during the period 1967 to 1972 in Magugu below the Rift Valley, rains flooded the area and rendered it unsuitable for larvipositing forcing tsetse into drier areas which were in the course of regenerating suitable vegetation for larvipositing.

In Africa, tsetse flies are rarely found in places with less than 500 mm of rainfall per annum, except where they have managed to penetrate drier areas by following the vegetation along a watercourse (Nash, 1969). The rainforest region, with over 1500 mm of rainfall per annum, surrounded by savannah, ending in desert or the sea, is closely related to the distribution of the different species of tsetse (Nash, 1969). For example, G. longipalpis and G. m. submorsitans occur in clearly defined belts where annual rainfall is between 600 and 1400 mm (Mohammed, 1980).

5.7.4 SEASON

Major seasonal changes in the fly distribution have been observed. Reporting on the effect of the

great drought of 1971 to 1973 in West Africa on the distribution of tsetse, Laveissière (1976) observed that this drought altered the distribution of some species of tsetse along the northern distribution limit. Nevertheless, Okiwelu et al. (1981) and Touré et al. (1979) suggested that this drought seemed not to have caused a permanent regression in the distribution of G. m. submorsitans in Mali.

Glasgow (1963) summarizes reports on seasonal alteration of breeding sites, including Burtt's (1952) observation that during the wet season puparia of G. swynnertoni are scattered on the surface of the soil while in the dry season they occur in large aggregations under deciduous thicket and in tree hollows. Harly (1954) and Glasgow (1961b) record similar seasonal shift of breeding sites used by G. morsitans, which use warmer sites in the cool weather and cooler sites in the hot weather.

G. m. submorsitans has been observed to retreat from the savannah into riverine vegetation in the dry season (Mohammed, 1980; Diallo, 1981). In a study of the spatial distribution of G. m. morsitans in an area of Sudano-Guinean savannah in Mali, Diallo (1984) found a contagious or aggregative distribution

for both sexes in the rainy season, while both sexes showed a more even distribution in the dry season except for a short period when females showed a contagious distribution and the males an even distribution.

McLennan (1967) has reported that in the Sudan vegetation zone in the dry season G. morsitans and G. tachinoides are confined to flood plains. Nash (1937) had reported that in the hot season tsetse are concentrated in forest patches, riparian forest and thicket in, or associated with, water courses. Pilson and Pilson (1967) have also found G. m. morsitans to be especially abundant in the riverine vegetation in the hot dry season.

Although it is not clear which factors are responsible for determining the distribution of tsetse flies, seasonal changes appear to play a major role in determining their distribution. As Tauber et al. (1986) have noted, most biotic and abiotic factors that organisms can use or must cope with in their environment are directly or indirectly related to seasonal changes.

5.7.5 ALTITUDE

Until recently, tsetse flies had not been found at altitudes above 2000m, but Tikubet et al. (1984) found G. m. submorsitans distributed between 2000 and 3000m in the Finchaa river valley. Earlier on, Swynnerton (1936) and Glasgow (1970) had reported that G. pallidipes was found up to 1800m above sea level at the equator and suggested that this limit decreased as the latitude increased.

5.8 SUMMARY ON DISTRIBUTION

The distribution of tsetse changes with changes in the ecosystem. Several factors that affect the tsetse distribution have been reported. Rogers and Randolph (1986) found the northern distribution limit of G. palpalis and G. fuscipes to correspond best with the joint condition that temperature and saturation deficit should not exceed 27^{o}C and 14 mmHg, respectively. Matechi and Muangirwa (1981) have reported an accelerated advance of tsetse flies in northern Tanzania as a result of movement of game in a dry period. Studies done in Zambia have shown that the limits of the G. m. centralis and G. m. morsitans fly belts are very unstable responding to complex inter-related climatic, vegetational and nutritional factors (Baldry and Evison, 1981).

Similarly, Glasgow (1970) has suggested that tsetse population react either to changes in the distribution of hosts, to the amount of shade, to temperature or to some combination of these.

Food has been considered to be the least important of the three groups of factors (seasonal, vegetational and food) that affect the distribution of tsetse flies (Nash, 1937). It may also be argued that the limiting factor is the vegetation or indeed the food as argued in the section on vegetational factors affecting distribution, and not any abiotic factor, though Nash (1969) argues that the distribution limits are determined primarily by the climate, and secondarily by the vegetation. Altitudinal limits could be thought of generally as being due to low temperature. Whatever the explanation, certainly, both biotic and abiotic factors play major roles in the distribution of tsetse flies.

5.9 GEOGRAPHICAL INFORMATION SYSTEMS

In the study of the tsetse fly movement and distribution, an integrative approach is essential due to the large volume of data involved. One such approach is the use of Geographical Information

Systems (GISs). In a GIS, the data is referenced in a manner which allows retrieval, analysis and display based on spatial criteria (Tomlinson, 1972).

GIS data may be alphanumerical, pictorial/ graphic or remotely sensed digital data (Lo, 1986). Acquiring alphanumeric data which is already in computer-readable form is straightforward. The input of pictorial data, such as maps, requires the use of a digitizer which converts the features into strings of coordinate values in a vector format (Marble and Peuquet, 1983); or an optical scanner or a scanning densitometer which automatically converts graphic material to computer-readable raster form (Lo, 1986). Remotely sensed data which are already in a raster format can be incorporated into the GIS with little difficulties (Meyer, 1984).

Hugh-Johns (1989) reports that remote sensing was first used for tsetse control in 1976 in the riparian forests of Mali. He reviews the characteristics, uses and limitations of satellite imagery for mapping potential habitats of parasites and disease vectors.

5.10 ACTIVITY

Activity of the tsetse flies was defined by Jackson (1941) as their readiness to appear to catchers. More recently, Glasgow (1967) defined tsetse activity as the ability of flies to respond, in such a way as to become catchable, to a given stimulus. Recently, with the availability of traps, the activity of tsetse flies can be defined as their readiness to be attracted to the trap and be captured. It is said that if there are more insects flying, then there is more activity (Southwood, 1978).

5.10.1 FLIGHT ENERGY AND SPEED

Tsetse fly activity depends on their fat reserves. Randolph and Rogers (1984) found that flies with little fat were relatively inactive, while those that had more fat were more active. Langley (1977) has reviewed the energetics of tsetse flies. In laboratory studies on circadian rhythms in adult tsetse, Brady (1970) lists five characteristics of apparently spontaneous activity and shows that the amount of activity increases roughly exponentially during the course of starvation. He further observed activity of adult G. m. orientalis in rocking-box actographs and found that the duration of the

activity bursts, has a maximum length of the order of 1 to 2 minutes.

Proline is believed to be the major direct source of energy for flight in tsetse flies (Bursell, 1963; Bursell and Slack, 1970) and observations have been made on the relations among wing beat frequency, flight duration, levels of proline and temperature. Hargrove (1980c) conducted his experiments in a flight mill and found that wing beat frequency at flight initiation in mature male G. morsitans rose approximately linearly from 213 Hz at 20°C to 263 Hz at 32°C and that an increase of temperature to 36°C produced no further effect. Earlier on, Hargrove (1975) had noted a decline in wing beat frequency during flight and attributed it to the rapid decline in the levels of thoracic proline. He also found that the flight duration of G. morsitans on flight mills in the laboratory is limited to bursts of less than 2 to 3 minutes (Hargrove, 1975). In another study, Bursell (1978) observed that flight duration was positively correlated with the concentration of haemolymph proline prior to flight.

Tsetse flies are inactive at extremes of temperature. At low temperatures the tsetse will not

fly off until a threshold thoracic temperature is reached, and at high temperatures oxidation of reserves of proline is rapid. These facts may explain Hargrove's (1980c) finding that high temperatures caused a more rapid overall decline in wing beat frequency.

Tsetse flies spend most of their time resting. Bursell and Taylor (1980) estimated the daily flight duration to be between 15 and 30 minutes for males in the hot and cold seasons, respectively, while the flight duration for females was found to be limited to a few minutes (1 to 3 minutes). Randolph and Rogers (1981) found a daily flight duration of about 32 minutes for G. m. centralis at the end of the rainy season. Previously, they had found higher values of between 32 and 50 minutes (Randolph and Rogers, 1978). Hargrove (1975) and Bursell (1978) working in laboratories observed a daily flight duration of between 1 and 5 minutes. It appears that at any one time the tsetse has enough reserves of proline for 5 minutes of flight (Bursell, 1978).

Several authors have estimated the flying speed of tsetse flies. Buxton (1955) put the maximum air speed at 6 to 7m per second lessened to 1 to 2m per

second immediately after a blood meal. Hargrove (1975) measured an average speed of tsetse flies in flight mills of about 4m per second in the laboratory, while field measurements carried out by Gibson and Brady (1988) in Zimbabwe gave a mean speed of about 6m per second and a maximum speed of 10m per second. In their preliminary study, Gibson and Brady (1985) reported mean flight speeds of about 5m per second and ranging from 2.5 to 7m per second for both G. pallidipes and G. morsitans.

5.10.2 ACTIVITY PATTERNS

Observed activity patterns for tsetse flies differ with respect to species and method of sampling. Here we concentrate on G. pallidipes and G. longipennis, the two species found at Nguruman. Using stationary vehicles to catch the flies, van Etten (1982) showed that catches of G. pallidipes peaked in the afternoon, especially for males. Using biconical traps in the Lambwe valley in Kenya, Turner (1987) found the same activity pattern for G. pallidipes and essentially the same pattern was found using handnets to capture flies off stationary oxen at Lugala in Uganda (Harley, 1965). In contrast, Jaensen (1981) using a slow moving vehicle observed a bimodal activity pattern for G. pallidipes at Kibwezi

in Kenya, but using Moloo traps the flies showed an activity pattern similar to that found by van Etten (1982) in Nguruman, Kenya. Several sampling methods and different activity patterns have been reported for G. pallidipes (van Etten, 1982).

G. longipennis is known to be most active at dawn and dusk. In sampling G. longipennis, Power (1964) used fly round sampling, while Kyorku (1989) used electric screens and biconical traps baited with cow urine, acetone and octenol. They both found that the activity pattern for G. longipennis shows two peaks, a lower peak at dawn and a higher one at dusk. During the day, between these two active periods the fly is very inactive (Neave, 1912; Lewis, 1942) but will approach moving vehicles.

Differences in the timing of male and female peaks of activity have been observed. The peak of activity in female G. p. palpalis occurred before that of males (Carnevale and Adam, 1971). The same situation was observed by Glasgow and Duffy (1961). In contrast, the peak of activity for female G. p. gambiensis (Challier, 1973) and G. f. quanzensis (Elsen, 1973) occurred later than that for males.

van Wettere (1975) has studied the effect of age on activity. He found that in the wet season teneral G. p. palpalis were more active in the early morning while older males were more active at midday; in the dry season teneral males were also active in the late afternoon.

Activity cycles have also been studied in relation to feeding and pregnancy. A 4-day feeding interval has been reported for male G. pallidipes (Turner, 1987), G. p. palpalis (Rogers et al., 1986), G. morsitans (Jackson, 1933a), G. swynnertoni (Jackson, 1933a; Glasgow, 1961a) and G. f. fuscipes (Rogers, 1977). A 9-day interlarval period has been observed for female G. p. palpalis (Rogers et al., 1984; Rogers et al., 1986), G. swynnertoni (Glasgow, 1961a) and G. pallidipes (Turner, 1987).

5.10.3 CLIMATIC FACTORS ASSOCIATED WITH ACTIVITY

Climatic factors associated with activity have been studied both in the laboratory and in the field. The activity pattern of Glossina may be influenced by irradiance, temperature, wind, rainfall, humidity and saturation deficit.

5.10.3.1 LIGHT

There is laboratory evidence to suggest that tsetse fly activity is regulated by light intensity. Barrass (1962) studied activity in the laboratory with temperature and humidity held constant while varying light intensity. He found that G. pallidipes was active during the simulated day and inactive at night. Barrass argued that light intensity acts as an environmental trigger and is sufficient to maintain a rhythm of activity under otherwise constant laboratory conditions. He also found that many flies showed a decreased activity in constant darkness. Cloudsley-Thompson (1962) also observed that activity was regulated by light intensity.

Field experiments have also shown that most tsetse species are only active during day-light. Gruvel (1975) has reported that G. tachinoides is active when the light intensity ranges from 0.17 to 11000 lux. Light intensities above 2500 lux inhibit feeding (Huyton and Brady, 1975) and since activity is linked to feeding, tsetse flies are inactive during these high light intensities. Most tsetse species are not active at night (Challier, 1982) but G. pallidipes has been caught after 19:00h (Kangwagye, 1971). Fuller (1978) also caught both

this species and G. longipennis at night when there were no lights. Power (1964) caught more G. longipennis as the light intensity decreased, until the light was too poor for efficient catching. He reports that activity had continued after dark as flies could be heard in flight.

Tsetse activity appears to be spontaneous and controlled by an endogenous circadian clock (Brady, 1972a; 1975b). The explanation by Brady that there is an endogenous rhythm entrained by light does not fully explain why some tsetse activity have been observed in the darkness. If the activity was controlled by an endogenous circadian clock, then we would expect no activity immediately the light was off, but this has not always been the case as reviewed above.

5.10.3.2 TEMPERATURE AND RELATIVE HUMIDITY

Temperature increases the rate of metabolic processes, and hence the activity of the tsetse flies. Several authors have studied the relation of temperature to tsetse activity. Flies generally become active at sunrise when the temperature exceeds 16° to 18°C (Challier, 1982). In the galley forest of Niger, G. tachinoides was observed to be inactive

before 10:00h when the temperature was still below 20°C. Thereafter, activity closely approximated the daily temperature profile until 16:30h (Turner, 1980b). Power (1964) found that under natural conditions G. longipennis was active when temperatures exceeded about 20°C. Gruvel (1975e) noted that beyond 30.5°C the activity of G. tachinoides decreased and no flies were caught when the temperature exceeded 39°C. It has been observed that tsetse generally exhibit a bimodal activity pattern during the hot season, and a unimodal pattern during the cold and rainy seasons (Challier, 1982).

Temperature and relative humidity are closely interrelated so that it is extremely difficult to distinguish their effects under field conditions. It has been reported that the level of activity for G. longipennis at low light values was influenced by temperature or saturation deficit (Power, 1964).

5.10.3.3 WIND

Wind may indirectly enhance the activity of tsetse flies by carrying with it odours to which tsetse flies respond. A number of odours have been tested and the following have been found to be

potential baits for G. pallidipes and G. longipennis in trapping programmes: carbon dioxide (Vale, 1984; Warnes, 1989; 1990; Torr, 1990); acetone (Vale, 1984; Takken, 1984; Owaga, 1985; Vale et al., 1986; Saini and Dransfield, 1987; Brightwell et al., 1987; Torr, 1990; Dransfield et al., 1986; 1990); ox breath (Warnes, 1990); urine (that of cows or buffalos) (Owaga, 1985; Dransfield et al., 1986; 1990; Brightwell et al., 1987); and 1-octen-3-ol (Vale et al., 1986; Saini and Dransfield, 1987; Torr, 1990; Oloo, 1990). Cow urine and acetone provide a useful combination of baits for G. pallidipes in community tsetse control schemes (Dransfield et al., 1986). A combination of acetone, cow urine and 1-octen-3-ol has been found to be an effective bait for G. longipennis (Kyorku, 1989). The range over which these odours attract tsetse flies may depend on the wind speed. Slower wind speeds of less than about 1m per second leads to a decrease in that range (Gibson and Brady, 1988).

Whereas a lot of effort has been concentrated on identifying odours that may provide useful baits for tsetse flies in trapping programmes, little work has been done on the importance of wind on the activity

of tsetse flies and more work is needed on the relation of wind to activity of tsetse flies.

5.10.4 SUMMARY ON ACTIVITY

Activity patterns for tsetse flies have been well documented. Temperature, humidity and light appear to be the most important climatic factors affecting activity pattern. But there is still a need for further studies on activity patterns for tsetse flies using the improvements in technology for measuring weather variables so that we may obtain better understanding of climatic factors affecting activity pattern.

5.11 DISPERSAL

There are a number of ways in which insects can move. They can migrate in swarms or spread out evenly (dispersal) or concentrate (locusts by weather) or forage. When organisms diffuse, their movement is essentially random. They are not moving to or from anything. But the result is that they do spread out. These are the principles of the process of diffusion which were first elaborated in the study of the random Brownian motion of small particles suspended in liquid and the diffusion of compressible fluids (see for example Reif, 1965). The

applicability of models based on such processes to a given system depends on the extent to which the random motion dominates other forms of change such as mortality and reproduction (Rudd and Gandour, 1985).

Tsetse flies can disperse by random diffusion or by moving in a directed fashion in relation to an environmental gradient.

5.11.1 THE PATTERN OF DISPERSAL

Two views of tsetse dispersal have been put forward. These are the "feeding grounds" hypothesis as set forth and substantiated by Jackson (1930; 1933a; 1937; 1941; 1944; 1948) and the "random movement" hypothesis propounded and substantiated by Bursell (1970), Vale (1974), Rogers (1977), Freeman (1977), Hargrove (1981), Vale *et al.* (1984) and Hargrove *et al.* (1989).

Jackson divided tsetse habitats into the "feeding grounds" and "home grounds" of the fly. The "feeding grounds" are relatively open areas, while "home grounds" are in areas of homogeneous woodland. The tsetse flies move between these areas and rarely move away from them. Bursell (1970) has discussed

evidence for and against the "feeding grounds" hypothesis.

The "random movement" hypothesis is based on the assumption that the direction of movement of tsetse flies is random (Bursell, 1970). Clark (1962) and Skellam (1951) have discussed the assumptions underlying a two-dimensional random walk.

Bursell (1970) citing work of Jack and Williams (1937) and that of Pilson and Leggate (1962a) suggested that tsetse flies might direct their flights towards shaded areas during hot times of the day, and towards lighted areas during cool times of the day. Glasgow (1963) concluded from the study done by Nash (1942), that adult tsetse moved into the centre of the forest because of the negative phototaxis operating at temperatures above 30 to 32oC. Observations such as these may have led Jackson to formulate his feeding ground hypothesis but it may be possible to account for these observations by changes in the diffusion coefficient in relation to an environmental gradient, in this case in relation to changes in temperatures in the woodland and open areas. Changes in the diffusion coefficient can produce a net displacement in a fly

population, imposing an apparently directed movement on the diffusive movement at certain times of day. One does not have to evoke the "feeding ground" hypothesis to explain these observations.

Experiments have been done to see if diffusion provides an adequate explanation of fly movement or if a more sophisticated model is needed.

5.11.2 EXPERIMENTAL DESIGNS ON DISPERSAL

A number of experiments have been done to study the dispersal of tsetse flies by placing traps around a central release point at set distances to measure the rate of dispersal of tsetse flies. Rogers (1977) simulated a situation in which traps were placed around a central release point forming concentric circles and monitored the number of flies captured on each circle with time. Earlier on, Jackson (1946, 1948b), Hargrove (1981) and Hargrove et al. (1981) designed their experiments in which a release point was surrounded by a rectangular spiral. Vale et al. (1984) used a central release point surrounded by groups of three traps in two concentric circles. Doane (1963) placed recapture traps at increasing distances in the form of a cross. In a homogeneous environment, uniform sampling would be appropriate

for experiments aimed at measuring the rate of dispersal. Where the environment is heterogeneous, a stratified type of sampling covering all vegetation types would be needed and setting up traps at random would be impractical due to the inaccessibility of certain areas.

5.11.3 RATES OF DISPERSAL

Few authors have estimated rates of dispersal for tsetse flies, and these have been found to be different for different species of tsetse flies, and different for the same species of tsetse flies in different locations. Rogers (1977) analyzed 14 data sets of fly movement for G. swynnertoni, G. longipennis, G. f. fuscipes, G. palpalis and for four species and subspecies of G. morsitans. He was able to show that the data were consistent with a random diffusion model. Thus, assuming that tsetse flies moved in a large number of small random steps, the mean distance moved away from a release point in a given time should be proportional to the step length and the square root of the number of steps. On this basis he calculated daily dispersal rates of 100 to 500m in one day for the above mentioned tsetse flies.

Hargrove (1981) argued that a correction factor of 0.9 should be applied to Rogers (1977) formula for the rate of dispersal but using this correction factor leaves the dispersal rate that Rogers (1977) found almost unchanged at 110 to 550m per day. Vale et al. (1984) using Hargrove's (1981) model for the dispersal of tsetse flies computed a dispersal rate of about 822m per day for combined male and female G.pallidipes, and for combined male and female G.m.morsitans of about 700m per day.

5.11.4 FACTORS AFFECTING DISPERSION

Female tsetse flies have relatively little energy for flight (Bursell and Taylor, 1980). But, it has been observed that females disperse more than males do (Vale et al., 1984; Cuisance and Itard, 1973b). Therefore, female tsetse flies must make fewer changes of direction in flight than males do (Vale et al., 1984).

Weather and vegetation may affect the dispersal of tsetse flies. There is some critical low temperature, below which tsetse flies are inactive and above which the activity of tsetse flies increases with a rise in temperature, until a critical high temperature is reached when the

activity starts to diminish. Vale et al. (1984) found that an increase in dawn temperatures, from 17.5 to 27.5°C, was associated with an increase in the rate of movement of G. pallidipes in the early morning. Laveissière (1988) observed that riverine species of Glossina travelled very long distances in the hot season, while in the wet season they travelled shorter distances. This could be explained by the fact that in the rainy season the vegetation adjacent to the rivers regenerates and as a result tsetse flies tend to spread out from the riverine vegetation, thus reducing their net displacement as reviewed in the proceeding paragraph. In a savannah vegetation type, Glasgow et al. (1961b) noted that dispersal of G. pallidipes was greatest in the wet, cool half of the year, when there was an extension of the tsetse habitat due to the regeneration of the marginal vegetation.

The finding by Glasgow (1963) that the rate of dispersal along riverine vegetation is greater than in the savannah is to be expected, since in a linear habitat (riverine vegetation) the movement is restricted to one dimension, while in the savannah, the flies can move freely in two dimensions.

Tsetse flies may disperse actively or passively. Passive movement may have been facilitated by people (Randolph et al., 1984), wind (Molyneaux et al., 1979a) or cattle (Lambrecht, 1972), although Jackson (1941) suggested that wandering game animals have very little effect in aiding dispersal of tsetse.

More information is needed on the rate of dispersal of tsetse flies. In particular, we need to know the rates of dispersal by species of tsetse flies with respect to weather and vegetation for control purposes.

5.12 MODELS OF ACTIVITY, DISPERSAL AND DISTRIBUTION

Different types of models have been used to study the activity, dispersal and distribution of tsetse. Activity models have mainly been regression models. Dispersal models are mainly concerned with diffusion processes and models of distribution are mainly cartographical.

5.12.1 REGRESSION MODELS OF ACTIVITY

Model I regression methods have been used to identify the environmental factors that determine activity. For example, Turner (1987) has regressed changes in the numbers of G. pallidipes caught

against corresponding changes in temperature, saturation deficit and light intensity, and found significant positive regression coefficients in all three cases. Power (1964) regressed the catch of non-teneral males of G. longipennis on both the light intensity and the saturation deficit, and found that the catch rose as the saturation deficit increased and as the light intensity decreased. He observed that although the regression suggests that light intensity was a major factor governing the size of the catch, the light intensity fell so uniformly each evening that a "trigger effect" cannot be ruled out. He further suggested that the saturation deficit does not trigger the evening peak since it began over a wide range of saturation deficits.

5.12.2 DIFFUSION MODELS OF DISPERSAL

A typical experiment to study dispersal involves releasing a number of insects at a given point and periodically returning to measure the population density of released insects as a function of the distance from the release point and time (Rudd and Gandour, 1985). The general approach to the analysis of data from such experiments is to regress the population density on the distance from the centre of dispersion (Andrewartha and Birch, 1954; Kettle,

1951). These model I regression equations are not based on known biological responses. Therefore, little information is obtained from the knowledge of the values of the parameters in such models.

Models of tsetse fly dispersal have been proposed with the assumption that the flies move in a random walk in which they execute a very large number of very small steps, the direction of each step being randomly and uniformly distributed around a circle (Bursell, 1970; Rogers, 1977; Hargrove, 1981). The root-mean-square distance from the starting point is then equal to the product of the step length and the square root of the number of steps (Gamow, 1962). Bursell (1970), Rogers (1977), Hargrove (1981a) and Vale et al. (1984) have used this model to calculate the rates of dispersal of tsetse flies.

Rudd and Gandour (1985) extend the diffusion equation by allowing for the possibility that individuals might leave the system. The additional term in the diffusion equation gives a decrease in the number of individuals at a rate proportional to the number of individuals present at any time.

In order to account for population regulation (see for example Rogers, 1979), a density-dependent term should be added to the diffusion model. At Nguruman where the fly population is suppressed by trapping, it would be appropriate to add to the diffusion model an additional term to allow for trapping in studies of the population dynamics of the flies.

5.12.3 CARTOGRAPHICAL MODELS OF DISTRIBUTION IN SPACE

Cartographical models have been used to study the distribution of the tsetse in space based on tsetse surveys. The tsetse numbers together with the trap positions are then plotted on a map of the area. The distribution maps can be used to check on advances and recessions of the tsetse distribution (see for example Baldry and Evison, 1981; Takken, 1988). Eventually we would like to be able to use simulation models of tsetse populations (Rogers, 1979) to predict the tsetse fly densities and plot these on the maps of the areas so that we can study seasonal changes in fly distributions.

5.12.4 INCORPORATING MOVEMENT INTO POPULATION DYNAMICS MODELS

Tsetse are particularly amenable to modelling because their life cycle may be divided into three essential stages: puparia, newly emerged adults (tenerals) and mature adults (Rogers, 1979). Nevertheless, models of tsetse population dynamics require a great deal of data from different fields, such as entomology and climatology.

The only study designed to develop a tsetse population model in relation to a specific field population was conducted at Nguruman, Kenya by a multi-displinary team from the International Centre of Insect Physiology and Ecology (ICIPE). Simultaneous studies on G. pallidipes population dynamics and trypanosome infection were carried out between May 1983 and July 1990 on a Maasai group ranch. This study is particularly important because, previously, scientists of different professions (entomologists, parasitologists and so on) have worked in isolation in quite different habitat types, and it has been difficult or impossible to use data from one habitat to interpret those of another (Berryman and Rogers, 1986).

In their population model, Dransfield and Brightwell (1989) assumed that immigration was equal to emigration and that tsetse produced one larva every 8 to 10 days. They were, therefore, concerned mainly with assessing the mortality rates at the various stages in the life cycle of the tsetse fly. They constructed a simulation model using the relations between these mortality rates and biotic and abiotic factors. The climatic factors that were considered included rainfall, relative humidity and temperature. The model runs on a time interval of 1 day. The model tends to overestimate some changes in population size and underestimate others.

As a result of their study, Dransfield and Brightwell (1989) suggested that some changes in population size resulted more from fly movement than from changes in mortality rates, and therefore fly movement must be incorporated in the model. This could be done by calculating emigration and immigration rates separately or by calculating mortality rates from Moran curves (Rogers, 1979) to deduce mortality and/or emigration rates (Taylor and Taylor, 1977). It may not be necessary to consider both relative humidity and temperature in one model because they are negatively correlated in nature.

Predominant wind direction, especially in the late afternoon when wind direction is less variable, should also be considered as there is evidence to suggest that tsetse may be dispersed by wind (Molyneux, Baldry and Fairhurst, 1979).

5.13 MARK-RELEASE-RECAPTURE STUDIES

5.13.1 INTRODUCTION

Many mark-release-recapture studies have been carried out using tsetse flies. These studies have been done to estimate population densities (Omoogun et al., 1987; Turner, 1980; Jackson, 1941), to determine movement patterns (Laveissière, 1988; Randolph et al., 1984; Rogers, 1977; Jackson, 1953; 1941; 1933a), to investigate the distribution, activity pattern, feeding cycle and losses of the released flies (Rogers, 1977; Jackson, 1941), to study insemination rates of male flies (Turner, 1980; Azevedo et al., 1970), to study mortality rates of flies (Laveissière, 1988; Jackson, 1941), to determine resting sites for flies (Turner, 1980; Hadaway, 1977) and other aspects of tsetse behaviour.

5.13.2 MATERIALS AND METHODS USED IN MARK-RELEASE RECAPTURE STUDIES

Several methods have been used to mark tsetse flies. Lamborn (1915), for example, marked flies by amputating portions of one leg. Such marks are most distinctive and not likely to be found in nature. But for a mark to be easily visible it may be proportionally so large as to affect the insect's behaviour (Southwood, 1978).

Marking individual tsetse flies with artist's oil paint, which comes in a variety of colours, has been extensively used since the 1930s (Southwood, 1978; Scott, 1931; Jackson, 1933b). For example, Jackson (1933b) marked individual tsetse flies on the thorax with 2 to 5 spots of artist's oil paint.

Entomologists have used fluorescent stains or dyes which are not conspicuous in normal light, but are very bright under ultraviolet light. Laveissière (1988), Turner (1980), Hadaway (1977), Scholz et al. (1976), Vale et al. (1976), Tibayrenc et al. (1971), Jewell (1958; 1956) and McDonald (1960) have reported the use of fluorescent lacquer enamels, fluorescent pigments with gum Arabic glue, and fluorescent powders with isopropyl alcohol to mark tsetse flies. Marked flies have been spotted in darkness in the field at a distance of up to 8 to 10m by the use of a beam of ultraviolet light (McDonald, 1960).

Paints or concentrated solutions of fluorescent powders may be applied by use of an ordinary perfume sprayer, a small pointed brush, a small wire, an entomological pin, an electric needle, a pointed stick, or a dry grass blade or stem. Jackson (1933b)

marked tsetse flies by use of a fine dry grass stem. Scholz et al. (1976) applied fluorescent powders suspended in isopropyl alcohol at a strength of 1.5% by means of an ordinary perfume sprayer. Emerging flies have been marked by spreading fluorescent powder over sand (Tibayrenc et al., 1971) so that the young flies pick up the powder when they emerge from their puparia in the soil.

Radioactive substances have also been used to mark tsetse flies. Isotopes may be used as labels outside the tsetse fly or alternatively incorporated in the blood meal of the fly. If fed on, the mark is invisible to predators and may be passed on to the next generation as it is incorporated in tissues (Beard, 1965). Bois et al. (1977) used 59Fe in a solution of iron (III) chloride to mark tsetse flies by placing 0.46 microlitre drops of the solution on the thorax. Flies could be detected at a distance of up to 1.5m with a scintillation counter. Cavalloro et al. (1971) and Cuisance et al. (1970; 1971) fed female tsetse flies on iron and zinc isotopes in order to detect the flies and their offspring. They also fed tsetse flies on 59Co and 51Cr but these were not transferred to the offspring. Other radioactive substances used to label tsetse flies are aqueous

solution of (32P) phosphate and (14C) isoleucine (Hamann and Langley, 1978), isotonic solutions of sodium (32P) phosphate (Hamann and Iwannek, 1978; 1979) and (two 14C) thymidine (Azevedo et al., 1970).

Tsetse flies are sensitive to radiation and the dose rate has to be carefully chosen. In addition, great care should be exercised when working with radioactive materials not to contaminate the environment. Whenever radioactive materials are to be used, it is recommended that long persisting isotopes, say those with half life of more than 200 days, should not be used in ecology.

Marking on specific locations on the thorax of the tsetse fly will require the fly to be still and tsetse flies are usually held between the thumb and the forefinger (DITH, 1986; Southwood, 1978)

Information on movement of individual tsetse flies can be obtained by using one colour in different patterns on different flies (DITH, 1986; Jackson, 1953) or marking individual flies with the same pattern but different colours. It is desirable to use the minimum number of colours in marking individual insects, as changing colours increases the

handling time, which should be kept to the minimum (Southwood, 1978). Some marking patterns for tsetse flies have been devised by Jackson (1953). The number of individual flies to be marked and the number of available colours will determine which method to adopt.

Release sites for marked flies need to be carefully chosen. Southwood (1978) suggests that the release points should be scattered uniformly throughout the habitat to ensure that the marked and unmarked flies mix freely. This is less important for tsetse flies as they are powerful fliers and disperse rapidly and uniformly, provided the habitat is homogeneous. In this case a single release point may suffice. Moreover, capturing and then releasing flies at one site will reduce the time they spend in the marking cage. This time spent should be kept short as possible to minimize stress on the flies. Marked flies should not remain in the cage for more than 15 minutes at most (Dransfield* pers. comm.). Sampling can then be done after sufficient time has passed for the released flies to have mixed

* ICIPE, Tsetse Research Programme, Box 30772, Nairobi, Kenya.

thoroughly with the unmarked ones (Iwao et al., 1963). Typically 24 to 48 hours (Buxton, 1955; Peterson, 1953) should be sufficient for mixing to have occurred. Southwood (1978) states that if the animal has definite times at which it is inactive, for example, if it is strictly diurnal or nocturnal, then it should be released during its inactive period. But at the same time one must still avoid excess stress imposed by keeping tsetse flies captive for too long. It is important that release sites should be carefully chosen. For instance, tsetse flies should be released under a shade tree near a stream to provide conditions of high humidity and only apparently healthy, unharmed individuals should be released.

5.13.3 EFFECT OF MARKING

Marking tsetse flies will always have some effect on them and it is important to decide if the marking adversely affects the tsetse behaviour or mortality. Marking tsetse flies by amputating legs is apparently least harmful if the right or left leg is severed through the center of a metatarsus or tibia, especially on a mesothoracic leg (Peterson, 1953).

Jackson (1948) suggested that newly emerged insects may be more sensitive to toxic substances used in marking materials than older insects, though the evidence is that the toxicity of good quality oil paints is slight (Jackson, 1936; 1941). Jackson (1941) observed that the marked male tsetse flies do not live as long as unmarked flies in the field but Potts (quoted by Jackson, 1941) showed that very large numbers of captive, painted tsetse flies survived as long as unpainted control flies kept under identical conditions. It has been argued that marked tsetse flies are more vulnerable to predators such as dragon flies (Southwood, 1978), but Potts (quoted by Jackson, 1941) concluded that colours such as black and purple, which are less conspicuous to human eye than others, such as light blue, do not appear to increase mortality of released flies.

The flight efficiency of painted tsetse flies may be adversely affected by the additional weight of the paint. However, Potts (quoted by Jackson, 1941) estimated the weight of paint applied on the fly to be between 0.5 and 2.0 mg depending upon how many times the fly was marked and concluded that this had little effect.

5.13.4 CONCLUSION ON MARK-RELEASE-RECAPTURE STUDIES

Artist's oil paint has been used successfully in mark-release-recapture experiments. And since it has been demonstrated that side effects of the paint on tsetse behaviour are insignificant, the method of marking tsetse flies with artist's oil paint should be used more widely than before in mark-release-recapture experiments. Use of radioactive materials in ecology should be kept to a minimum to reduce environmental contamination.

CHAPTER 6

GENERAL MATERIALS AND METHODS

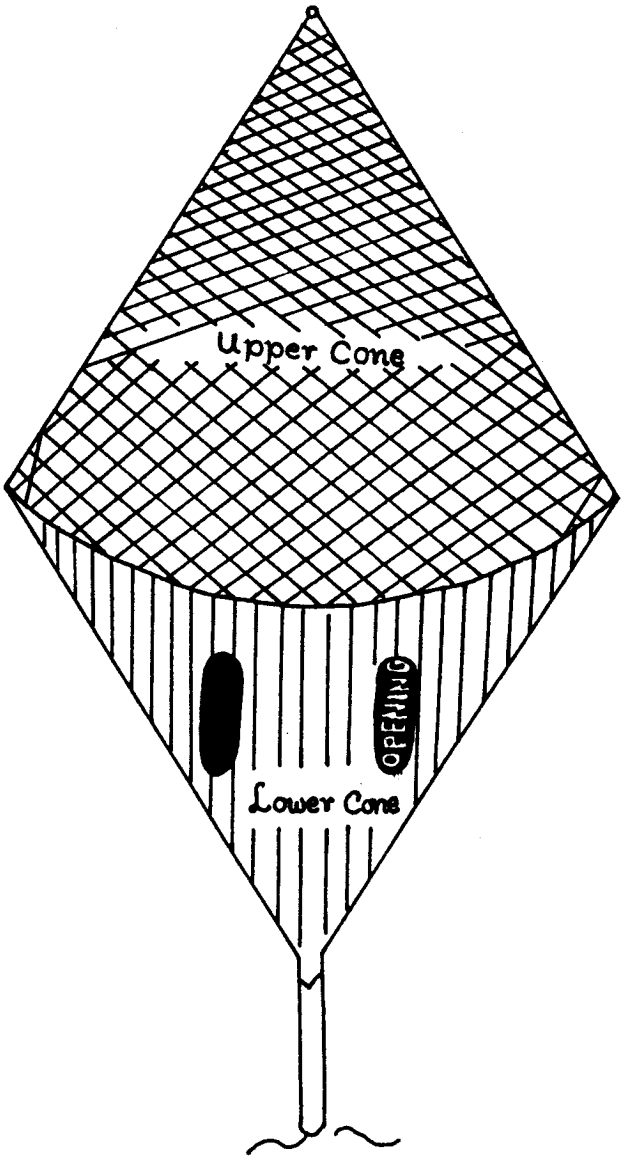
6.1 BICONICAL TRAP

The Biconical trap (Figure 6.1) (Challier et al., 1973; 1977; Laveissière et al., 1979) has been used to catch tsetse flies. It consists of two cones joined together at their bases. The bases are mounted on a wire ring of about 80 cm in diameter. The lower cone is made of royal blue cloth while the upper cone is made of white mosquito netting. The lower cone has four vertical openings which lead to four compartments separated by four black screens. The compartments rise to about two thirds up the height of the trap. The trap stands above the ground supported by a pole which passes through the centre of the cone; and at the top, the trap is supported by a cone on which a collection cage is put when used for monitoring flies. The pole is greased close to the ground to prevent ants entering the trap and removing flies from the collection cage.

Tsetse flies are attracted to a baited biconical trap, first by the odours and then by the blue colour of the trap. If they enter the trap they find

FIGURE 6.1

Biconical trap



themselves in one of the four compartments. Once inside the compartments which are dark, the flies are attracted to the lighted top and eventually enter the collection cage.

6.2 NGURUMAN TRAP

Another trap that has been used to catch tsetse flies is the Nguruman (NG2G) trap (Figure 6.2), (Brightwell et al., 1991). The design of this trap is based on the F1 and F2 traps (Flint, 1985) and on the Nguruman version 2B (NG2B) trap (Brightwell et al., 1987).

The NG2G trap is supported by three external poles and a central pole of about 1.5m long. It takes the shape of a triangular prism with a `wing' attached to it. The top is a triangular cone made of a white mosquito netting. Both the target and the shelf are made of black cloth and the rest of the trap is made of royal blue cloth. The trap is about a metre high.

Tsetse flies are attracted to the unbaited Nguruman trap in the same way they are attracted to the unbaited biconical trap. That is, the overall blue colour of the trap attracts the flies first.

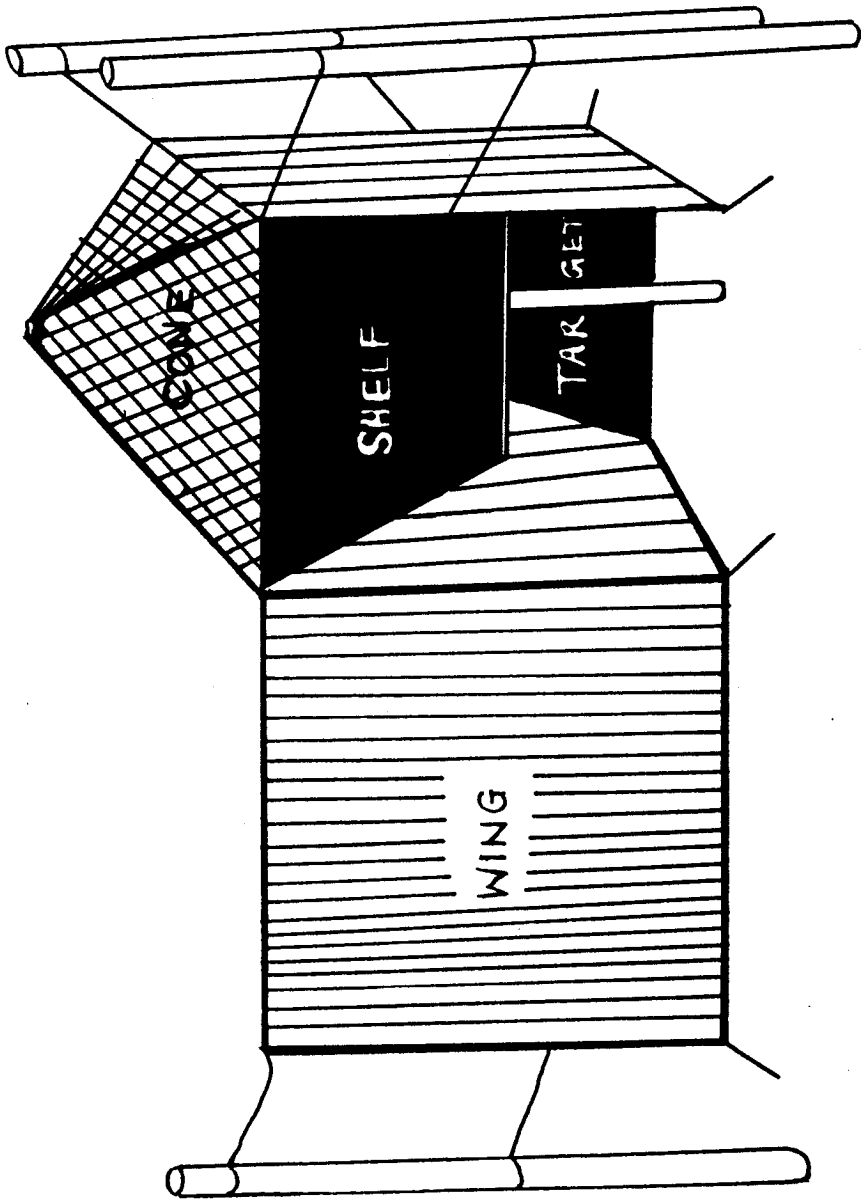


FIGURE 6.2

Nguruman (NG2B) trap

The black colour of the shelf and the target encourages the flies to land. Once they have landed on the target, the white netting of the cone encourages the flies to move up towards the light and find their way into the collection cage on top of the cone.

The flies may regard the unbaited trap as a refuge when they fly towards it. In the case of a baited trap, the flies may regard the trap as a source of food.

6.3 IDENTIFICATION OF *GLOSSINA PALLIDIPES* AND *G. LONGIPENNIS* IN THE FIELD

The two species of tsetse flies, *G. pallidipes* and *G. longipennis* have been distinguished using the method of Nash (1969), while the sexes of the flies have been determined using the method of Austen (1903). Both methods are described in chapter 5 section 5.2.

Teneral and non-teneral flies can be distinguished by squeezing the thorax between the finger and the thumb. The thorax feels soft in teneral flies and firmer in non-teneral flies (Pollock, 1982).

6.4 SAMPLING

Transects have been cut through the different vegetation types covering the study area. Along these transects, biconical and Nguruman traps were set and emptied at intervals ranging from 1 to 4 days. The flies were separated into species, sexed and counted to give data on the distribution of tsetse flies both in space and time.

6.5 WEATHER STATION

6.5.1 DELTA-T

Climatic conditions were monitored from the middle of May 1989 to June 1990 using the Delta-T weather station, which consists of a set of sensors and a Delta logger.

The Delta-T weather station mast is 2m high and is supported by four guy ropes. A solar radiation sensor is mounted at the top of the mast. A horizontal cross-bar, mounted near the top of the mast, supports an anemometer and windvane. The relative humidity and air temperature sensors are housed in a screen, which is attached to an offset mounting arm just below the cross-bar. The rain-gauge is anchored to the ground about 5m away from