# ECOLOGY AND VECTORIAL CAPACITY OF *GLOSSINA FUSCIPES FUSCIPES* NEWSTEAD 1910 ON RUSINGA ISLAND AND ALONG THE SHORES OF LAKE VICTORIA, KENYA

by

Mwangelwa Inambao Mwangelwa

B.Sc. (UNZA), M.Sc. (Nairobi)

A thesis submitted in partial fulfilment of the requirements of the degree of Doctor of Philosophy of the University of Zambia

July, 1990

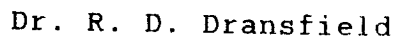
# DECLARATION

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

Signed:

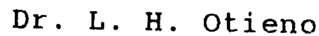
Mwangelwa Inambao Mwangelwa

This thesis has been submitted with our approval as supervisors:

Signed: 

Dr. R. D. Dransfield

ICIPE, P. O. BOX 30772, NAIROBI, KENYA

Signed: 

Dr. L. H. Otieno

ICIPE, P. O. BOX 30772, NAIROBI, KENYA

Signed:

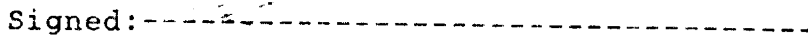
Dr. K. J. Mbata

UNZA, BIOLOGY DEPT., P. O. BOX 32379
LUSAKA, ZAMBIA

## APPROVAL

This thesis of Mr. Mwangelwa Inambao Mwangelwa is approved as fulfilling the requirements for the degree of Doctor of Philosophy in Biology of the University of Zambia.

Internal Examiners:



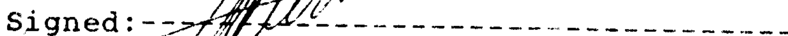
Signed:----------------------------------

Dr. Y. D. Deedat
UNZA, School of Agriculture, P. O. Box 32379
LUSAKA, ZAMBIA

Signed:----------------------------------

Dr. K. J. Mbata
UNZA, Biology Dept., P. O. Box 32379
LUSAKA, ZAMBIA

External Examiner:



Signed:----------------------------------

Prof. Y. Tsutsumi
UNZA, School of Veterinary Medicine
P. O. Box 32379
LUSAKA, ZAMBIA

for: Prof. C.P.M. Khamala
University of Nairobi, Department of Zoology
P. O. Box 30197
NAIROBI, KENYA

## DEDICATION

For Lilian Chaze who missed me throughout the period this study was carried out.

# TABLE OF CONTENTS

Page

TITLE....................................................i

DECLARATION..............................................ii

APPROVAL.................................................iii

DEDICATION...............................................iv

LIST OF TABLES...........................................ix

LIST OF FIGURES..........................................xii

ABSTRACT.................................................xv

CHAPTER 1: GENERAL INTRODUCTION AND LITERATURE REVIEW......1

General Introduction.....................................1

Literature review........................................7

Systematics..............................................7

Distribution of tsetse flies..............................9

Changes in the distribution of *palpalis* group of tsetse flies.............14

Ecology and population dynamics of *G. f. fuscipes*.......15

The use of odour-baited traps/targets for sampling and controlling tsetse flies.........19

Vectorial capacity of tsetse flies.........30

Historical aspects of sleeping sickness in South Nyanza, Kenya............37

Control of *G. f. fuscipes* in Kenya.........41

CHAPTER 2: STUDY AREA....................................44

Geographical location....................................44

Landscape....................................44

Climate....................................46

Vegetation....................................46

Wildlife....................................47

Human and livestock populations....................................48

CHAPTER 3: DISTRIBUTION AND DIEL ACTIVITY PATTERNS OF *G. F. FUSCIPES* ON RUSINGA ISLAND AND THE MAINLAND....................................50

Introduction....................................50

Materials and methods....................................51

Results....................................53

Discussion....................................57

CHAPTER 4: POPULATION DYNAMICS OF *G. F. FUSCIPES* ON RUSINGA ISLAND AND THE MAINLAND IN MBITA, SOUTH NYANZA, KENYA....................................61

Introduction....................................61

Materials and methods....................................62

Meteorological data....................................62

Sampling procedure....................................62

Dissection of flies....................................63

Analysis of ovarian age data....................................66

Mark-release-recapture experiments....................................68

Results....................................73

Meteorological factors....................................73

Apparent density....................................73

Age composition........................76

Reproductive abnormalities...............82

Mark-release-recapture studies...........88

Feeding and pregnancy cycles..........88

Absolute population size..............89

Dispersal.............................91

Discussion................................94

CHAPTER 5: RESPONSES OF *G. F. FUSCIPES* TO ODOUR BAITS AND TRAP TYPES ON RUSINGA ISLAND, KENYA...........................101

Introductio...............................101

Materials and methods.....................102

Chemical baits........................102

Dispensers............................105

Dose rates............................105

Trap types............................107

Experimental design of trials.........115

Results...................................117

Discussion................................124

CHAPTER 6: REARING *G. F. FUSCIPES* FOR VECTORIAL CAPACITY STUDIES ...................130

Introduction..............................130

Materials and methods.....................132

Tsetse insectary......................132

Tsetse fly collection..................133

Tsetse fly rearing....................134

Results...................................135

Discussion................................138

**CHAPTER 7: STUDIES ON VECTORIAL CAPACITY OF *G. F. FUSCIPES*** .......... 141

Introduction .......... 141

Materials and methods .......... 142

Field collected tsetse flies .......... 142

Host determination .......... 143

Laboratory studies .......... 143

Laboratory animals .......... 143

Infection of rats and tsetse flies .......... 148

Results .......... 149

Field studies .......... 149

Host determination .......... 152

Laboratory studies .......... 152

Trypanosome infection in flies .......... 152

Discussion .......... 159

**CHAPTER 8: GENERAL DISCUSSION** .......... 167

**SUMMARY** .......... 173

**REFERENCES CITED** .......... 178

**ACKNOWLEDGEMENTS** .......... 227

**LIST OF ABBREVATIONS** .......... 230

**APPENDICES** .......... 231

## LIST OF TABLES

Table Page

1. Species and subspecies of the genus *Glossina*..........8

2. Reproductive abnormalities in *G. f. fuscipes* in samples from Rusinga Island and the mainland collected from February 1988 to January 1989.........86

3. The frequency of empty uteri and abortions recorded in *G. f. fuscipes* in samples from Rusinga Island and the mainland from February 1988 to January 1989.......................................87

4. The distances from the release point at which *G. f. fuscipes* was recaptured and the times taken after marking.................................92

5. Best fit values of lambda to estimate root-mean-square displacement per hour for *G. f. fuscipes* on Rusinga Island.................93

6. Dose rates of odour baits determined in a series of experiments on Rusinga Island from February 1988 to July 1989...................................108

7. The effect of acetone and cow urine on the catches of *G. f. fuscipes* on Rusinga Island.........118

8. The effect of acetone, 1-octen-3-ol, cow urine, TF 841, TF 89/1 and TF 89/4 applied either singly or in combinations on the catches of *G. f. fuscipes*.....................................119

9. The effect of cow and human urine and washings from a monitor lizard and a goat on the catches of *G. f. fuscipes*...................................120

10. Summary of odour baits used in various experiments on Rusinga Island for *G. f. fuscipes*....121

11. Analysis of numbers of *G. f. fuscipes* caught by different types of traps on Rusinga Island.......122

12. Performance of the *G. f. fuscipes* colony at the ICIPE Mbita Point Field Station from November 1988 to September 1989.....................136

13. Weight of pupae produced by wild and laboratory reared *G f. fuscipes* from April 1988 to August 1989 arranged in class weights. In brackets is the percentage number of total weight for each class.......................................137

14. The number of *G. f. fuscipes* dissected and examined for trypanosome infection from Rusinga Island and the mainland in Mbita, South Nyanza District, Kenya.......................................150

15. Results of tsetse blood meal analysis of *G. f. fuscipes* caught from Rusinga Island and the mainland.......................................151

16. Trypanosome infection rates in *G. f. fuscipes* and *G. pallidipes* infected with a *T. congolense* stock F1.......................................153

17. Trypanosome infection rates in *G. f. fuscipes* and *G. pallidipes* infected with a *T. congolense* stock F2.......................................154

18. Trypanosome infection rates in *G. f. fuscipes* and *G. pallidipes* infected with a *T. congolense* stock Maruma.................................155

19. Trypanosome infection rates in *G. f. fuscipes* and *G. pallidipes* infected with a *T. brucei* stock F4.......................................156

20. Trypanosome infection rates in *G. f. fuscipes* and *G. pallidipes* infected with a *T. brucei* stock F6.......................................157

21. Trypanosome infection rates in *G. f. fuscipes* and *G. pallidipes* infected with a *T. brucei* stock F27 .......... 158

## LIST OF FIGURES

Figure page

1. Map of study area (Rusinga Island and the mainland) and its environs....................45

2. Map of Rusinga Island and the mainland showing tsetse distribution............................54

3. Hourly profiles of (a) male (____) and female (---) ***G. f. fuscipes*** caught in traps on Rusinga Island; (b) solar radiation intensity; (c) relative humidity; (d) ambient temperature and (e) windspeed recorded on Rusinga Island.........56

4. Map of Rusinga Island and the mainland showing trap positions during the second mark-release-recapture experiment for ***G. f. fuscipes*** from 8 November 1988 to 12 December 1988....................72

5. (a) Mean maximum soil temperature (____) and mean maximum ambient temperature (---) recorded at 9.00 h; (b) mean minimum soil temperature (____) and mean minimum ambient temperature (---) recorded at 9.00 h; and (c) percentage relative humidity recorded at 9.00 (____) and 15.00 (---) h on Rusinga Island with histograms showing rainfall recorded at Mbita.........74

6. ***G. f. fuscipes*** catches from (a) Rusinga Island and (b) the mainland showing males (____) and females (---) and (c) rainfall recorded at Mbita..............75

7. Percentage female ***G. f. fuscipes*** of the total catch on Rusinga Island (____) and the mainland (---)..........................................77

8. Age composition of (a) male and (b) female ***G. f. fuscipes*** from Rusinga Island (shaded) and the mainland (clear)...................................78

9. Age composition and pregnancy stages of *G. f. fuscipes* on Rusinga Island (shaded) and the mainland (clear) caught in traps from February 1988 to June 1989....................................80

10. Apparent mortality rates of *G. f. fuscipes* on Rusinga Island (____) and the mainland (---) estimated using the ovarian age analysis method......81

11. The relationship between rainfall and mortality rates of female *G. f. fuscipes* on Rusinga Island obtained using the ovarian age analysis method......83

12. Moran plots derived from arithmetic means per trap per day data for *G. f. fuscipes* plotted on a logarithmic scale, (a) males and (b) females from Rusinga Island and (c) males and (d) females from the mainland....................................84

13. Mortality rates of male (____) and female (---) *G. f. fuscipes* on (a) the mainland and (b) Rusinga Island, estimated from Moran plots..................85

14. Corrected recapture rates of (a) male and (b) female *G. f. fuscipes* on Rusinga Island showing peaks for females at intervals of about 4 and 7-9 days following marking.....................90

15. Monitor lizard from which skin scrapings and body washings baits were derived.....................104

16. Some of the dispensers used for 1-octen-3-ol, acetone and cow urine baits in trapping trials for *G. f. fuscipes* on Rusinga Island and the mainland........................................106

17. The biconical trap used in the trapping studies.....109

18. The NG2B trap used in the trapping studies..........110

19. The NG2G trap used in the trapping studies..........111

20. The F3 trap used in the trapping studies............112

21. The Vavoua trap used in the trapping studies........113

22. The pyramidal trap used in the trapping studies.....114

23. The decline in the catches of ***G. f. fuscipes*** over the four days of testing various odour baits in latin-square designed experiments on Rusinga Island, (a) males and (b) females........123

## ABSTRACT

Studies were carried out on Rusinga Island and the mainland in the Mbita Division of South Nyanza District, Kenya, from November 1987 to December 1989 to determine the distribution and diel activity patterns, population dynamics and responses of ***Glossina fuscipes fuscipes*** Newstead 1910 to various odour attractants and trap types. The vectorial capacity of ***G. f. fuscipes***, a vector of both human and animal trypanosomiasis, was also examined in the field and in the laboratory. The details of the current tsetse/trypanosomiasis situation were assessed in view of the frequent outbreaks of human trypanosomiasis in the neighbouring regions.

The distribution of ***G. f. fuscipes*** was confined to strips of thick vegetation along the lake shores. Tsetse flies were caught all around the island. Apparent densities of ***G. f. fuscipes*** were found to be remarkably stable on both Rusinga Island and the mainland varying by a factor of five and seven, respectively, during the study period. Low trap catches were recorded during and immediately after the rainy season. In one of the study sites on Rusinga island, the absolute population density was estimated at 301 males and 559 females per hectare from mark-release-recapture studies. The mortality rates for the flies derived by two methods (i.e. ovarian age analysis and Moran curves technique) were

not significanlty correlated. Mortality rate estimates by ovarian age analysis showed a higher mortality on Rusinga island than on the mainland. This high mortality was recorded during the rainy season on the island. Reproductive abnormalities in female flies did not exceed 2 % indicating that the populations were not under stress. Using a random diffusion equation, fly movement was estimated at 112 m per day. The short distance travelled implied that if control programmes involving traps were to be initiated they would have considerable effect on the tsetse fly populations in areas within the vicinity of traps (e.g. villages). However, control of the flies from large areas would be difficult.

Studies of odour attractants indicated that the use of cow and human urine, acetone, 1-octen-3-ol, phenolic fractions and washings from a monitor lizard and a goat as attractants did not enhance trap catches. Trap catches of females were inconsistent when acetone and cow urine were added to traps. At times the fly catches increased and at other times decreased. Females were strongly repelled by combinations of acetone, cow urine and phenolic fractions. The causal factors for this response are discussed. Of the six trap designs compared, the biconical trap was the most effective followed by the pyramidal trap, NG2B and NG2G, Vavoua and F3 traps.

Trypanosome infection rates in wild-collected flies were very low (0 % on Rusinga island and 0.1 % on the mainland). Laboratory studies indicated that although ***G. f. fuscipes*** was significantly less susceptible to mature infection with ***T. congolense*** and ***T. brucei*** than ***G. pallidipes*** there were no significant differences in immature infections between the two fly species. It was unlikely that an epidemic of human trypanosomiasis transmitted by ***G. f. fuscipes*** would occur on Rusinga island and the immediate area on the mainland. This is because of the confinement of the fly distribution to strips of vegetation along the lake shores, the nature of fly feeding patterns and the absence of trypanosome reservoir hosts in the area.

# CHAPTER 1

# GENERAL INTRODUCTION AND LITERATURE REVIEW

## GENERAL INTRODUCTION

Tsetse flies (***Glossina*** species) are the vectors of the pathogenic salivarian trypanosomes that cause African trypanosomiases. These parasites affect both man and his domestic livestock causing sleeping sickness or human trypanosomiasis and nagana or animal trypanosomiasis, respectively. Tsetse flies and the diseases they transmit occur in an area of about 10 million square kilometres spanning 37 sub-Saharan countries (FAO, 1979; WHO, 1987).

Recent estimates by (WHO) (1987) indicate that 50 million people living in or around areas where the disease is endemic are at risk of infection. Only 10% of this population is under surveillance and the World Health Organisation (WHO) aims to raise this figure to 80% by 1992. On the average about 20,000 new cases are reported each year. African human trypanosomiasis is considered by WHO as one of the six major tropical diseases including malaria, schistosomiasis, filariases, leshmaniases and leprosy.

FAO (1979) reported that "animal trypanosomiasis is probably the only disease which has profoundly affected the

settlement and economic development of a major part of a continent." In light of the magnitude of the problem presented by the disease the Food and Agricultural Organisation of the United Nations (FAO) considers the control of the disease obligatory and as a high priority issue for increasing agricultural production in support of general economic development in Africa.

The impact of animal trypanosomiasis is both direct and indirect. The direct effect is in the form of deaths of livestock due to the disease and the financial requirements for control operations. The disease indirectly affects agricultural productio.. and rural and national economies by the deprivation of benefits that would be obtained from cattle (Wilson *et al.*, 1963; FAO, 1979).

It is impossible to quantify the losses caused by animal trypanosomiasis. This is because there are so many other factors that may contribute to its fatality such as other diseases, problems of availability of water and pasture for livestock development and the difficulties of access to some affected areas to determine mortality. However, despite these constraints some authorities (OAU/STRC, 1980; Jordan, 1986) consider that animal trypanosomiaisis is often the single most important constraint preventing the exploitation of the vast potential of livestock development in Africa.

FAO (1979) estimated the potential for meat production in tsetse infested areas, if the disease was cleared in Africa. The area that is tsetse infested which could be used for livestock production was estimated to be about 7 million square kilometres. The average potential carrying capacity was estimated at 20 cattle per square kilometre and the total potential population of tsetse fly infested zone at 140 million cattle. At that time the cattle population in this area was only 20 million. The average cattle productivity in Africa was estimated at 12.5 kilogrammes per head per year and additional meat production at 1.5 milion tons per year. The value of additional meat production taken at a cost of 50 US cents per kilogramme was estimated at US $ 750 million. Thus there is vast potential for livestock production in tsetse infested areas but that this potential is not exploited because of the presence of tsetse flies. This has restricted livestock production to areas where tsetse flies cannot survive causing pressure on land usage as a result of shortage of pasture. If food production is to be increased to meet the requirements of the African human populations, there is need to claim the tsetse infested areas.

There are various approaches to trypanosomiasis control and these have been discussed in detail by Jordan (1986). Methods of control can be directed at the parasites or the

vectors. For the former, potential methods include the use of trypanocidal drugs, immunisation and the use of trypanotolerant breeds of livestock. Of these methods the use of trypanocidal drugs is the most common. Although drugs can be highly effective if proper treatment regimes are followed, the high costs involved and the development of drug resistant strains of trypanosomes limit their use (Jordan, 1986). With no trypanosocidal drug developed for many years a search for alternative methods is essential. The use of trypanotolerant breeds of cattle, sheep and goats in tsetse fly infested areas is an important alternative. In West Africa, for example, several breeds of cattle can survive and reproduce in tsetse fly infested areas without chemotherapy. The disadvantages of the use of trypanotolerant breeds of cattle include the need for high financial inputs required coupled with slow economic returns due to the slow breeding cycle of the cattle. Additionally, there is cultural resistance to small breeds of cattle, characteristic of the trypanotolerant breeds identified in West Africa.

Vector control methods include avoidance of hosts from contact with tsetse flies, clearing of vegetation, destruction of wild animals, application of insecticides, sterile male release techniques and the use of traps and insecticide-impregnated targets. Vector control in its various forms has contributed considerably to the control of

the disease. Earlier methods employed such as game elimination and clearing of vegetation are no longer favoured because of the wastage of natural resources and environmental damage (Jordan, 1986). The use of insecticides is still the most common vector control method today. There is as yet no strong evidence indicating the detection of resistance to any insecticide in tsetse flies (Jordan, 1986; but see also Turner and Golder, 1986). This method has come under critisism from environmentalists due to pollution and the adverse effect it has on non-targets organisms. Intensive research into the ecology, behaviour and physiology of the fly is, therefore, being carried out to develop environmentally safer methods. Among these are the rational uses of chemotherapy, the use of traps and targets, identification and use of tsetse attractants and the release of sterilized male tsetse flies to reduce tsetse populations.

This project was an attempt to provide further information on the biology and population dynamics of ***G. f. fuscipes*** that would be needed for its control, with particular reference to the use of traps. The objectives of the study were therefore to:

1. determine the distribution of ***Glossina fuscipes fuscipes*** on Rusinga Island and along the shores of Lake

Victoria in Mbita Division, South Nyanza District, Kenya.

2. investigate the population dynamics of ***G. f. fuscipes*** in the study areas with a view to designing better control methods for the subspecies.

3. elucidate the efficacy of various trap-types for the capture of ***G. f. fuscipes*** in the field as a control technique.

4. determine the vectorial capacity of ***G. f. fuscipes*** for trypanosomes of the ***congolense*** and ***brucei*** types and to determine its role in trypanosomiasis transmission.

5. give insight into the current tsetse/trypanosomiasis situation on Rusinga Island and the immediate mainland in Mbita area in view of the frequent outbreaks of trypanosomiasis in the neighbouring regions.

6. provide data which would assist the Government of Kenya to make decisions on whether or not it it is necessary to carry out control measures in localities dominated by this subspecies of tsetse flies.

# LITERATURE REVIEW

## Systematics

All tsetse flies are placed in the genus *Glossina*. In recent years authorities have placed the genus in an independent family, Glossinidae (Brues *et al.*, 1954; Haeselbarth *et al.*, 1966). According to Glasgow (1970a) the genus comprises 22 species. The revised list (Table 1) of species and subspecies was recently reported by Jordan (1986).

The genus is subdivided into three groups on the basis of the characters of the male and female genital armatures namely; the *fusca*, *palpalis* and *morsitans* groups (Newstead, 1911; Newstead *et al.*, 1924). These groups, which were initially established on the basis of morphology only, have been confirmed by studies of the general habitat preferences of the flies and their genetics (Jordan, 1974). *Glossina fuscipes fuscipes* belongs to the *palpalis* group and has the status of a subspecies together with *G. f. quanzensis* and *G. f. martinii* following the taxonomic revision of Machado (1954, 1959, cited by Potts 1970a).

Table 1. Species and subspecies of the genus *Glossina*
(from Jordan, 1986)

*fusca* group

*G. fusca*
- *fusca* (Walker) 1849
- *congolensis* Newstead & Evans 1921

*G. tabaniformis* Westwood 1850

*G. longipennis* Corti 1895

*G. brevipalpis* Newstead 1910

*G. nigrofusca*
- *nigrofusca* Newstead 1910
- *hopkinsi* van Emden 1944

*G. fuscipleuris* Austen 1911

*G. medicorum* Austen 1911

*G. severini* Newstead 1913

*G. schwetzi* Newstead & Evans 1921

*G. haningtoni* Newstead & Evans 1922

*G. vanhoofi* Herard 1952

*G. nashi* Potts 1955

*palpalis* group

*G. palpalis*
- *palpalis* (Robinean-Desvoidy) 1830
- *gambiensis* Vanderplank 1949

*G. tachinoides* Westwood 1850

*G. pallicera*
- *palicera* Bigot 1891
- *newsteadi* Austen 1929

*G. fuscipes*
- *fuscipes* Newstead 1910
- *martinii* Zumpt 1933
- *quanzensis* Pires 1948

*G. caliginea* Austen 1911

*morsitans* group

*G. longipalpis* Wiedemann (1830)

*G. morsitans*
- *morsitans* Westwood 1850
- *submorsitans* Newstead 1910*
- *centralis* Machado 1970

*G. pallidipes* Austen 1903

*G. austeni* Newstead 1912

*G. swynnertoni* Austeni 1903

* An eastern form, *ugandensis* Vanderplank 1949, of this subspecies is recognised by Machado (1970)

## Distribution of Tsetse flies

Ford (1970, 1971) has described the zoogeography of the genus ***Glossina***. At present tsetse flies are found only in sub-Saharan Africa. However, there is evidence of there having been a much wider distribution of tsetse flies in the past from observations made in Arabia by Carter (1906, cited by Ford, 1970), and from the fossil records of tsetse dating back to 40 million years ago found in the Oligocene shales of Florissant, Colorado, in North America.

The first edition of tsetse distribution maps were complied by Potts in 1953-1954. These were updated and revised by Ford and Katondo (1977a, 1977b) and published as the second edition. These authors took into account recent changes in the systematics of tsetse species. In his review Challier (1982) summarized all available information on tsetse distribution from 1970-1981 and more recently Katondo (1984) revised the second edition of the tsetse distribution maps to indicate the recent retreats and expansions of the tsetse belts as well as tsetse cleared areas following control operations.

The distribution of tsetse flies in Africa generally falls between latitudes 14° N and 29° S representing an area of about 10.8 million square kilometres (Eouzan, 1977). Eouzan also stated that climate, vegetation and availability

of animal hosts of the flies determine the extent of the distribution. He further observed that the Sahara Desert forms the northern limit of the distribution because of the arid conditions which are unsuitable for the survival of tsetse flies. Cold temperatures due to mountainous areas and the hot Kalahari Desert limit the distribution in the south-east and south-west of the African continent, respectively.

The distribution of the ***fusca, palpalis*** and ***morsitans*** groups was recently reviewed by Jordan (1986). This review reveals that the distribution of the species of the ***fusca*** group is less known than the other two groups because they are economically important and secondly, their presence is difficult to detect. These species were shown to mostly occupy various types of rain forests whereas ***G. haningtoni, G. nashi. G. tabaniformis, G. vanhoofi, G. severini*** and in some cases, ***G. nigrofusca*** inhabited lowland rain forests. However, ***G. fusca, G. schwetzi, G. fuscipleuris, G. medicorum*** and in some cases, ***G. nigrofusca*** occurred in forested areas outside the lowland rain forests such as the edge of the rain forest, in forest along water courses and forest islands (relic forest) (Jordan, 1986). In East Africa two species of this group, ***G. brevipalpis*** and ***G. longipennis***, occupy atypical habitats. The former occupies islands of forest, often associated with water courses while the latter inhabits semi-arid areas.

The species of the ***palpalis*** group like those of the ***fusca*** occupy the lowland rain forests, but the distribution of these species extend into the drier savannas along rivers and streams. They occur along river systems draining into the Atlantic Ocean, Mediterranean Sea and the inland drainage systems of some of the big African lakes, but not along river systems draining into the Indian Ocean (Jordan, 1986). ***G. p. gambiensis*** and ***G. p. palpalis*** occur in lowland rain forests and are also found in drier savanna areas associated with water courses. The former species occurs to the west and north of an irregular line from the coast in Sierra Leone to northern Benin, while the latter occurs to the south and east of this line extending south, along the western part of Africa, to Angola (Jordan, 1986). ***G. pallicera*** occurs in the rain forest and ***G. caliginea*** in the coastal mangrove communities but penetrates into the rain forest in West Africa. ***G. tachinoides*** mainly occupies areas along rivers and streams in the savannas of West Africa outside the lowland rain forests but it can invade areas cleared of forest.

***G. fuscipes*** mostly occupies the Congo Basin, but the distribution extends further north and east into the basin of the Upper Nile (Ford, 1970). Ford considered that the original ***G. fuscipes*** populations inhabited a large part of the Congo forest which was rooted in Kalahari sands. Dry

epochs that occurred around 75,000-52,000 and 10,000 years ago followed the emptying of the Miocene lake and the reduction of the peri-lacustrine forests occupied by this species in the region, to mere gallery forests. This process led to a segregation of the populations of ***G. fuscipes*** occupying the northern parts of the basin from those of the Kasai and other main tributaries that follow a meridional course across the Congo Basin from the region of the present day Angola border. This isolation led to the development of ***G. f. quanzensis*** which is a gallery forest tsetse fly in derived savanna or forest mosaic vegetation. ***G. f. martinii*** evolved independently as a result of the isolation of Lake Tanganyika long after the final formation of this lake in the middle Pliocene. The distribution of ***G. f. martinii*** which is mainly in the Lualaba Valley in Zaire, extending into the Luapula Valley in Zambia, is smaller than that of the other two subspecies. This is a gallery forest tsetse fly of the Miombo woodlands dominated by ***Brachystegia*** trees. ***G. f. fuscipes*** has a far wider distribution than either of the other two ***fuscipes*** subspecies. It occupies the great central rain forest of the present day Zaire; the distribution extends north to Chad, the Central African Republic, Cameroun, Gabon, and to the north-east and east to Sudan, Ethiopia, Uganda, Kenya and Tanzania (Ford, 1970, 1971). In Kenya, the distribution of ***G. f. fuscipes*** is restricted to the area around Lake

**Changes in the Distribution of *palpalis* group of Tsetse flies**

The distribution of the *palpalis* group, unlike that of the ***morsitans*** group, has changed very little with respect to changes in human populations and their activities (Rogers and Randolph, 1986a). As Jordan (1986) has observed, "it is likely that these species occupy much the same area today as they occupied when man first became a dominant feature on the African scene." Studies of ***G. tachinoides***, for example, in the forest/savanna mosaic zones of southern Nigeria carried out by Baldry (1964, 1980) and Madubunyi (1986) and, of ***G. palpalis palpalis*** in Ivory Coast by Gouteux and Laveissiere (1982), have demonstrated that these species have adapted to habitats modified or created by man. These habitats include sacred groves, oil palms, banana, coffee and cocoa plantations. Under such conditions, their original preferred hosts having been either eliminated or driven away, the tsetse flies utilize available alternative hosts like reptiles, man and his domestic animals. Baldry (1980) suggested that there is a close association between foci of the West African human trypanosomiasis and the presence of pigs.

**Changes in the Distribution of *palpalis* group of Tsetse flies**

The distribution of the *palpalis* group, unlike that of the ***morsitans*** group, has changed very little with respect to changes in human populations and their activities (Rogers and Randolph, 1986a). As Jordan (1986) has observed, "it is likely that these species occupy much the same area today as they occupied when man first became a dominant feature on the African scene." Studies of ***G. tachinoides***, for example, in the forest/savanna mosaic zones of southern Nigeria carried out by Baldry (1964, 1980) and Madubunyi (1986) and, of ***G. palpalis palpalis*** in Ivory Coast by Gouteux and Laveissiere (1982), have demonstrated that these species have adapted to habitats modified or created by man. These habitats include sacred groves, oil palms, banana, coffee and cocoa plantations. Under such conditions, their original preferred hosts having been either eliminated or driven away, the tsetse flies utilize available alternative hosts like reptiles, man and his domestic animals. Baldry (1980) suggested that there is a close association between foci of the West African human trypanosomiasis and the presence of pigs.

Evidence is accruing from the environs of Lake Victoria in Uganda and Kenya that *G. f. fuscipes* can also be closely associated with man and utilize peridomestic habitats (Willett, 1965; Okoth, 1980; Okoth and Kapaata, 1987). In Busoga and Lugala, Uganda, Abaru and Matovu (1981), Ssebalijja (1981) and Okoth (1982) reported that the population of *G. pallidipes* and *G. brevipalpis*, once abundant species, were declining while that of *G. f. fuscipes* was gradually increasing because of the increase in human settlements. *G. f. fuscipes* increased in numbers probably because it could utilize peridomestic habitats such as plantations and hedges of *Lantana camara* and because of its opportunistic feeding behaviour. The presence of humans could have reduced the prefered hosts of the other species.

## Ecology and Population Dynamics of *G. f. fuscipes*

Population ecology of *Glossina* species was reviewed by Buxton (1955), Glasgow (1970b) and more recently by Rogers and Randolph (1985). In their review they outlined the general theory of regulation of populations and applied it to explain changes in the distribution and abundance of tsetse populations. They further outlined the problems associated with sampling tsetse flies and related them to the interpretation of data relevant to tsetse control strategies.

Studies on the population dynamics of ***G. f. fuscipes*** in Kenya are scanty. Glasgow (1954) while assessing the feasibility of bush clearing as a method of controlling tsetse in Central Nyanza, estimated changes in apparent densities of ***G. f. fuscipes*** in blocks of vegetation he demarcated near the lake shore for a period of up to six years and three months. In one of the blocks, in addition to relative estimates, he also estimated absolute population densities by marking, releasing and recapturing non-teneral males. He observed that although there were long term fluctuations in apparent densities these were neither annual nor related to season. However, populations in lake-side blocks fluctuated together and so did the riverine blocks, but the two groups fluctuated indepedently of each other. He estimated the population in one of the blocks to be about 250 males per hectare with a mean death rate of 26 % per week (4.2 % per day) and a mean longevity of 27 days. On the basis of the proportions of tenerals, non-teneral females and males in the catches biting man he came to the conclusion that riverine ***G. f. fuscipes*** were more hungry than flies of the same species caught on the lake shore because the proportions of each group biting man were higher along the river than along the lake shore. Bursell and Glasgow (1960) reported the opposite after observing that riverine puparia and flies were slightly larger than those caught from the lake shore. They concluded that the latter

were under stress as compared to the former and suggested that climatic factors (temperature and saturation deficity) were responsible. They suggested that higher temperatures at their study area along the lake shore led to rapid utilisation of food reserves in flies, which in turn led to an increase in the percentage of males caught and production of smaller puparia by females.

McConnell (1912) who observed the habits of ***G. f. fuscipes*** in Uganda noted that the most favourable habitat was the "conjuction of a tree or scrub shade, water and rocky clean bank." Fiske (1920) and Gibbins (1941) confirmed this finding and showed that ***G. f. fuscipes*** mostly inhabited riparian forests within which flies were mostly caught less than 91 m from the edge of the water. However, flies could range up to a few kilometres inland if conditions, such as shelter, animal hosts and breeding grounds were suitable. Chorley (1944) working in Busoga, Uganda, observed that *G. f. fuscipes* bred as far away as 19 km from the lake shore.

Rogers (1977) working in South Busoga in Uganda investigated the population ecology of ***G. f. fuscipes***. He reported that the distribution of flies was related to the amount of light reaching any particular area and hence was determined by the vegetational cover. Oloo (1983) who studied the ecology of the same subspecies at Gunga in Kenya

also observed that of the physical factors (temperature, relative humidity and light intensity) light intensity was the key factor controlling fly activity within the temperature range of 20-36 °C when the flies were active. Within this temperature range, fly activity did not significanly vary in relation to changes in temperature. There was also no significant correlation between changes in relative humidity and numbers of tsetse flies caught.

Harley (1965) reported that in Lugala in Uganda diel activity patterns of ***G. f. fuscipes*** occured between 5.00 and 19.00 h. He observed that maximum activity occured between 10.00 and 16.00 h and that peak activity varied from site to site and season to season. Oloo (1983) obtained results falling within this range at Gunga in Kenya where he recorded peak activity to occur at 10.45 h.

From mark-releasese-recapture studies Rogers (1977) estimated that male flies had a feeding interval of four days as reflected by regular peaks obtained in the recapture rate. He observed that the concentration of marked flies decreased regularly with distance from the point of marking and release and suggested that this was a result of random movement of the flies. Using a simulation model he estimated the distance moved by male ***G. f. fuscipes*** to be 338 m per day. However, Gibbins (1941) had earlier reported that movement of this fly along the rivers in Uganda was

quite considerable, flies covered 6-8 km in 7-8 hours during the day.

Oloo (1983) reported that ***G. f. fuscipes*** larviposited in three sites near the lake shore including the sloping edges of drainage systems, flat surfaces between buttresses of trees, below inclined stems and in holes in the stems or in the ground covered with vegetation. Resting sites observed included rock surfaces, fallen branches twigs and upper sides of leaves. Studies conducted in Busoga, Uganda, by Okoth (1986a) indicated that ***G. f. fuscipes*** was peridomestic, breeding in coffee, banana and ***Lantana camara*** thickets as well as under house verandahs and, on one occasion inside a hut.

**The use of Odour-baited Traps/targets for Sampling and Controlling tsetse flies.**

The first recorded use of trapping mechanisms (in this case screens) to catch tsetse flies dates back to 1910 when Maldonado (cited by Buxton, 1955) had his workers wear on their backs a black piece of cloth covered with "bird lime" to catch ***G. p. palpalis*** on the Island of Principe, off the west coast of Africa. This was part of an exercise directed at controlling an epidemic of sleeping sickness which had developed among the workers engaged on the cocoa and coffee

plantations. Lamborn (1915) and Ruttledge (1928) also used "bird lime" to catch tsetse flies but with little success. However, screens without adhesive substances were used by Jack (1941) and Barrass (1960) as a means of attracting tsetse before being caught with hand nets.

The first trap "proper" was designed by Harris (1930) (cited by Buxton, 1955) in Zululand, South Africa, for use against ***G. pallidipes.*** This proved successful and was used in a control campaign against this species. Harris's trap was tried by other workers elsewhere, either in its original or modified form, for other tsetse species including ***G. f. fuscipes*** but with varying degrees of success (Swynnerton, 1933, 1936; Jack, 1941, Langridge, 1975 and Moloo, 1973). Many other designs of traps were developed with similar successes (Chorley, 1933; Lloyd, 1933; Lewillon, 1945, quoted by Buxton, 1955; Morris and Morris, 1949 and Morris, 1960).

Swynnerton (1933) remarked about the relative readiness with which ***G. f. fuscipes*** entered traps and suggested that trapping could be used to destroy this fly. Despite the early promising results, the old traps were cumbersome to handle and were not very effective. Until the late 1960s most of the data on ecological studies were based on samples collected using hand nets supplemented by data for catches from various traps (Vale ***et al.***, 1985). Jordan (1986) in a

discussion of the use of traps in control campaigns concluded that up to about 1960 there were clear indications that traps could be used to control the ***palpalis*** group of flies with linear distribution along water courses or infesting islands but not the ***morsitans*** group with a much wider dispersal.

The design of the biconical trap (Challier and Laveissiere, 1973) and its improvement (Challier, ***et al.***, 1977) rekindled the interest in the use of traps for ecological studies. Following this, the effectiveness of various traps was again assessed (Hargrove, 1977; Owaga, 1981 and Ryan and Molyneux, 1982).

Studies by Vale (1974a, 1974b) on the responses of tsetse flies to mobile and stationary baits gave insight into the understanding of the behaviour of tsetse flies. He observed that the presence of man in the field (in an upright posture) depressed the catches, especially of females. Hargrove (1976) confirmed results obtained earlier by Vale and Vale (1979) further showed that lactic acid which occurs on human skin was a repellent to flies. In his previous studies Vale (1978) had exposed the weaknesses of the previous methods involving the use of hand nets. He asserted that the basic problem was that such methods undersampled the female component of the tsetse populations though it was known that in nature the sexes emerged from

the puparia in equal proportions and that females outlived males. Thus, this served as an impetus to researchers for improving trap designs for sampling the ***morsitans*** group of flies (Hargrove, 1977; Vale, 1982a, 1982b; Flint, 1985), using odour baits (Hargrove, 1977; Vale, 1985a, 1985b; Owaga, 1984, 1985; Dransfield ***et al.***, 1986). The development of more accurate methods of testing traps using electric screens (Vale and Hargrove, 1979) contributed a great deal to the improvement of trap design. Following these developments, Brightwell ***et al.*** (1987, 1990) designed a more effective trap for controlling ***G. pallidipes***.

The biconical trap of Challier ***et al.***, (1977) proved effective for a wide range of tsetse species particulary those of the ***palpalis*** group for which it was designed. To reduce costs, variants of this trap were developed mainly for the ***palpalis*** group of flies, that is, the monoconical trap (Lancien, 1981), the pyramidal trap (Gouteux and Lancien, 1986) and the Vavoua trap (Laveissiere, 1989). Some of these variants were more cost-effective but not necessarily superior to the original biconical trap.

Swynnerton (1933) described various traps some of which incorporated animal baits to enhance catches. He observed that the presence of a calf in a trap raised the catch of ***G. pallidipes*** even if the calf was not visible to the flies. In his discussion of scent as a bait he noted that animal

products such as urine, dung, blood and hides, however, were unattractive to ***G. swynnertoni*** and ***G. pallidipes***. He concluded, "Naturally we cannot sprinkle a large piece of country with calf-traps. Our effort now is to ascertain which of the scents of an animal is the one (if there be only one) that attracts the tsetse and then ask the chemists if they can reproduce it. We shall also test scents empirically...". Lloyd (1935) working in Shinyanga, Tanzania, reported similar results on ***G. swynnertoni***. Chorley (1933) working in Uganda smeared the fat of cormorants and crocodiles, and extracts of animal glands (sebaceous and other) on his traps and found that these were attractive to ***G. f. fuscipes***. Bax (1937) observed that ***G. swynnertoni*** responded to a herd of cattle and men passing at a distance of about 55 metres but not 91 metres. Chorley (1948) tested cattle dung and urine for attractiveness to tsetse flies in shelters near which they were captured with hand nets. He caught more tsetse flies near baited shelters than elsewhere. He also observed that in the field, ***G. morsitans*** congregated around herds of elephants, ***G. pallidipes*** around buffaloes and ***G. palpalis*** around hippopotamus. Hughes (1957a) reported that ***G. morsitans*** responded to various acids, alcohols and other compounds in the laboratory. In another study Hughes (1957b) found that vapour distillates from sump oil had no effect on ***G. palpalis*** contrary to observations made by Bax (1937) on ***G. swynnertoni***. Langridge (1960) applied lanolin (a

preparation made from sheep-wool grease), and hair and skin scrapings of pigs treated in benzene, on vegetation in ***G. pallidipes*** infested areas of Shimba Hills, Kenya. He observed that such applications increased the catch of flies two and five times, respectively, along treated sectors of the transect. By applying hot-water washings of pigs treated with petroleum spirit on the hessian of tsetse traps Persoons (1966) improved the catches of ***G. pallidipes*** and ***G. f. fuscipes*** in Uganda.

Interest in odour attractants then declined until the 1970's when the rediscovery of electric-nets that made it feasible to determine the responses of flies to baits in the absence of man (Vale, 1974a, 1974b). Vale's study demonstrated that host odour released at the base of traps significantly raised the catch of ***G. morsitans*** and ***G. pallidipes***. There was a positive correlation between the amount of host odour dispensed with the number of flies caught. Hargrove and Vale (1979) suggested that it was possible to employ odour baited traps for tsetse control. Although host odour was identified as attractive to ***G. morsitans*** and ***G. pallidipes*** it was expensive and inconvenient to use live animal baits in the field. There was, therefore, need to determine the chemical components that constituted host odour. Frezil and Carnevale (1976) working independently in Congo observed that carbon dioxide raised the catch of ***G. f. quanzensis***. By applying carbon

dioxide as dry ice to traps they increased the catch 40 times. They suggested that, apart from ecological studies, biconical traps could be used for control of sleeping sickness in Congo. Vale (1980) found that carbon dioxide and acetone increased by up to six times the catches of ***G. m. morsitans*** and ***G. pallidipes*** when dispensed separately or together in the field in Zimbabwe.

Owaga (1984, 1985) raised catches of ***G. pallidipes*** by addition of buffalo urine to biconical traps in Nguruman, Kenya. Buffalo urine was found to be ten times more effective than the control and about three times more attractive than acetone. Hall ***et al.*** (1984) identified and isolated 1-octen-3-ol as one of the active components of cattle odour. They found that it elicited electroantennograghic responses from ***G. m. morsitans*** and ***G. pallidipes*** with a dose-response curve about $10^6$ times more potent than acetone. 1-octen-3-ol was observed to be attractive to tsetse flies by itself in the field and appeared to play a synergistic role by increasing the attractiveness of ox odour and mixtures of carbon dioxide and acetone. Dransfield ***et al.*** (1986) working in Nguruman, Kenya, tested various ketones, 1-octen-3-ol, cow and buffalo urine as odour attractants for ***G. pallidipes***. They found that acetone, methyl ethyl ketone and 1-octen-3-ol increased catches by 9-25 times and that cow urine was as effective as buffalo urine. They suggested that the combination of cow

urine with acetone could be used as baits for community participation tsetse control schemes. Hassanali *et al.* (1986) identified seven phenols (phenol, 3-methylphenol, 4-methylphenol, 3-ethlyphenol, 4-ethlyphenol, 3-n-propylphenol and 4-n-propylphenol) in buffalo urine as the main phenolic components. Following this discovery Gough *et al.* (1987) identified eight phenolic fractions of cow urine two (4-methylphenol and 3-n-propyphenol) of which were as attractive to *G. pallidipes* as the total mixture. Similar observations were reported by Owaga *et al.* (1988) who used buffalo urine. Further studies by Vale *et al.* (1988) indicated that catches of *G. m. morsitans* and *G. pallidipes* in traps baited with acetone and 1-octen-3-ol were increased by the addition of a synthetic mixture of eight phenols found in cattle urine to propotions equal or greater than those in natural urine. The addition of natural urine to the synthetic mixture did not increase catches further, indicating that the phenols accounted for essentially all the attractiveness of cattle urine. Vale and his team also observed that 4-methylphenol and 3-n-propylphenol were the attractive fractions in cattle urine while 2-methoxyphenol reduced attractiveness. They found that 4-methylphenol was slightly attractive to both species, but only for males, increasing catches by about 50 %. 3-n-propylphenol increased catches of both species by about 50 %. Recently Warnes (1989) reported that ox sebum

significantly increased the catches of ***G. m. morsitans*** and ***G. pallidipes*** in field trials in Zimbabwe.

Most of the work on odour attractants has been conducted on savannna species, particulary ***G. pallidipes*** and ***G. morsitans***. Apart from studies reported by Frezil and Carnevale (1976) on ***G. f. quanzensis***, very little appears to have been done on the ***palpalis*** group until the mid 1980s. Galey ***et al.*** (1986) increased the catch of ***G. tachinoides*** more than three fold by releasing carbon dioxide near traps. Merot ***et al.*** (1986) increased the catch of ***G. tachinoides*** in Burkina Faso by applying ox odour. Cheke and Garms (1988) doubled the catch of ***G. p. palpalis*** in Liberia by incorporating acetone and 1-octen-3-ol to traps. But they found that phenols or a combination of all the three chemicals did not increase the catch. Spath and Kupper (1989) working in Ivory Coast raised the catch of ***G. tachinoides*** in biconical traps by 40 % by using a mixture of 3-methylphenol, 4-methylphenol and 1-octen-3-ol in the ratio 1:1:2. Merot (1989) reported that odours emanating from a man, a pig and a cow acted as attractants for ***G. tachinoides***. He further noted that the combination of m-cresol and 1-octen-3-ol was effective for the same species especially when used at the end of the dry season. When applied singly 1-octen-3-ol had no effect on ***G. tachinoides***. He did not explain how seasonality influenced the catches.

Research in central and west Africa concentrated on the development of the visual attractiveness of traps and targets. In southern Africa investigations focussed on the improvement of insecticide-impregnated targets with odour baits. Vale *et al.* (1986) demonstrated that insecticide-impregnated odour baited targets were effective for reducing populations of ***G. m. morsitans*** and ***G. pallidipes*** on Antelope island in Zimbabwe. They estimated that on this island of 4.5 $km^2$, targets baited with acetone and 1-octen-3-ol were required at densities of 5 per $km^2$ for ***G. m. morsitans*** and 2 per $km^2$ for ***G. pallidipes*** to kill 2 % of each species. They suggested that targets had several advantages over other tsetse control methods because they were simple to construct and deploy, required a reduced demand for imported skills and materials and had a reduced risk of ecological damage. Targets had another advantage in that they could be deployed any time of the year while conventional methods of tsetse control could only be applied effectively during restricted seasons. Recently, some researchers (Vale, 1974b; Bursell, 1977; Hargrove, 1977; Langley and Weidhass, 1986; Langley and Hall, 1986) have concentrated on the development of odour-baited traps that would capture, sterilize and release wild flies. However, Dransfield ***et al.*** (in press) considered that the high costs of maintaining automatic devices in the field or synthentic juvenile hormone analoques would be prohibitive. Such an approach would also negate the participation of local

communities, an approach stressed in east Africa. Brightwell *et al.* (1987, 1990) designed a simple trap which was reported to be very effective for *G. pallidipes.* The effectiveness of the trap was enhanced by the use of acetone and cow urine (see Dransfield *et al.*, 1986). In the Nguruman area of Kenya Dransfield and his team mobilized the rural communuties of Masai to construct such traps which the Masai also assisted in deploying and maintaining near their homesteads. This approach reduced populations of *G. pallidipes* by 99.9 % with the concomintant reduction of the threat of nagana to several thousands head of cattle.

For the riverine species, Gouteux and Challier (1978) employed unbaited biconical traps impregnated with decamethrin to control *G. p. palpalis* in Ivory Coast. Eouzan *et al.* (1981) tried to control *G. f. quanzensis* and *G. p. palpalis* using blue screens impregnated with decamethrin in Congo. The results were poor but there were indications that biconical traps which were used for sampling were themselves effective in reducing fly populations. There has since been several trials in Central and West Africa involving the use of screens and traps for tsetse control with some success (Lancien *et al.*, 1981; Laveisseire and Couret, 1981, 1983a, 1983b; Kupper *et al.*, 1984; Kupper *et al.*, 1985; Laveisseire *et al.*, 1986; Gouteux *et al.*, 1986). Laveissiere *et al.* (1986) and Laveissiere (1987) also involved rural communities to control human

trypanosomiasis with traps and screens in the Ivory Coast with success. A similar approach was reported by Okoth (1986b) in Uganda to control ***G. f. fuscipes***. Further research is needed to determine odour attractants that would increase the effectiveness of screens and traps for the ***palpalis*** group as is the case for the ***morsitans*** group. This review has revealed that no odour baits are in use for the control of ***G. f. fuscipes***.

Vectorial Capacity of 'Tsetse flies

Pathogenic trypanosomes that infect tsetse flies were reported (Buxton, 1955; Hoare, 1972; Pollock, 1980) to follow certain routes in the fly during the course of their development. These routes or sites have been used to categorize trypanosomes into broad groups. Thus, trypanosome infection of the hypopharynx and labrum only are attributed to the trypanosome subgenus ***Duttonella*** (or the ***vivax*** group), of the hypopharynx and gut to the subgenus ***Nannomonas*** (or ***congolense*** group), and that of the hypopharynx, salivary glands and gut to the subgenus ***Trypanozoon*** (or ***brucei*** group). The duration of trypanosome development in the tsetse fly was also reported by Buxton, Hoare and Pollock to differ in relation to the life cycle of each subgenus; those of the ***vivax*** group generally taking the shortest time and the ***brucei*** group the longest.

Determination of the many factors that influence the development of trypanosomes in *Glossina* has been a subject of extensive research reviewed by many authors (Buxton, 1955; Hoare, 1970, 1972; Jordan, 1974, 1976; Molyneux, 1977, 1980; Moloo, 1980). Molyneux grouped all the factors that are involved under three broad headings. These include: (a) endogenous factors associated with the fly (fly age at infective feed, sex of fly, genetic differences between fly species or within species, behaviour, physiological and biochemical state of fly and concurrent infections of fly that is, viral, bacterial and fungal infections); (b) ecological factors (climate, availability of infected hosts, hosts available for subsequent feeds); (c) parasite and host (parasite numbers available to fly, type of parasite and its infectivity to fly - immune state of host, subspecies - strain, susceptibility, intercurrent infection, behaviour and attractiveness to fly).

The earliest studies on the vectorial capacity of *G. f. fuscipes* were undertaken following the great epidemic of Gambian sleeping sickness that occured early this century around the Lake Victoria region. Duke (1933a) reviewed all records from both field and laboratory studies available then on trypanosome infection rates and noted that in any of the tsetse species investigated it was a rare occurrence to get 20 % infection rates. In the field it was rare to find

more than 0.1 % or 0.2 % of flies infected with the ***brucei*** type of trypanosomes although 20 % or 30 % of the game animals from which flies derived their blood meals carried trypanosomes. Gibbins (1941) working in the Nile District of Uganda dissected 2,122 ***G. f. fuscipes*** (721 males and 1,401 females) but found none infected with trypanosomes despite that 215 cases of sleeping sickness had been diagnosed in the same area. Laboratory experiments involving 320 males and 503 females yielded the same results.

The vectorial capacity of ***G. f. fuscipes*** has been compared with other tsetse species in the laboratory by various workers. Duke (1933a, 1933b, 1936) found that ***G. morsitans*** was significantly more susceptible to infection with ***T. b. brucei*** and ***T. b. rhodesiense*** than ***G. f. fuscipes***. In one such study 6.5 % of 3,119 ***G. morsitans*** were found with positive salivary glands while only 2.9 % of 3,236 ***G. f. fuscipes*** dissected were infected. Harley and Wilson (1968) compared ***G. f. fuscipes***, ***G. pallidipes*** and ***G. morsitans*** infected with ***T. congolense***. They found that ***G. f. fuscipes*** was a poor vector with an infection rate of 2.9 % as compared to 11.6 % in ***G. morsitans*** and 13.2 % in ***G. pallidipes***. The poor vectorial capacity of the ***palpalis*** group of flies for ***congolense*** type trypanosomes has been reported by other authors (Godfrey, 1966; Distelmans ***et al.***, 1982; Stephen, 1986). In another study, Harley (1971) found

that infection rates due to *T. rhodesiense* in *G. f. fuscipes* were not significantly different from those recorded for *G. pallidipes* while none of the 202 *G. brevipalpis* used failed to pick infection. Van Vegten (1971a), however, found significant differences in salivary gland infection rates of *G. f. fuscipes* (2 % of 151 dissected) and *G. pallidipes* (13 % of 30) although the latter figure may be argued to be rather a small sample. Recently, Moloo *et al.*, (1985, 1988) while investigating the effect of gamma irradiation on infection rates of seven species (*G. m. centralis, G. austeni, G. p. palpalis, G. p. gambiensis, G. f. fuscipes, G. tachinoides* and *G. brevipalpis*) concluded that *G. m. centralis* was the most efficient vector of trypanosomes.

Field and sometimes laboratory studies have often revealed conflicting results by various researchers on the differences in susceptibility to trypanosome infection by sexes of *Glossina*. Burtt (1946b), Fairbairn and Culwick (1950), Clarke (1969), Otieno *et al.* (1983) and Mwangelwa *et al.* (1987) showed that males were more susceptible to infection than females, but others Duke (1933c), Moloo *et al.* (1973) and Harley (1971) reported the opposite. Field results are conflicting because variations in sampling arise due to the different techniques employed which have a bias towards a certain group of the population, for example, age, sex, hunger stage, etc (Glasgow and Phelps, 1970). Man-fly rounds for instance, tended to catch more male flies than

traps which do the opposite. In view of all the factors involved it is inevitable that field results on the same subject have sometimes varied not only seasonally but also from locality to locality. Differences in laboratory results obtained by different workers could be explained in terms of different techniques, trypanosome and tsetse fly strains used by various workers.

Various researchers observed that the age of the tsetse fly at the time of the infective feed influenced infection rates. Young flies were more infected with ***T. congolense*** and ***T. brucei*** type of trypanosomes than older ones (van Hoof ***et al.***, 1937; Wijers, 1958; Harley, 1966a, 1966b; Moloo ***et al.***, 1973; Clarke, 1966, 1969; Ward, 1968; Willett, 1966; Elce, 1974; Ryan ***et al.***, 1982; Distelmans, 1982). Willett (1966) suggested that the peritrophic membrane lining the gut of tsetse flies was not fully developed in younger flies. As a result trypanosomes could reach the ectoperitrophic space around the region of proventriculus or easily penetrate through the freshly secreted membrane. The peritrophic membrane was considered to be well developed in older flies and only a few trypanosomes could reach the ectoperitrophic space by passing round the end of this membrane in the midgut or hindgut. Gingrich ***et al.*** (1982), however, demonstrated that even old flies could be readily infected with trypanosomes if starved for four days indicating that there were other factors involved other than

the physical one. Maudlin and Welburn (1987) and Welburn *et al.* (1989) suggested that lectins in the fly midgut could be responsible for the low trypanosome infetion rates in fed flies. Trypanosomes were killed more quickly in flies which had been fed on a clean blood meal prior to the infective feed than in teneral flies which had not fed before. They suggested that starvation probably reduced the level of lectins in non-teneral flies thereby rendering them more susceptible to trypanosome infection. These authors cautioned against drawing conclusions from studies conducted on laboratory colonies and constrated such findings with the vector potential of wild flies since the former may have undergone selection for example, for refractoriness and susceptibility to trypanosome infection during the course of rearing.

Raised temperature speeded up the development of trypanosomes in the tsetse fly (Kinghorn *et al.*, 1913; Taylor, 1932; Duke, 1933d) and also influenced the development of the puparia with concomitant susceptibility to trypanosome infection of the adult flies that emerged from them (Burtt, 1946a; Fairbairn and Culwick, 1950; Fairbairn and Watson, 1955; Dipeolu and Adam, 1974).

Lloyd *et al.* (1924) working in Nigeria related trypanosome infection rates in the fly to the food sources of flies. Duke (1933c) recorded similar observations in

Uganda. The development of more accurate methods of identifying the source of tsetse blood meals (Weitz, 1956) allowed investigations to determine the relatonship between trypanosome infection rates in tsetse flies and the identity of the animals on which the flies fed. It was established that suids were less heavily infected with trypanosomes than bovids (Ashcroft, 1959). Although suids were easily infected with the *brucei*-type of trypanosomes, the parasitaemia was low while bovids remained infected for long periods. Following Jordan's (1965) work on the relationship between infection rates and hosts of flies, Harley (1966a) also observed that infection rates in *G. pallidipes*, *G. f. fuscipes* and *G. brevipalpis* were influenced by the extent to which the flies fed on bovids. *G. f. fuscipes* derived 53 % of its feeds from man, reptiles and birds while these hosts formed only 3 % of feeds of *G. pallidipes*. Since *T. vivax* and *T. congolense* do not naturally infect these hosts *G. f. fuscipes* had half the chance of contracting trypanosome infection compared to *G. pallidipes* which fed mostly on bovids. *G. brevipalpis* had the least chance of being infected having the least proportion of its feeds from bovids.

Little is known of the vectorial capacity of *G. f. fuscipes* from Rusinga Island and the immediate neighbourhood on the mainland shore of Lake Victoria. However, this area is in proximity with Busia in Kenya and Busoga in Uganda

where human trypanosomiasis is endemic. Rusinga Island also lies close to the Lambwe Valley, another area endemic with trypanosomiasis.

**Historical aspects of Sleeping Sickness in South Nyanza, Kenya**

Willett (1965), Ford (1971) and Onyango (1974) have reported in detail historical aspects of African human trypanosomiasis in the Nyanza region of Kenya. It is generally held by these authors that the Gambian sleeping sickness spread into the Nyanza area in about 1901-1902 from the great epidemic in Uganda and that transmission of this disease was associated with ***G. f. fuscipes***. It is reported that from 1901-1906 about 200,000 people died from this disease in the areas affected (Bell, 1909). According to Onyango (1974) the epidemic that followed affected the islands of Rusinga and Mageta first before spreading to the mainland around Kadimo in Central Nyanza and Kaksingiri in South Nyanza. From there it spread further to contiguous locations in the Lake Victoria Basin infested with ***G. f. fuscipes***.

Once introduced, the disease remained endemic but occasionally flared up into epidemics in various places particulary between the periods 1902-1908, 1920-1930 and

1940-1950. As a result vigorous control measures comprising active case detection, treatment of diagnosed cases, hand-catching of the flies, bush clearing and later, the spraying of riverine vegetation with insecticides were instituted. It is asserted that following these control measures, the Gambian sleeping sickness disappeared from its foci in South Nyanza.

The Rhodesian form of the disease was introduced into the Samia location of Kenya from Uganda in about 1942 (Mackichan, 1944). The disease spread from there to Central Nyanza at the time *G. pallidipes* was also increasing in density in that locality. Later, the disease spread to other areas such as Yimbo, Sakwa, Uyoma and Alego and the spread was mainly associated with the presence of *G. pallidipes* (Willett, 1965; Ford, 1971). Cases of Rhodesian sleeping sickness were also reported from Mara near the Kenya/Tanzania border where transmission was thought to be through *G. swynnertoni*. Onyango (1974) considered that a residual population of *G. pallidipes* that was left out during control measures in Lambwe Valley, South Nyanza, became a focus of *Trypanosoma brucei rhodesiense*. Onyango who listed the number of sleeping sickness cases notified in Kenya between 1950 and 1971 further reported that the Rhodesian form of the disease replaced the Gambian form due to *T. b. gambiense* around the early 1950s and became endemic

in Samia, Alego, Kadimo and Sakwa, as well as Lambwe Valley and its contiguous areas.

The role played by ***G. f. fuscipes*** and ***G. pallidipes***, the two tsetse species then found in Samia, Alego, Kadimo and Sakwa in Central Nyanza during the Rhodesian sleeping sickness epidemics that occured in these areas in the 1950s and 1960s was not clear-cut. Initially, ***T. b. gambiense*** and Gambian sleeping sickness were generally associated with flies of the ***palpalis*** group, and ***T. b. rhodesiense*** and Rhodesian sleeping sickness with the ***morsitans*** group. However, it was later shown that either group could transmit either disease (Willett, 1965). Willett associated the increasing number of Rhodesian sleeping sickness cases with the increasing level of contact between man and ***G. f. fuscipes*** and attributed the explosive epidemic in Alego and the surrounding locations in 1964 to this factor. He considered the peridomesticity of this fly in ***Lantana*** thickets and vegetation surrounding the homesteads as an additional factor that contributed to the epidemic. He further considered that heavy rains in the preceding years had promoted vegetational growth that was favourable to the survival of ***G. f. fuscipes*** which extended its distribution further inland from the lake shore. Wijers (1974b, 1974c), however, was of the opinion that this species played a minor role in the transmission of the disease. He regarded the epidemics that occured in Alego in 1963-1964, and in Busesa

in 1971 as due to exceptional circumstances that brought man and the fly into increased contact. His opinion was that the invasion by ***G. f. fuscipes*** of the new vegetational areas near homesteads was not the direct cause of the epidemic but part of the normal range of its adaptation. Further, that man-fly-man transmission occured occasionally if not sporadically. He considered cattle to be the main reservoir of the disease from which flies obtained their infection during outbreaks and the degree of contact between cattle, fly and man around watering sites determined the severity of the outbreaks. Wijers based his arguement on the evidence that most of the sleeping sickness cases were observed in areas adjacent to bush infested with ***G. pallidipes*** and that it was such areas which harboured game animals that were the reservoirs of the disease. In the lake shore areas infested with ***G. f. fuscipes*** wild animals were scarce and dissection of non-teneral flies caught in these areas revealed mostly ***T. vivax*** infection.

It seems that ***G. pallidipes*** whose preferred hosts are game animals some of which are the reservoirs of trypanosomiasis could have initially introduced the disease into cattle. ***G. fuscipes*** could have then picked up the infection from cattle and passed it on to people at watering points.

More recently in Busoga, Uganda, Kangwagye (1975) and several other workers (Matovu, 1982; Katabazi, 1983; Abaru, 1985 and Mbulamberi, 1989) reported that transmission of Rhodesian sleeping sickness was mainly due to ***G. f. fuscipes***. Social and political disturbances which interupted the normal services in health care and vector control led to increased man-fly-man contact as ***G. f. fuscipes*** inhabited areas with human activity.

**Control of *G. f. fuscipes* in Kenya**

Efforts to control ***G. f. fuscipes*** in Kenya appear to have been stimulated mainly by the need to control sleeping sickness epidemics, as stated earlier, rather than nagana for which comparatively little is published in relation to control of this subspecies. Early control strategies were based on the results from studies of the bionomics of ***G. f. fuscipes*** conducted by various workers mainly in Uganda.

On the basis of the linear distribution of the fly habitats along water courses, Symes and Vane (1937) and Symes and Southby (1938) employed a method of blocks along the tributaries of the Kuja River in South Nyanza District from which they systematically caught flies by hand. Glasgow and Duffy (1947, 1951) also employed the same strategy to control flies along the Sari River and the main

Kuja River in the same District. Hand-catching was effective in isolated areas with low to medium fly densities. However, it proved to be costly and ineffective in areas heavily infested with tsetse flies because of reinvasion (Wilson, 1953). This led to the abandonment of the method in preference to bush clearing. Wilson (1953) and Glasgow (1954) assessed the feasibility of bush clearing along rivers in Central Nyanza Distict. They found that bush clearing caused a slow reduction in the fly populations but could in some cases achieve eradication. The problem, however, was the high cost of reslashing the regrowth of vegetation.

In the late 1940s trials involving the spraying of dichloro-diphenyl-trichloroethane (DDT) and benzene bexachloride (BHC) on fringing vegetation along water courses showed promise in Uganda. Adoption of this method in Kenya led to the eradication of ***G. f. fuscipes*** by several applications of DDT on vegetation along the Mbogo and Ainamotua Rivers in Central Nyanza (Wilson, 1953). Working in the same area, *Fairclough and Thomson (1957) reported similar results, having achieved eradication of flies along sections of the Nyando river. They, however, reported problems due to reinvasion of the cleared areas.*

The Tsetse Survey and Control Section of the Kenya Veterinary Department now under the Ministry of Agriculture

and Livestock Development was established in 1942 (Maina, 1979). Its main objective was to stop reinvasion by tsetse flies of the cleared areas. By that time some 349 km of riverine tsetse-infested bushes had been cleared along the Kuja/Migori and Nyando river systems where epidemics had occurred. This exercise helped to release 1,352 km$^2$ of land for settlement which hitherto had been rendered inhabitable due to the tsetse fly menace.

Control of *G. f. fuscipes* with the use of insecticides was initiated by the Department of Veterinary in 1952 (Maina, 1979). In the 1950s and 1960s large tracts of land along rivers and lake shore were sprayed with insecticides. During 1965/66 alone, 1,166 km$^2$ of land and 3,326 km of river and lake shores were sprayed. The expenditure on tsetse control in western Kenya only was KShs 2,580,000 every year. In 1977 estimates to clear reinfested areas had reached KShs 200,000,000 and there was no guarantee that epidemics would not reoccur (Maina, 1977). From that time up to the present, the Department of Veterinary Services sometimes sprays riverine and lake-side vegetation with insecticides to control *G. f. fuscipes*. Initially, dieldrin (1.8 % emulsifiable concentrate) was applied using motorized knapsack sprayers but synthetic pyrethroids such as cypermethrin at a concentration of 0.3% have now come into use (Mr. F. P. Oloo, Assistant Chief Zoologist, Department of Veterinary Services, personal communication).

# CHAPTER 2

# STUDY AREA

## GEOGRAPHICAL LOCATION

The study area comprising Rusinga Island and part of the mainland is located in the Mbita Division of South Nyanza District in Nyanza Province, Kenya. This region lies in the eastern part of Lake Victoria. It is located between latitudes 0° 20' and 0° 30' South and longitudes 34° 06' and 34° 15' East (Fig. 1). Rusinga Island joins the mainland at Mbita Point by a causeway about 50 m long. The island is about 43 $km^2$ in area.

## LANDSCAPE

The altitude lies between 1143 and 1500 m above sea level. The geology of the area comprises Tertiary sediments (National Atlas of Kenya, 1970). The soil is mainly loam with a gravel or stone surface. Rusinga Island is dominated by a large central hill with numerous small hills around it. The part of the mainland under study is also hilly. For this reason most of the cultivation both on the island and the mainland is done on strips of land of about a kilometre in width along the shores of the lake.

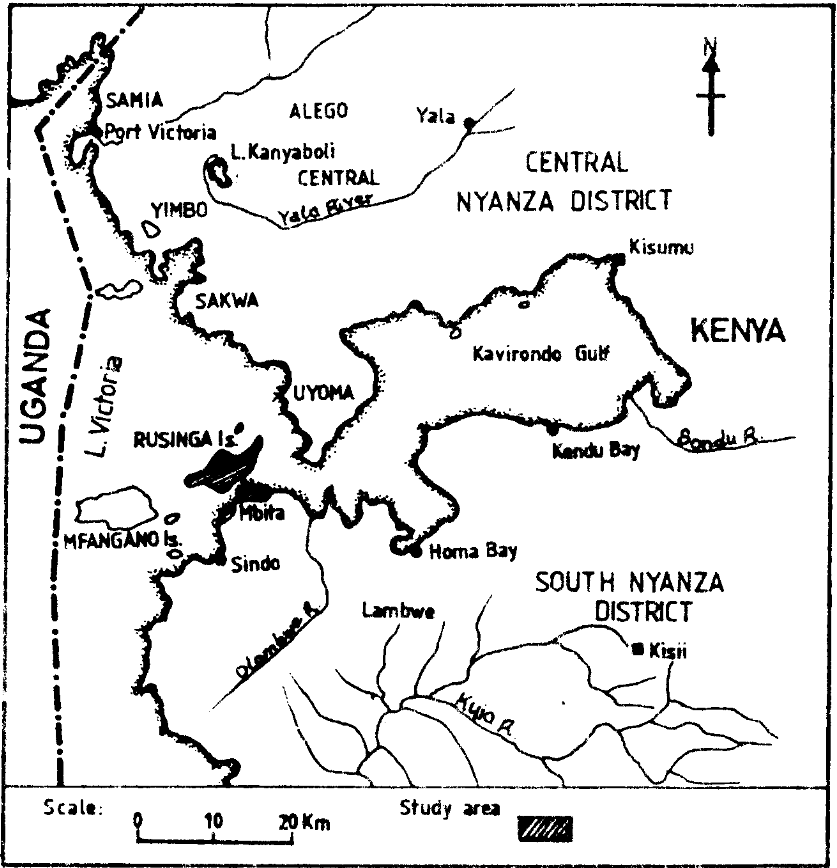



Fig. 1. Map of study area (Rusinga Island and the mainland) and its environs. (From National Atlas of Kenya, 1970).

## CLIMATE

The study area lies close to the equator and experiences a hot and humid type of climate most of the year. There are no definite seasons but rainfall is bimodal with peaks in April and December. According to the National Atlas of Kenya (1970) Rusinga Island and the lake shore area on the mainland fall in the region of the country that receives a mean annual rainfall of between 760-1015 mm and has minimum and maximum temperatures of 14-18° C and 30-40° C, respectively. Meteorological data collected during the course of this study are presented in Chapter 4.

## VEGETATION

The vegetation of the area which harbours the tsetse flies has been greatly influenced by human activities in terms of clearings made for cultivation of crops. On the island, hills with little or no human settlement are characterized by extensive bushland while low areas have been reduced largely to grassland with scattered shrubs. The local people have demarcated some of these areas with fences of ***Euphorbia tirucalii*** (L.) and in some localities also with ***Lantana camara*** (L.) to form homesteads and gardens. In some places ***L. camara*** has become a weed. Crops grown include maize, sorghum, cassava, bananas, sugar cane, sweet potatoes and vegetables. In areas which are not cleared, shrubs of several species occur. These include

***Triumfetta macrophylla*** (K. Schum), ***Mimosa pigra*** (L.), ***Phichea ovalis*** (Pers) and ***Ipomea hilderbrandtii*** (Vatke). Closer to the shoreline, within a distance of about 10 m, trees of the species ***Sesbania sesban*** (L.) Merrill and ***Aeschynomene elaphroxylon*** (Guill and Perr) Taub., often thrive, together with ***Phragmites*** and several species of creepers of the family Nyctaginaceae and genus ***Ipomea*** to form discontinuous thick vegetation.* Sedges, ***Cyperus immensus*** (C. B. Cl.) and ***C. articulatus*** (L.) are often found in association with these plant species.

**WILDLIFE**

There are several species of wild animals** on the island on which flies could feed. A list of those recorded by the International Centre of Insect Physiology and Ecology (ICIPE, 1985) on the evidence of sightings and spoors includes bushbuck (***Tragelaphus scriptus***) (Pallas, 1776), dik dik (***Madogua kirkii***) (Gunther, 1880), hippopotamus (***Hippopotamus amphibius***) (Linnaeus, 1758), monkeys (***Cercopithecus albogularis***) (Sykes, 1831), hares (***Lepus***

---

*Specimens of plants were collected and taken to Professor J. O. Kokwaro of University of Nairobi, Botany Department who identified them.

**The identification of these animals was partly based on the maps and description provided by Harternorth T. and Diller H. (1980). Where several species of animals of the same genus exist in the same locality these have only been identified to the genus level.

spp.) and monitor lizards (***Varanus niloticus niloticus***) (Laurenti). With the exception of monitor lizards these animals occur in low numbers.

On the mainland animals frequently seen include hippopotamus, monitor lizard and hare. Those which are occasionally seen are bush buck, leopard ***(Panthera pardus)*** (Linnaeus,1758), hyaena ***(Crocuta crocuta)*** (Erxleben, 1777), porcupines ***(Hystix africae australis*** (Peters, 1852) and ***H. cristata)*** (Linnaeus,1758) and several species of antelopes. About 30 km south of the study area lies the Ruma National park which is a sanctuary for a number of species of wild animals reported in detail by Allsopp and Baldry (1972). It is possible that some of the animals stray out of the park into the neighbouring areas including the study area.

## HUMAN AND LIVESTOCK POPULATIONS

A census carried out in 1979 indicated a human population of 9,905 on Rusinga Island comprising 4,805 males and 5,100 females (Kenya Population Census, 1979). Using an average national growth rate of 4 % the 1986 population of the island was estimated at 13,000. Mbita Point had an estimated human population of about 3,000. Ayot (1979) refers to the inhabitants of Rusinga Island and the lake region of South Nyanza as the Luo-Abasuba. The livestock kept includes the indigenous zebu cattle, sheep and goats.

A survey carried out by ICIPE (1985) showed that in March 1985 there were 6,228 cattle, 1,498 sheep and 1,377 goats on the island.

# CHAPTER 3

## DISTRIBUTION AND DIEL ACTIVITY PATTERNS OF *G. F. FUSCIPES* ON RUSINGA ISLAND AND THE MAINLAND

### INTRODUCTION

The distribution of ***G. f. fuscipes*** has not been studied in detail in recent years on Rusinga island and the nearby mainland areas. Earlier investigations (Symes and Vane, 1937; Symes and Southby, 1938; Glasgow, 1954) indicated that ***G. f. fuscipes*** inhabited thickets fringing the lake shore and rivers flowing into Lake Victoria. However, Willett (1965) observed that in Central Nyanza, ***G. f. fuscipes*** colonized ***L. camara*** thickets and rings of vegetation surrounding groups of huts locally known as bomas. Langridge and Mgutu (1971) also reported that although this subspecies was primarily associated with waterside vegetation, it could spread to places up to 20 km away from rivers provided that shade and humidity were adequate for its survival. The Tsetse Survey and Control Section of the Department of Veterinary Services sprays the lake-side vegetation occasionally with synthetic pyrethroids (for example, cypermethrin) to control ***G. f. fuscipes***. This affects the distribution of the flies in the sprayed areas.

However, during the course of this study which lasted for three years no spraying of insecticides was recorded in the study area.

Studies on diel activity patterns of *G. f. fuscipes* were carried out by Harley (1965) in Lugala, Uganda, who reported that this subspecies was diurnal and that maximum activity varied from site to site and season to season. Oloo (1983) working at Gunga which is located south of Sindo (Fig. 1) recorded biting activity of this subspecies from 8.15 to 13.15 hours. However, his work did not extend to the latter part of the day thus, neither the biting activity nor the availability of flies to man was studied throughout the day. The objectives of this study, therefore, were to: (1) investigate the distribution of *G. f. fuscipes* in the experimental area in order to know where to sample the flies and (2) to gain insight into its diel activity patterns so as determine when to do the sampling for various other studies.

## MATERIALS AND METHODS

A tsetse survey of Rusinga Island and the immediate mainland, from Sindo through Mbita to Homa Bay, was conducted from 20 November 1987 to 14 January 1988. Biconical traps (Challier *et al.*, 1977) were used to

determine the presence of tsetse flies. These were set at varying distances along transects traversing the island and along the lake shore only, on the mainland, as further inland the vegetation had been cleared for settlement and cultivation. Traps were set at various times between 8.00 and 18.00 hours and emptied after 24 hours from setting times. The traps were first placed in the western part of the island, then were progressively shifted eastwards until the whole area was covered. Flies caught in the traps were brought to the laboratory, killed using chloroform, sexed and classified as teneral or non-teneral. A subsample of the catch was selected randomly from the fly cages, dissected and examined for trypanosome infection as described in Chapter 7.

On completion of the survey, the area with the highest catches was selected for studies on diel activity patterns. On 17 February 1988 and 19 March 1988, six biconical traps were set at intervals of about 100 m in openings in the thickets near the lake shore. Traps were set by 6.30 hours and emptied at hourly intervals until 19.00 hours. Ambient temperature, relative humidity and solar radiation were simultaneously recorded with the use of dry and wet-bulb thermometers and a radiation meter (L1-1776, USA), respectively. From 14 to 16 October 1989, windspeed was recorded at hourly intervals from 6.00 to 18.00 hours at a height of 1.5 m from the ground at a government

meteorological station located about 7 km in the nothern part of the island. Catches for February and March were pooled together and the numbers of flies caught at different times of the day were related to environmental factors recorded at the same time (except windspeed) using linear stepwise multiple regression analysis.

## RESULTS

Fig. 2 and Appendix I (Tables 1.1 and 1.2) indicated that on Rusinga Island tsetse distribution was confined to strips of thick vegetation varying in width and of lengths extending up to about 2 km along the lake shore. All tsetse flies caught were ***G. f. fuscipes*** and these were trapped in or near the thick vegetation. Flies were caught in such vegetation all around the island but catches were highest in the Wakondo/Kakrigu area, in the southern part of the island where dense thickets stretch a little over two kilometres in length. Catches were also high in a similar type of vegetation in Kaswanga/Wanyama area in the northern side of the island. Catches were lowest in the western side where it was hilly and the vegetation was sparse. No flies were caught further than 100 m from the lake shore. The trend was the same on the mainland where the survey was confined to the lake shore only because of the vegetation clearings further inland. On the mainland catches were highest in

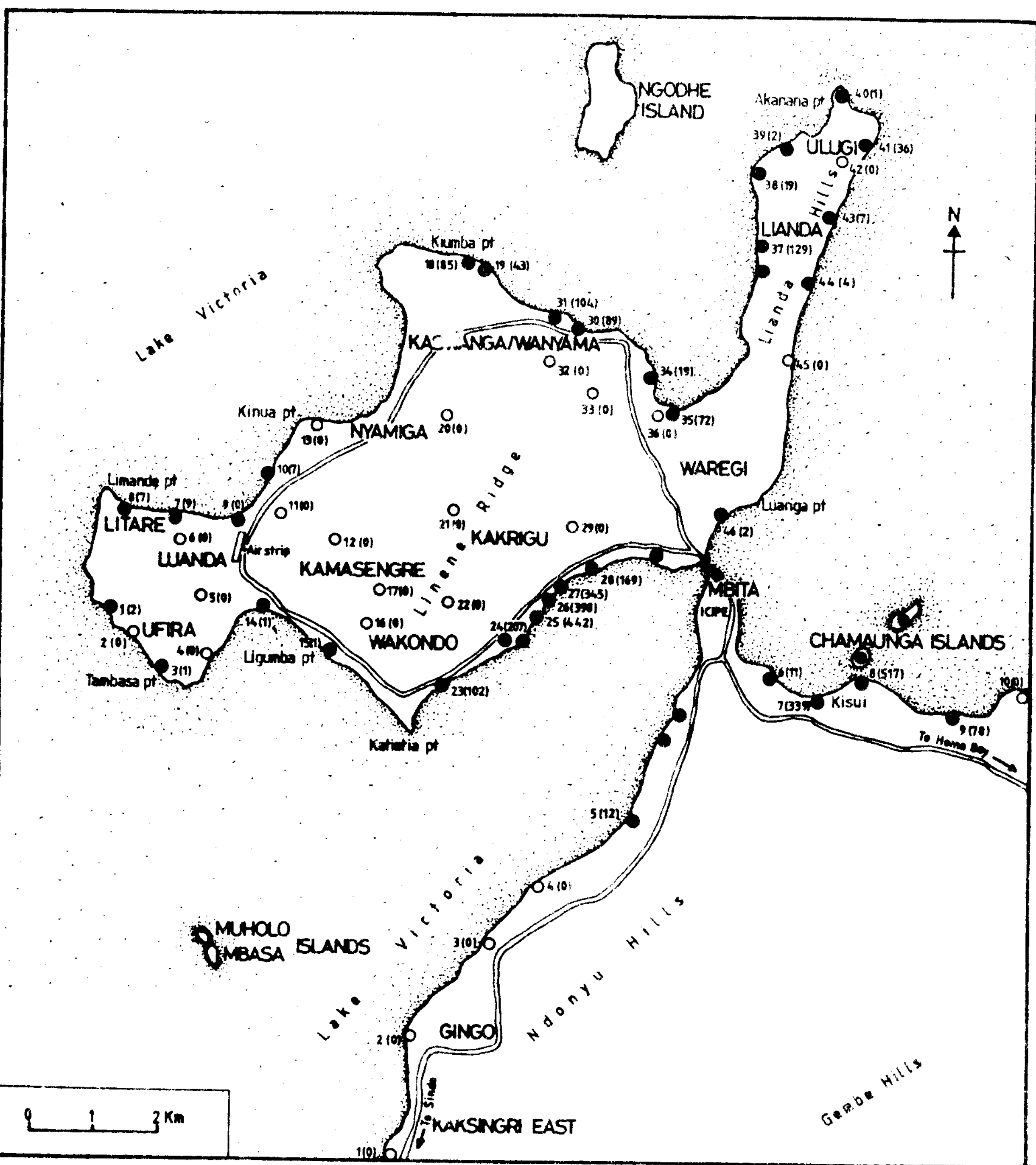



Fig. 2 Map of Rusinga island and the mainland showing tsetse distribution.
● = sites where *G. f. fuscipes* was caught.
o = sites where traps were set but no catches were recorded.
Figure outside brackets shows the trap number. Figure within brackets indicates the total number of flies caught at that site.

Kisui area. A fairly high number of flies was also caught on Chamaunga islands about a kilometre off the mainland in the north (Fig. 2). The presence of teneral flies in the catches indicated that breeding occured in or near places where they were caught. Such places were characterised by the highest fly catches and had relatively more extensive areas covered with thickets.

Flies were first caught in traps shortly after 7.00 h. The catches quickly increased in size reaching a maximum between 8.00-9.00 h for females and at 9.00-10.00 h for males (Fig. 3). Catches for both sexes were high until about noon, after which they gradually decreased in size to almost zero by 19.00 h (Fig. 3a). Only one male fly was caught at 19.00 h from a total catch of 325 males and 486 females. The trap catches suggested a unimodal diel activity pattern for both sexes for the conditions at the time of the study. Multiple regression analysis suggested that solar radiation intensity (Fig. 3b) and relative humidity (Fig 3c) were affecting the catch size of males. The regression equation describing the relation of the two factors and the catch size of males was $Y=-29.46 + 6.30X_1 + 0.40X_2$, ($r^2=0.59$, $P=0.0053$ and $P=0.0425$) for solar radiation and relative humidity, respectively, where $X_1$ = solar radiation and $X_2$ = relative humidity. No factor was significant at the 5 % level for females, but solar radiation was significant at the 10 % level ($Y=3.63 +$

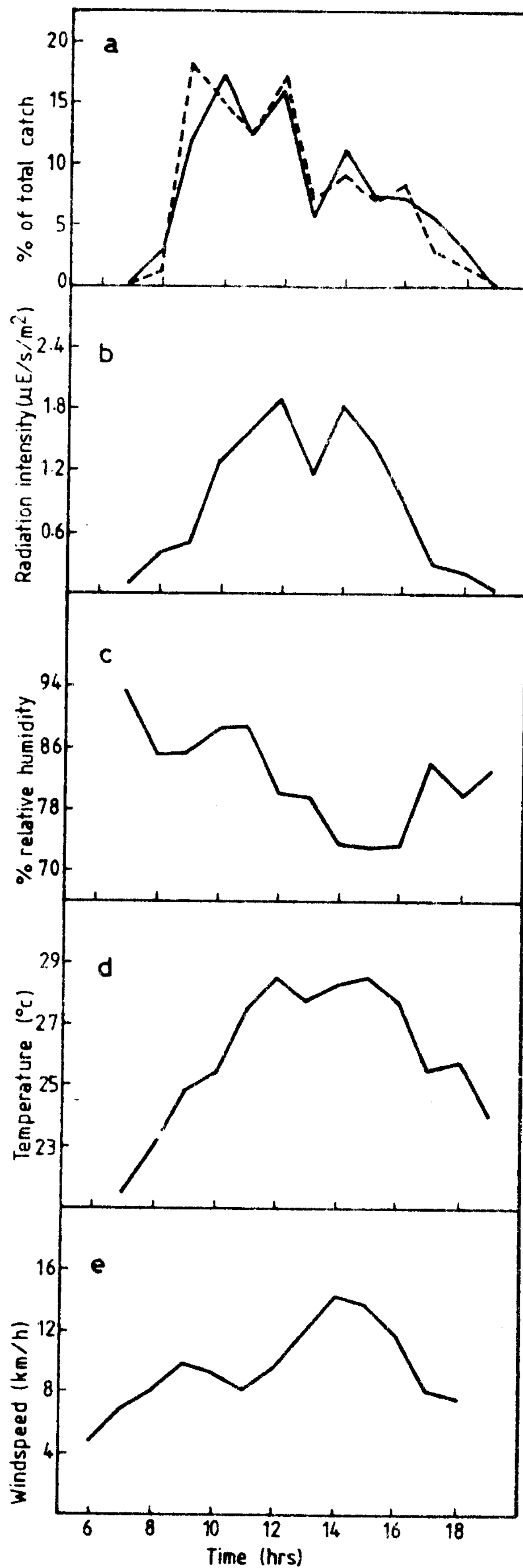



Fig. 3. Hourly profiles of (a) male (____) and female (---) *G. f. fuscipes* caught on Rusinga Island; (b) solar radiation intensity; (c) relative humidity; (d) ambient temperature and (e) windspeed recorded on Rusinga island.

$5.13X_1$, $r^2=0.20$, $P=0.0960$), where $X_1$ = solar radiation. Temperature (Fig. 3d) and windspeed (Fig 3e) did not signicantly influence the catch size of either sex.

## DISCUSSION

The distribution of ***G. f. fuscipes*** is known to be normally confined to the environs of water courses. Gibbins (1941) reported the distribution of this fly in the West Nile District of Uganda to be entirely confined to areas along the tributaries of the Nile river and along the shores of Lake Victoria. He further observed that ***G. f. fuscipes*** could be caught along tributaries at distances of up to 97 km from the main river or the lake. Chorley (1944) however working in Busoga District, Uganda, found breeding sites in dense, humid, forest near Lake Victoria and also found breeding sites up to 19 km from the lake. Glasgow (1954) while assessing bush clearing methods of eradicating ***G. f. fuscipes*** along the shore of Lake Victoria observed that flies were inhabiting narrow dense vegetation near the lake. He cleared the dense vegetation along the lake shore up to 274 m inland in order to control this fly. Glover ***et al.*** (1958) also exploited the knowledge of the distribution of this fly to control it. By a combination of spraying with insecticides and clearing vegetation along the tributaries

they claimed extermination of *G. f. fuscipes* along more than 483 km of the Kuja and Migori river systems of Kenya.

A major departure from the usual habitat of *G. f. fuscipes* was reported by Willett (1965) who observed that this subspecies was colonising new vegetational areas away from rivers, particulary *L. camara* thickets and the rings of vegetation surrounding groups of huts of the local people in Central Nyanza, Kenya. He suggested that the colonisation of this new habitat could have risen due to the successive heavy rainy seasons that produced suitable conditions for the survival of *G. f. fuscipes* away from its usual lacustrine and riverine habitat. Recently, Okoth (1985, 1986a) reported a similar situation in Busoga, Uganda, where the same subspecies had become peridomestic, breeding in coffee and banana plantations and *L. camara* thickets.

On Mfangano Islan which is about 5-7 km southwest of Rusinga Island, Wijers (1974a) encountered *G. f. fuscipes* practically everywhere along the lake shore and gulleys and streams. The present survey, which was conducted when it was relatively dry, from November 1987 to January 1988, indicated that this subspecies was confined to the lake shore areas as Wijers (1974a) observed on Mfangano island. It is possible that during very wet years, when there is regrowth of bush, this species extends its habitat inland for several kilometres as reported by Willett (1965) and

Langridge and Mgutu (1971). Vegetation cover was considered to be the limiting factor of the distribution of *G. f. fuscipes* along the lake shore on Rusinga island and the mainland. The vegetation was in turn affected by human activities in the form of clearings for cultivation. Spraying of insecticides was another factor that could have affected the distribution of flies especially on the mainland where the application of insecticides was more frequent than on the island.

The distribution of *G. f. fuscipes* in the study area was limited to the lake shores. This meant that sampling of this subspecies could only be done in some areas with thick vegetation along the lake shores. An expansion in cultivation would imply further reduction of the distribution of the subspecies as its breeding sites would be affected. Furthermore, the limited distribution of the fly implied that its effiency as a vector was resticted to only those hosts frequently visiting the thick vegetation along the lake shores.

Diel activity patterns of the same subspecies were earlier reported by Harley (1965) in Lugala, Uganda. His results showed that *G. f. fuscipes* was active between 5.00 and 19.00 h with a peak of activity between 10.00 and 16.00 h. The exact hour of maximum activity was found to vary from site to site and season to season. Nocturnal

activity was not observed. Similar results were reported by Okiwelu (1982) in Mali for a related species, ***G. p. gambiensis***, and in Nigeria by Tenabe (1983) and Ivory Coast by Gouteux and Monteny (1986) for another subspecies, ***G. p. palpalis***. This study which was carried out in February and March 1988 showed that the maximum activity for ***G. f. fuscipes*** occurred in the morning, from 8.00-10.00 h, and this falls within the range of activity reported by Harley (1965) whose studies lasted throughtout the year.

Of the physical f ctors recorded, solar radiation intensity appears to be the main factor influencing activity patterns of *G. f. fuscipes*. This is in agreement with the observations made by Oloo (1983) and Gouteux and Monteny (1986) who reported similar observations on ***G. f. fuscipes*** and ***G. p. palpalis***, respectively. In this study relative humidity was also observed to affect the catch which declined as humidity declined even though solar radiation remained high. Windspeed in this analysis did not seem to influence diel activity rhythms. It was however not measured at the same time as the trap catches were made and it is possible that strong winds in the afternoon may have been responsible for the decrease in fly catches at this time of the day. Sampling of ***G. f. fuscipes*** was, therefore, crucial by mid day bef e fly numbers started to decline.

# CHAPTER 4

# POPULATION DYNAMICS OF *G. F. FUSCIPES* ON RUSINGA ISLAND AND THE MAINLAND IN MBITA, SOUTH NYANZA, KENYA.

## INTRODUCTION

Apart from the work done by Glasgow (1954) very little information is available on population dynamics of ***G. f. fuscipes*** in Kenya. Extensive ecological studies have however been carried out on the same subspecies in the neighbouring Uganda which shares the same international border with Kenya relating to sleeping sickness epidemics in that country. Since the 1950s the Nyanza region of Kenya has experienced many ecological changes. Increased human settlement has led to changes in vegetation types and fauna of the region. The 1960s and 1970s were also a period of increased use of insecticides against tsetse in that region (Chapter 1). These factors could have had a profound effect on the populations of ***G. f. fuscipes***. An understanding of the ecology of tsetse flies is vital for its control. It is against this background that this study was initiated.

# MATERIALS AND METHODS

## Meteorological data

For the purpose of this study a standard Stevenson screen was set up in the experimental area, 15 m from the lake shore on the southern part of Rusinga Island to record the following: minimum and maximum temperatures and dry and wet-bulb thermometer readings for relative humidity estimates. Soil temperatures in the shade at a depth of 5 cm as well as rainfall were also recorded. Readings were taken at 9.00 h and at 15.00 h for ambient temperature and relative humidity. Due to logistical constraints meteorological readings were only taken during the first two weeks of each month during the study period. Complete data on rainfall were obtained from the main meteorological station of the ICIPE, Mbita Point Field Station, situated about 5 km from the study site, on the mainland.

## Sampling procedure

Sampling to determine changes in apparent density commenced in February 1988. A transect with five (but later reduced to three due to logistical problems) trapping stations at 150-200 m intervals was established along the lake shore in Wanyama area on Rusinga Island. A similar one

was also established along the lake shore in the Kombe/Kisui area on the mainland. Biconical traps were set at each station along the two transects which were worked consecutively each month. From February to September 1988, traps were emptied once a month but thereafter when the logistics improved they were emptied on three consecutive days every month. In February and March 1988, traps were emptied after 24 and 12 hours, respectively, but from then onwards three-hour samples were taken on the first day of sampling followed by 24-hour samples the next two days. Traps for three-hour samples were set by 7.00 h on the day of trapping and were emptied at intervals of three hours until 16.00 h. The three-hour samples were used to determine and record wing fray (Jackson, 1946), trypanosome infection rates (Lloyd and Johnson, 1924) (see Chapter 7), ovarian age (Saunders, 1960, 1962; Challier, 1965) and reproductive abnormalities (Madubunyi, 1975; Turner and Snow, 1984).

**Dissection of flies**

Flies caught in the field were brought to the laboratory alive in cages after every collection. Thirty male and 30 female flies were selected at random from each of the monthly samples from Rusinga Island and the mainland. The flies were squeezed on the thorax to immobilize them

before dissection. The rest were killed using chloroform and sorted out according to sex and whether or not they were tenerals.

The wing fray method of estimating fly age (Jackson, 1946) suffers from the main limitation that it is only a relative method and should ideally be calibrated with fly calender age. Even if it were calibrated, the method does not estimate the age of individual flies and will tend to over-estimate the age of flies if they are kept for several hours in trap cages. Although this technique was initially designed for the ***morsitans*** group of flies it is also applicable to other tsetse species.

Reproductive abnormalities were recorded during the period February 1988 to January 1989. These constituted any anatomical departures from what is considered normal ovarian development of the female tsetse as reported by Saunders (1960, 1962) and Challier (1965). Detection of abortions in wild flies is generally made difficult because there is usually no trace of it in the female fly. To detect abortions in female flies the method first described by Madubunyi (1975) and later modified by Turner and Snow (1984) was used. This method makes a distinction between a parturition and an abortion by measuring the size of the largest egg follicle which is compared to the mean size of

the intra-uterine egg that it shortly becomes. The standard deviate (**d**) is calculated as follows:

$$d = \frac{(x-\mu)}{\sigma}$$

where, x is the size of the largest egg follicle in the ovarioles of a female.

$\mu$ is the mean size of the intra-uterine egg.

$\sigma$ is the standard deviation of the size of intra-uterine eggs.

For a sample greater than or equal to thirty ($n \geq 30$), if **d** is greater than 1.96, there is less than 5 % chance ($P<0.05$) that the value of **x** lies outside the range of distribution. Challier (1973) observed that eggs produced by females in the ovarian age category 1 (see Saunders, 1960, 1962; Challier, 1965) were smaller than those produced by older age categories. The detection of abortions was therefore restricted to ovarian age categories 2-7 to avoid confusion that would arise if measurements of smaller eggs from category 1 flies were also considered in the calculations. Abortions were estimated on the basis of measurements of intra-uterine eggs of *G. f. fuscipes* caught on Rusinga Island and the mainland from February 1988 to January 1989.

Analysis of ovarian age data

Mortality rates were estimated by two methods; by ovarian age analysis (Rogers ***et al.***, 1984) and Moran curves (Rogers, 1979). The first method estimates mortality in adult female flies and is only valid if the population is stable, that is, when birth rate equals death rate (van Sickle and Phelps, 1988). If the population size is either declining or expanding estimates must be corrected by the rate of change of the population. Hargrove (1989) suggested that there is bias in capture probabilities of the different age categories of ***G. pallidipes***. In this study category '0' (nulliparous flies) were ommited as this group was considered to be undersampled by biconical traps (Challier, 1982). Data from flies of category 1-7 were analysed assuming that the interlarval period was 9 days on the basis of results obtained from mark-recapture-release studies (see section on feeding and pregnancy cycles). On this basis the proportion of parous flies in category 1 ($P_1$) is given as:

$P_1=(1-e^{-9m})$, where 'm' is the mortality and 'e' is the number 2.714.... Older categories are

given as follows;

$$P_2 = e^{-9m}(1-e^{-9m})$$

$$P_3 = e^{-18m}(1-e^{-9m})$$

$$P_4^+ = R.e^{-27m}$$

$$P_5^+ = R.e^{-36m}$$

$$P_6^+ = R.e^{-45m}$$

$$P_7^+ = R.e^{-54m}$$

where, $R=(1-e^{-9m})/(1-e^{-36m})$

A non-linear least squares fit method was used to estimate 'm'. Due to the small size of samples, data for two months were pooled together.

The estimation of mortality rates by the Moran curve method involves plotting the logarithm of a population density for one month against the logarithm of the same population for the previous month. A tsetse population is expected to double within this period and the maximum reproductive rate is compared with the observed rate of increase. The difference gives an estimate of population mortality over the period concerned, assuming there is no net emigration/immigration of flies in the study area. Thus the Moran curve technique (Rogers, 1979) gives an estimate of total mortality of a population.

**Mark-release-recapture experiments**

Two short-term mark-release-recapture experiments were carried out on Rusinga Island from 22 June to 2 July 1988 and from 8 November to 12 December 1988 to determine: i) feeding and larviposition cycles, ii) absolute population density, and iii) fly movement. In the first experiment (22 June to 2 July 1988) traps were set in a linear pattern along the lake shore in Kakrigu area. This area supported a high density of flies (Fig. 2) and was estimated to be of approximately 14 hectares in size. Traps were placed every 120 m from a release point in two directions (east-west) up to a distance of 720 m. Two more traps were sited 50 m away from the lake shore at roughly 60° angles from the release point. This pattern was similar to that used in the second experiment (Fig. 6). On the day of marking all the traps were placed in position by 8.00 h and were emptied at hourly intervals from 9.00 h until 17.00 h. Flies caught were marked with artist's oil paint (Rowney Georgian Oil Colours, England) on the thorax (Jackson, 1953) using small wires with rounded tips. A few drops of linseed oil were added to maintain its fluidity during the course of marking. Soon after marking, flies were released. Those recaptured after the first mark were given a new mark for that day and re-released. Different colours were used each day for three days. The three-day mark-release-recapture sessions were considerea to be three replicates, each marking day being a

separate experiment. From the fourth day onwards no further marking was done. On the fourth day the number of traps was increased to get more recaptures. On either side of the release point traps were set at intervals of 120 m up to a distance of up to 1,080 m. From the fourth day to the eleventh day, flies caught were not released but taken to the laboratory to check and record the marks. Corrected recapture rates (CRRs) were calculated using the method described by Jackson (1948) and later modified by Rogers and Randolph (1986b) to determine the absolute population density, feeding and larviposition cycles. The maximum likelihood estimate for the average corrected recapture rate on day '**n**' was described by Rogers and Randolph as:

$$Pn = \frac{\sum_{i=1}^{k} Rni}{\sum_{i=1}^{k} Coi.Cni} \times 10^4$$

with **k** replicates. **Pn** is the proportion of marked flies over the sum of marked and unmarked ones. **Rn** is the number of flies originally marked on day 0 (when the catch was **Co**) that are recaptured on day **n** in a total catch **Cn** flies. Hungry flies show a tendency to visit traps at intervals. Thus, by plotting CRRs against time the peaks that rise at regular intervals suggest feeding cycles. Peaks that occur at longer regular intervals and are superimposed on the shorter ones suggest larviposition cycles. Extrapolation of

the regression line to day 0, that i , the day before marking, makes it possible to estimate the population for that day (Jackson, 1948). This experiment lasted 11 days.

In one of the experiments a record was kept of the time taken between marking and the recapturing of flies and the distance the flies covered from the release point. The distances travelled by flies were estimated using a modified diffusion equation of Pielou (1977) given by Dr Brian Williams (personal communication). The modified equation is given as:

$$N_{(x,t)} = \frac{K}{\sigma} e^{-(x-x_0)^2/2\sigma^2}$$

where N=Number of flies diffused from the release point

x=distance from release point

t=time between marking and recapture

K=total number of flies recaptured

e=2.714....

$\sigma=\lambda^2 t$

In using this equation, the following assumptions were made; (i) that flies diffused in a random fashion and (ii) that since most of the flies were released from the selected release point between 9.00 and 10.00 h, nine hours was taken to represent zero time

Applying the above equation, evaluation was done with x equals 120 m (this being the intertrap distance), and with various times (t) at hourly intervals that is, 1-7 hours (representing time in hours after marking) while adjusting K so that the total number of flies estimated was the same as observed. Lambda ($\lambda$) was varied to get the best fit as measured by the sum of squares of the differences between observed and expected values.

The second experiment followed the same design as the first. The only differences being that this was of a longer duration, lasting 28 days, and comprised four mark-release-recapture sessions. The distance moved by flies per unit time was not estimated in the second experiment. On the fifth day traps were spread farther apart at distances of 0.5, 1.0, 1.5, 2.5 and 3.5 km on the eastern and western sides of the release point. On the western side, this spacings of traps was continued up to 5.5 km but on the eastern side one trap was set about 6 km from the release point on the mainland due to clearings for cultivation and human settlements (Fig. 4). This was to determine whether flies moved longer distances over time.

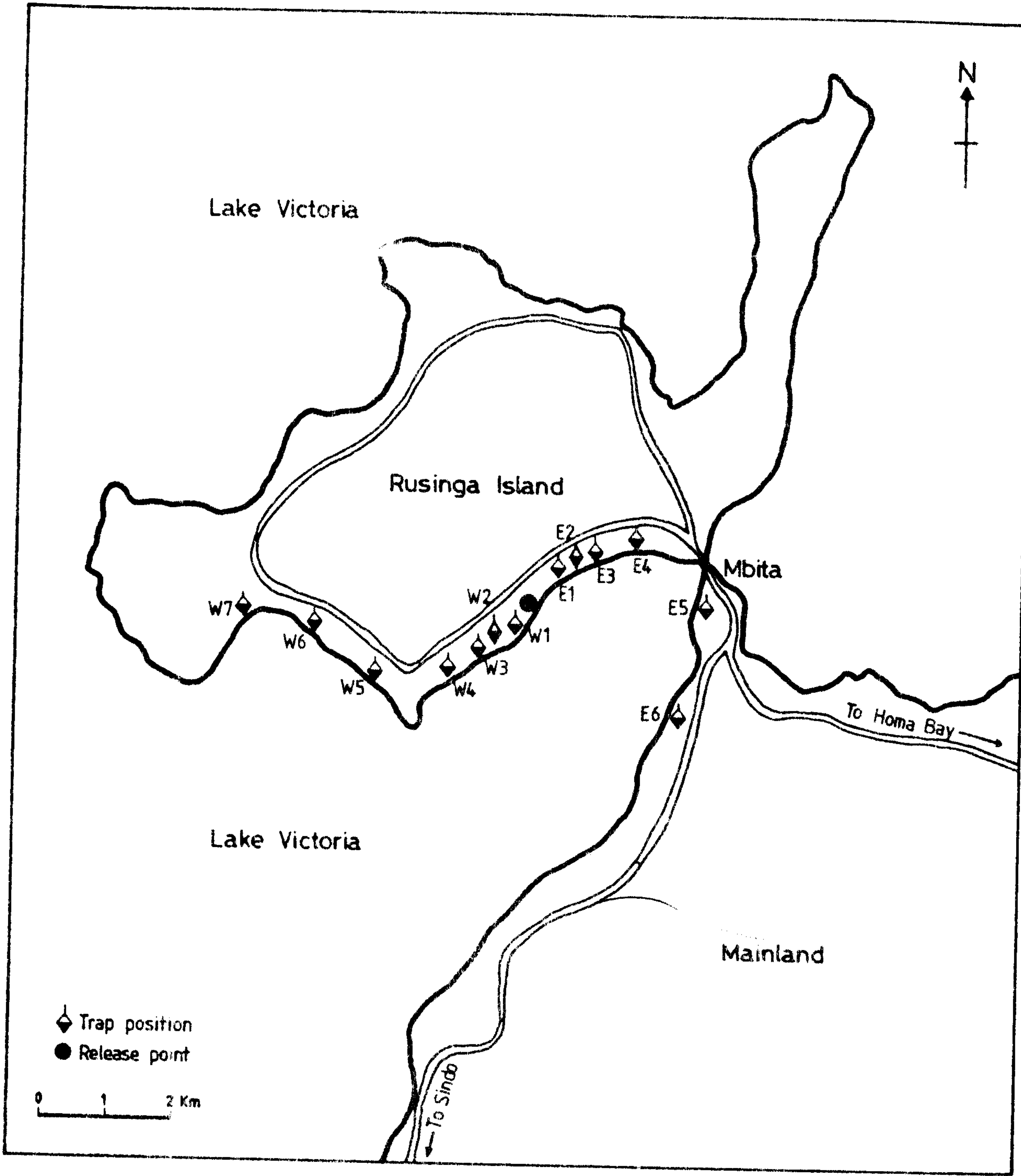



Fig. 4. Map of Rusinga Island and the mainland showing trap positions during the second mark-release-recapture experiment for *G. f. fuscipes* from 8 November 1988 to 12 December 1988.

# RESULTS

## Meteorological factors

Mean minimum and maximum temperatures (ambient and soil), rainfall and relative humidity are presented in Figs. 5a-5c. Ambient and soil temperatures fluctuated together. Mean maximum temperatures were highest in February, March, June and December. There was a drop in temperature during the rains. Mean maximum ambient temperatures fluctuated around 28 °C during the year. In January 1989 a low mean minimum soil temperature of about 25 °C was recorded. Relative humidity which was recorded at 9.00 h each day was also rather constant, fluctuating mostly between 80 and 90 %. There was rainfall each month except in January and June 1989. Peak rainfall figures were recorded in the months of April-May, September and December.

## Apparent density

Changes in apparent density of tsetse flies caught on Rusinga Island and the mainland (Figs. 6a and 6b) show that population size was remarkably stable during the course of the study, varying by only a factor of 5 on Rusinga Island and 7 on the mainland. However, rainfall appeared to influence their numbers. There was a drop in trap catches

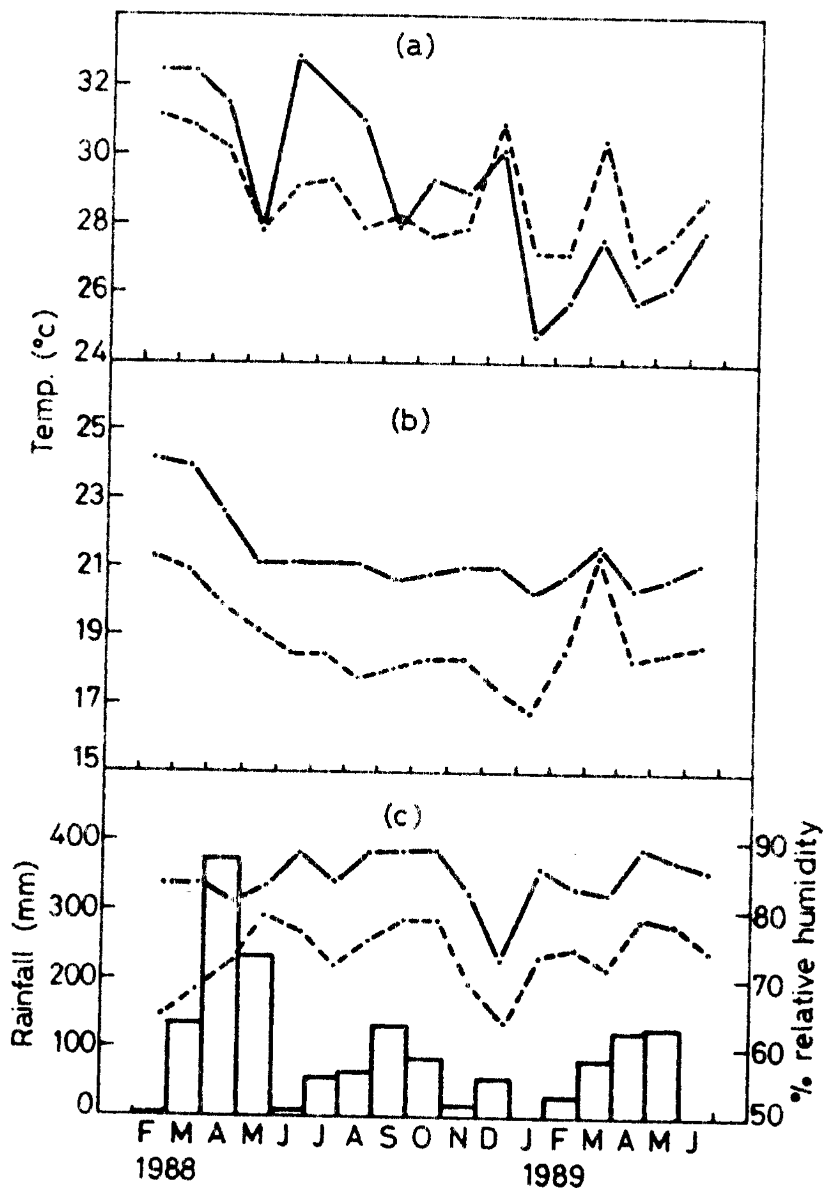



Fig. 5. (a) Mean maximum soil temperatures (____) and mean maximum ambient temperatures (---) recorded at 9.00 h; (b) mean minimum soil temperatures (____) and mean minimum ambient temperatures (---) recorded at 9.00 h; (c) percentage relative humidity recorded at 9.00 (____) and 15.00 (---) h on Rusinga Island with histograms showing rainfall recorded at Mbita.

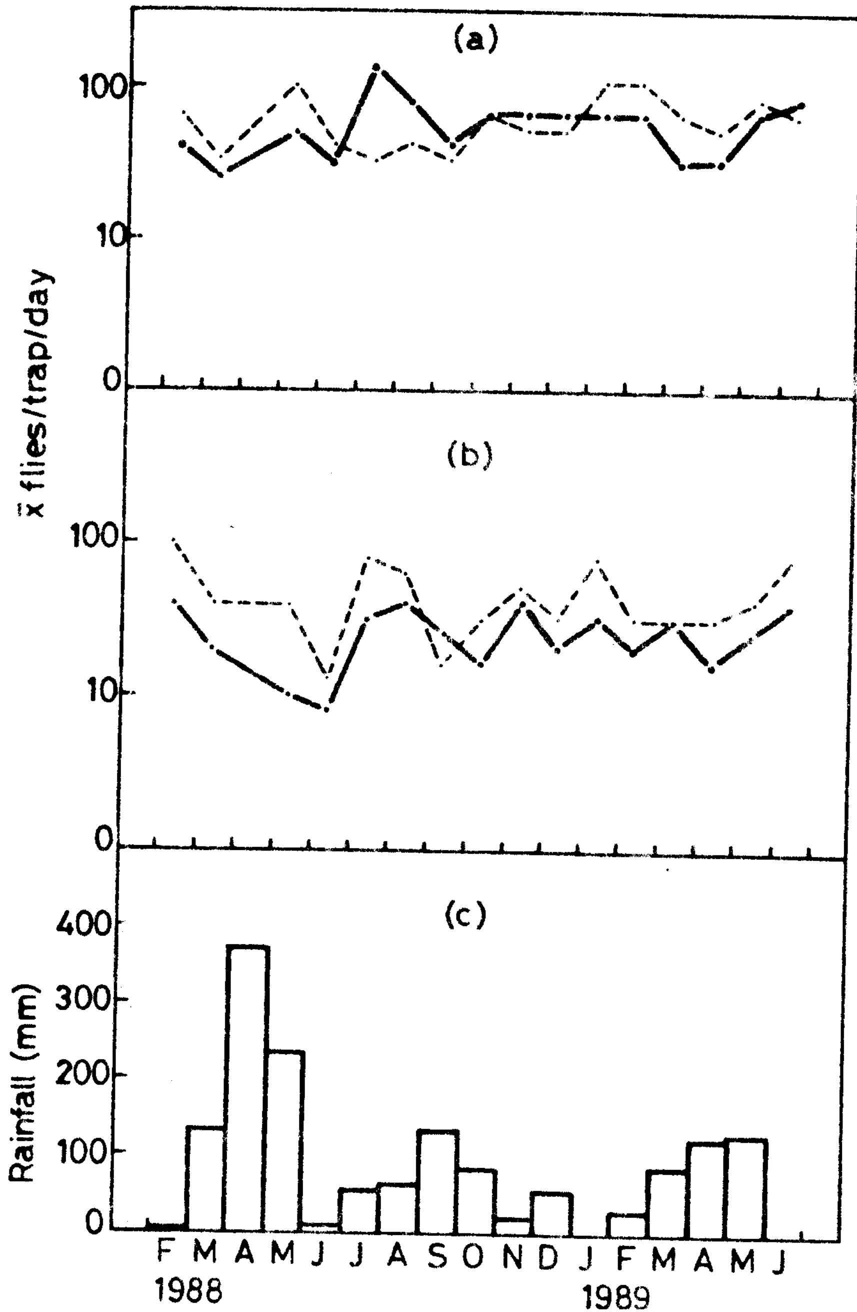



Fig. 6. *G. f. fuscipes* catches on (a) Rusinga Island and (b) the mainland showing males (____) and females (---) and (c) rainfall recorded at Mbita.

soon after the rainy season in June 1988 and during the rainy season in September-October 1988 and in March-April 1989. Unfortunately, ' data was collected at the peak of the rainy season in April 1988 due to operational problems. Heavy rainfall which culminated in floods coincided with the low catches. There were in general more flies caught per trap per day on the island than on the mainland. The sex ratio (percentage of females) was quite variable especially on Rusinga Island and could also be related to rainfall. On the island the percentage of females in the total catch dropped after the rains in July and November 1988 and in June 1989 (Fig. 7). This trend also occurred on the mainland. However, the drop in catches occurred about three months after the rains in comparison to the situation on Rusinga Island.

## Age composition

The age composition of male flies caught in traps on Rusinga Island and the mainland is shown in Fig. 8a and Appendix II (Table 2.1). The mean wing fray age of males was estimated using the correction factors provided by Potts (1970b) for ***G. morsitans***. In doing so it was assumed that the rate of tear of the wings of ***G. morsitans*** and ***G. f. fuscipes*** were similar. Using these correction factors, the mean wing fray age of males caught in traps on Rusinga

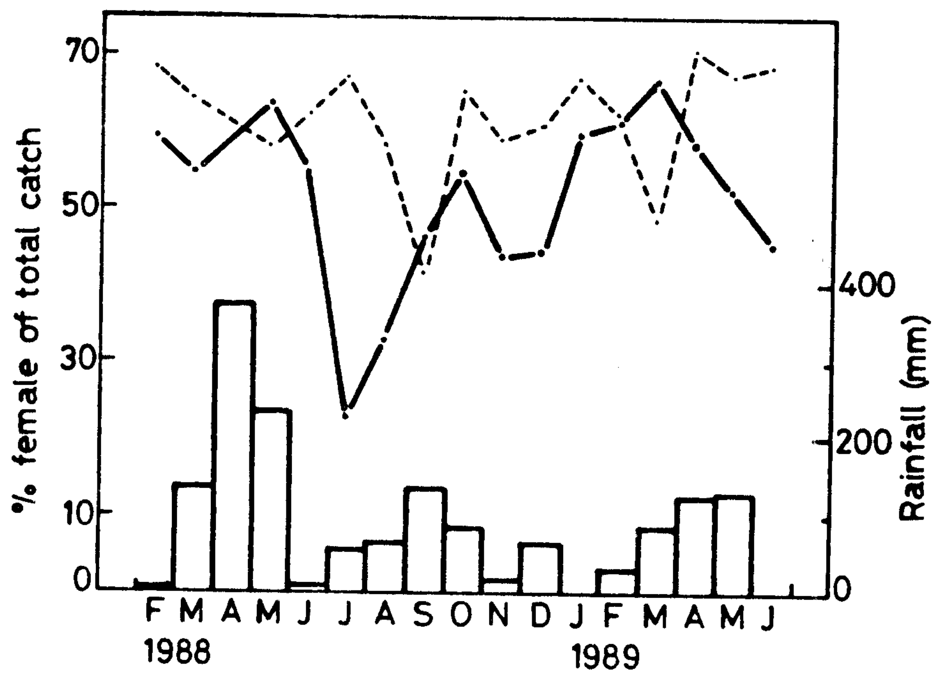



Fig. 7. Percentage female *G. f. fuscipes* of the total catch on Rusinga Island (____) and the mainland (---).

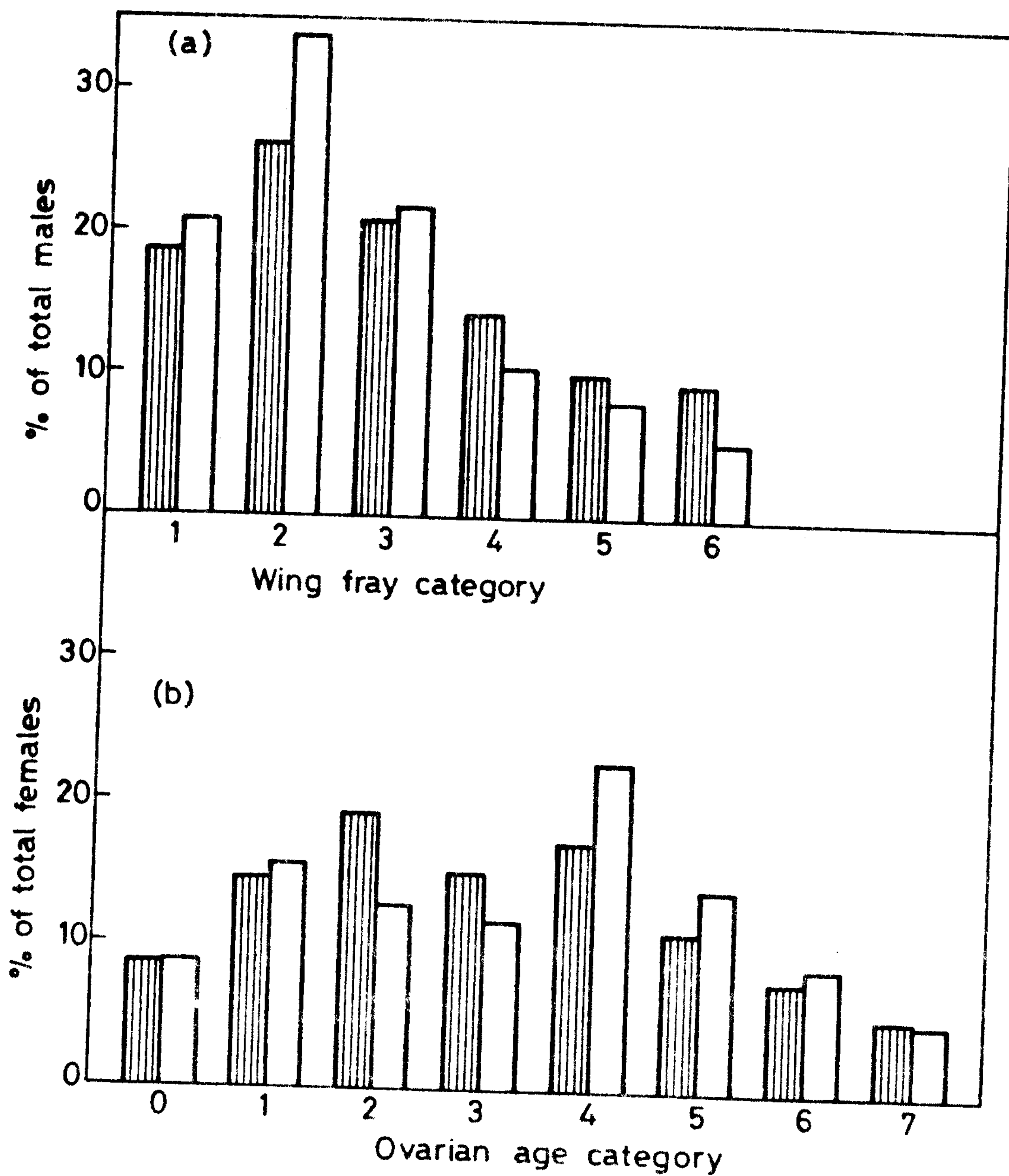



Fig. 8. Age composition of (a) male and (b) female *G. f. fuscipes* on Rusinga Island (shaded) and the mainland (clear).

Island and the mainland were estimated to be 24 and 21 days old, respectively (Appendix II, Table 2.1). This would give mortality rates of 4.2 % and 4.8 % per day, respectively. The age distribution of males from the island was significantly different from that of males from the mainland (N=914, $X^2$=13.92, df=5, P<0.05) (Fig. 8a).

All the ovarian age categories were represented in the ovarian age studies (Fig. 8b and 9). In the ovarian age category 0, Ob's (nullipars with the inside right follicle in this case taken to be greater than or equal to 0.60 mm) were more frequent than Oa's (nullipars with the right inside egg follicle equal or less than 0.60 mm). In parous females, those with eggs and second instar larvae in the uterus were the most frequent, while parous females with third instar larvae in the uterus were the least common. The age distribution of the females from the two localities was not significantly different (N=832, $X^2$=10.93, df=7, P>0.05 ns) (Fig. 8b).

Estimated mortality rates of the tsetse populations on Rusinga Island and the mainland derived from the analyses of age distribution (Fig. 10) show that mortality rates expressed as percentage per day ranged from 0.018 to 0.050. More flies died on Rusinga Island in May-June 1988 and March-April 1989 than on the mainland. This coincided with the long rainy seasons or the period following immediately

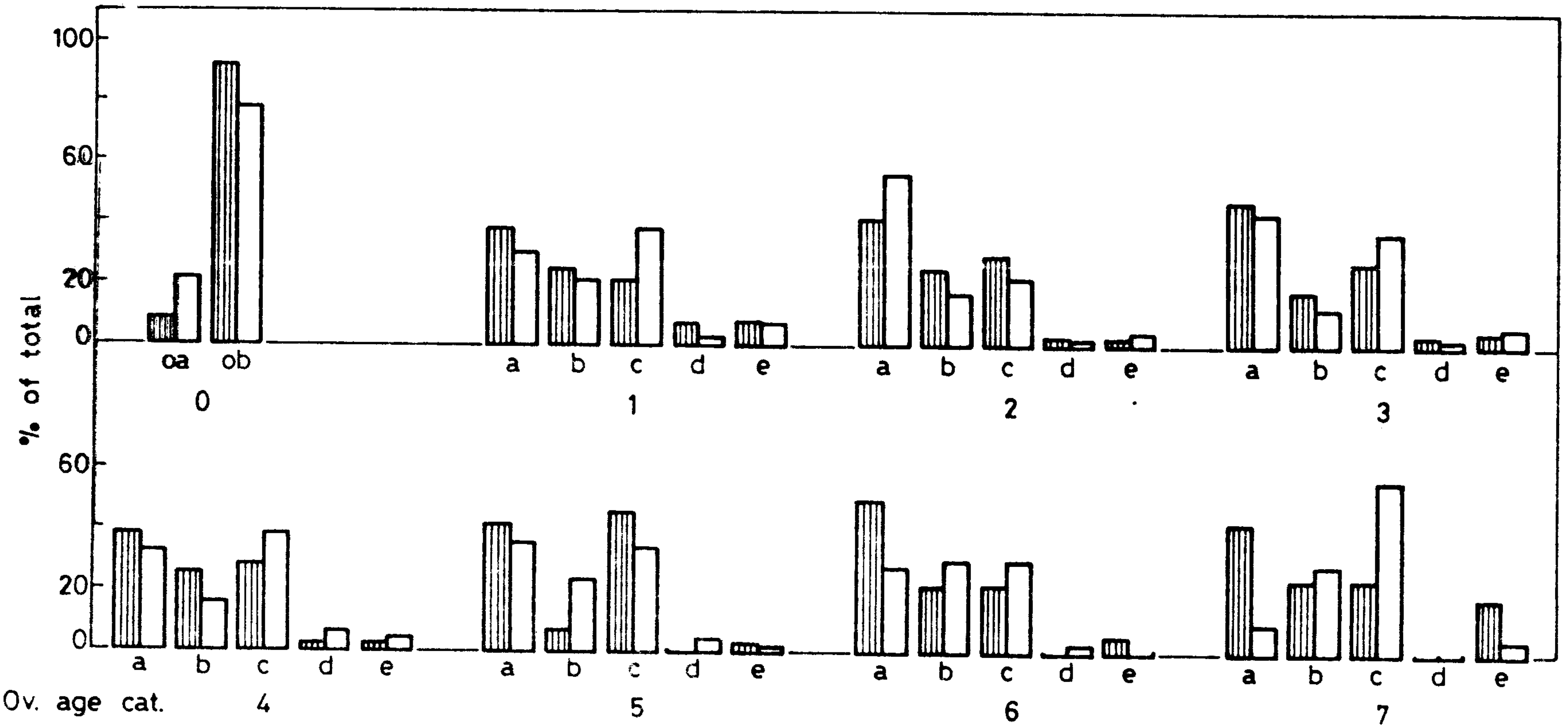



Fig. 9.. Age composition and pregnancy stages of ***G. f. fuscipes*** on Rusinga Island (shaded) and the mainland (clear) caught in traps from February 1988 to June 1989.

Oa=nullipars with inside right follicle ⩾ 0.60 mm.

Ob=nullipars with inside right follicle ⩽ 0.60 mm.

a=parous female with egg in uterus.
b=parous female with first instar larva in uterus.
c=parous female with second instar larva in uterus.
d=parous female with third instar larva in uterus.
e=parous female without egg or larva in uterus.

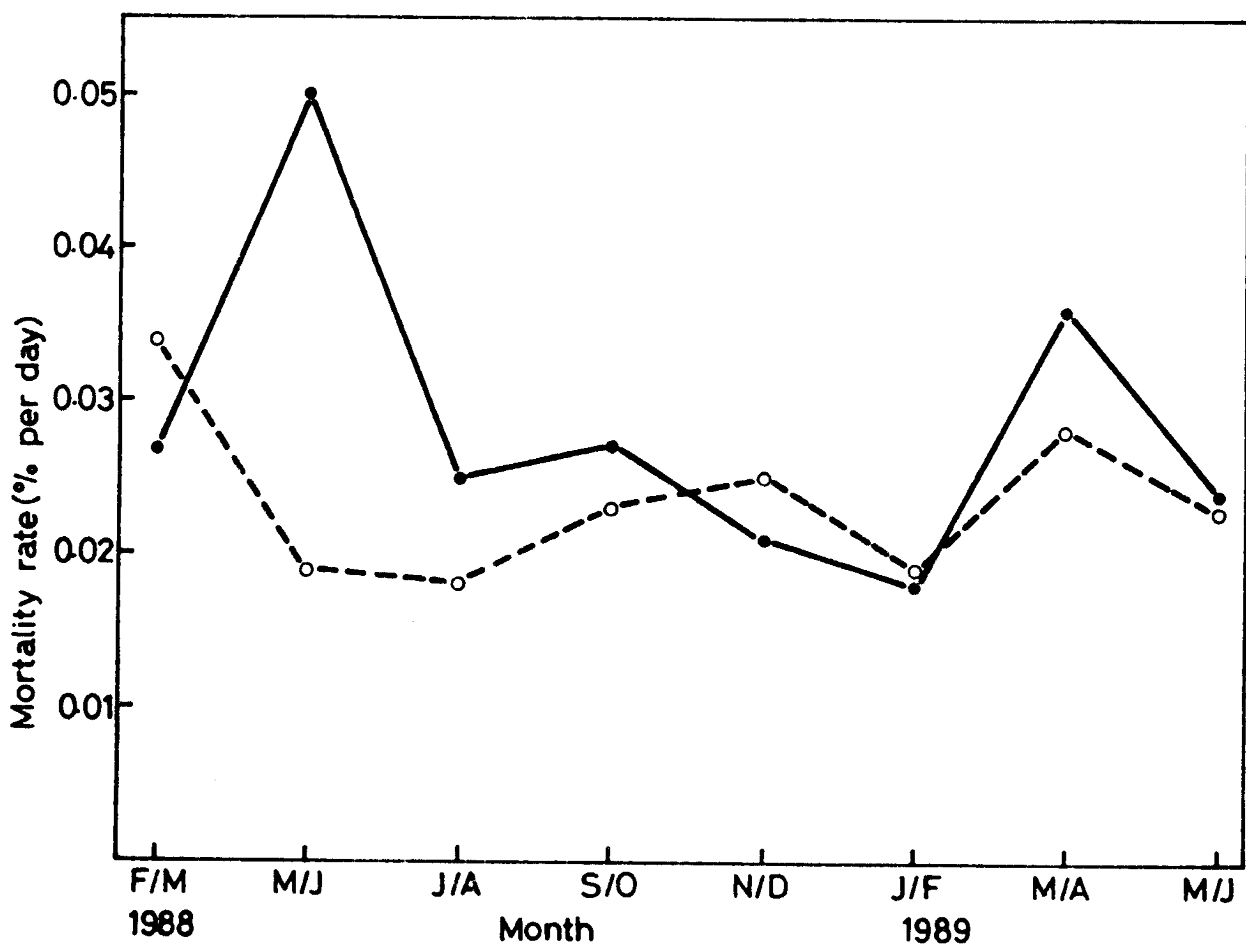



Fig. 10. Apparent mortality rates of *G. f. fuscipes* on Rusinga island (____) and the mainland (---) estimated using the ovarian age analysis method.

after these seasons. The trend was slightly different on the mainland where mortality rates were highest during the periods February-March 1988 and March-April 1989. However, the mortality rates for the two localities were not correlated. There was a positive correlation between mortality rates and amount of rainfall on Rusinga island ($Y=0.0115 + 0.0002X$, $r=0.8404$, $P<0.01$) (Fig. 11). Apart from rainfall there were no correlations between other physical factors and the mortality rates for the two localities.

Moran plots derived from geometric means of flies caught in traps on Rusinga Island and the mainland show that one or two points fell outside the expected reproductive rates of tsetse flies implying either immigration or random error in estimating density (Fig. 12). Mortality rates estimated from Moran plots fluctuated and no patterns due to seasonality were discernible (13). Mortality rates derived by Moran curve technique were not positively correlated to the physical factors. Furthermore, mortality rates derived by the two methods given above were not correlated.

**Reproductive abnormalities**

Reproductive abnormalities recorded in tsetse fly samples from Rusinga Island and the mainland (Table 2)

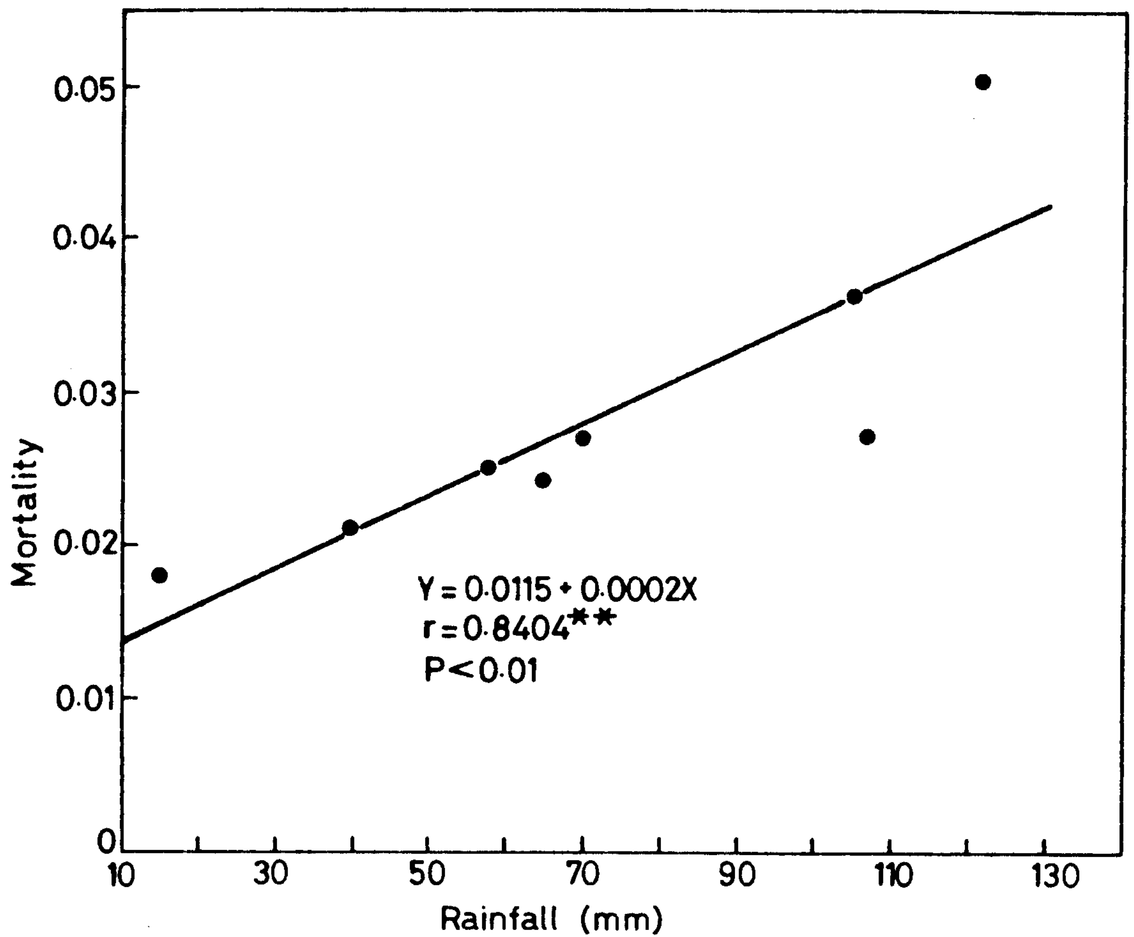



Fig. 11. The relationship between rainfall and mortality rates of female *G. f. fuscipes* on Rusinga Island obtained using the ovarian age analysis method.

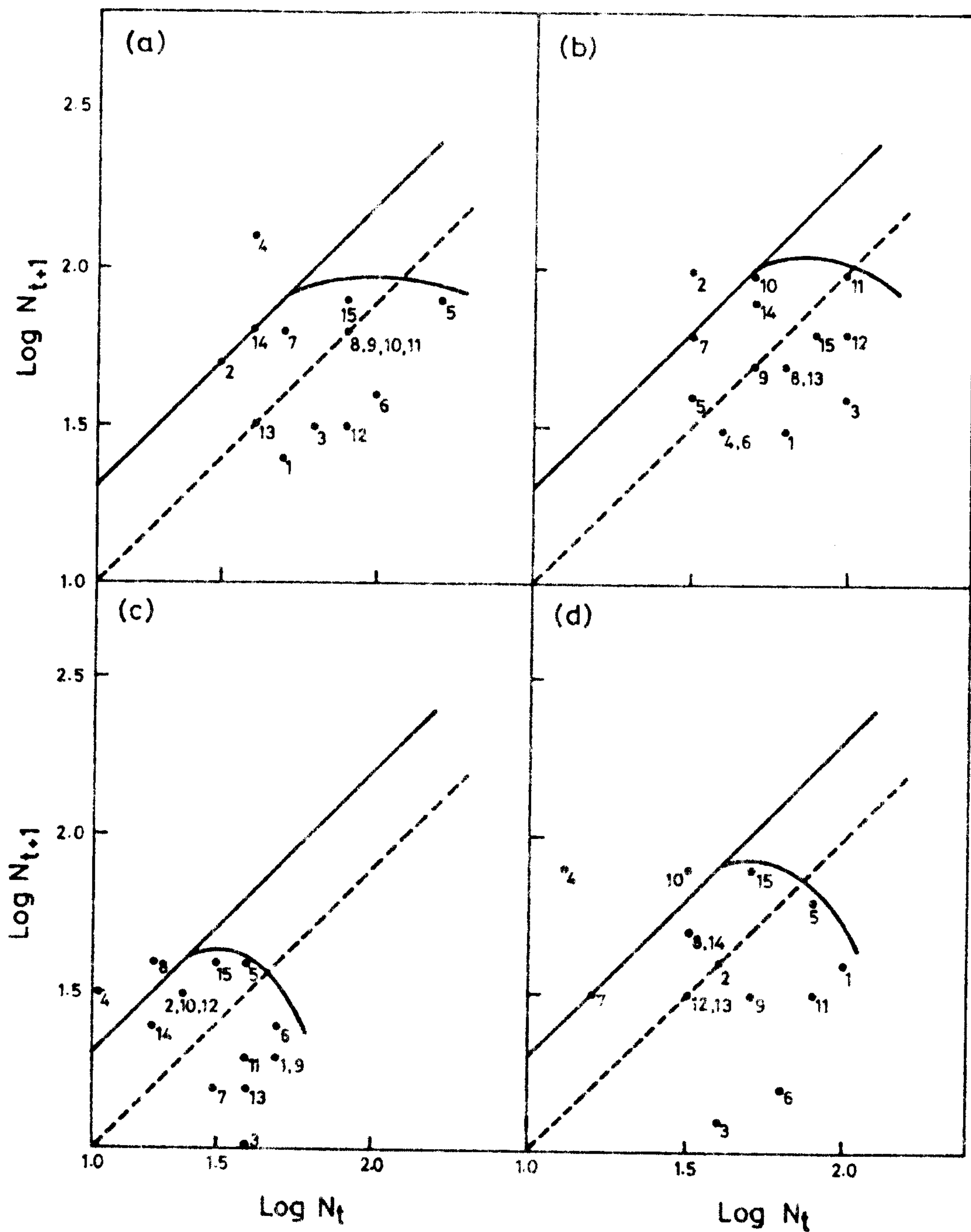



Fig. 12. Moran plots derived from arithmetic means per trap per day data for *G. f. fuscipes* plotted on a logarithmic scale. (a) males and (b) females from Rusinga Island and (c) males and (d) females from the mainland.

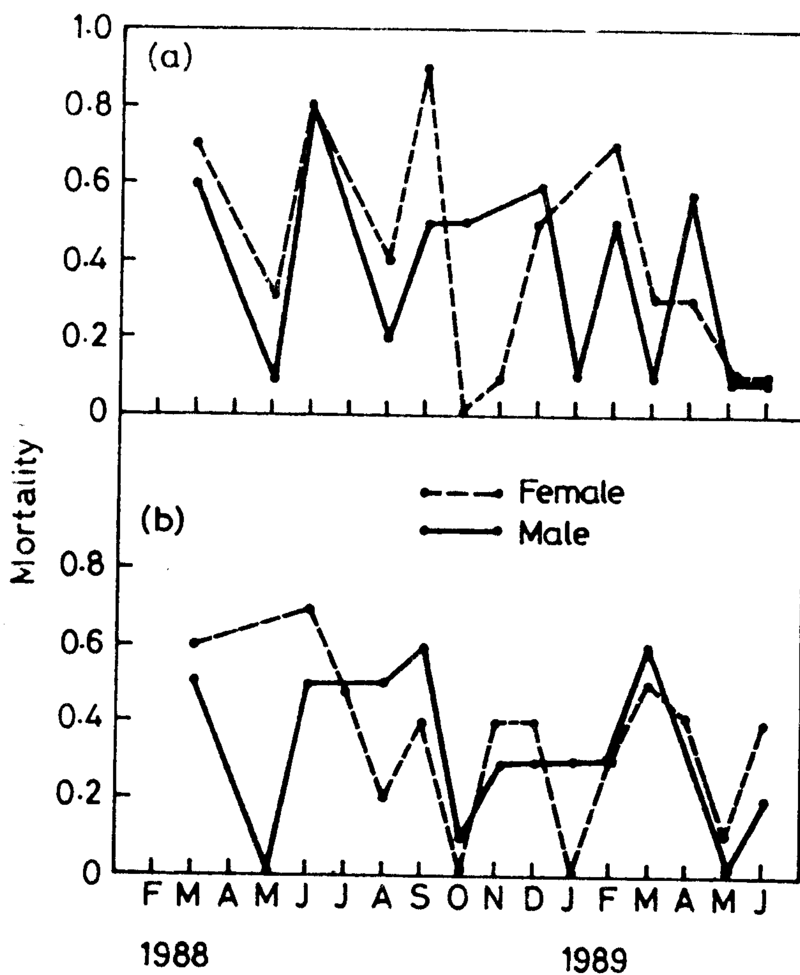



Fig. 13. Mortality rates of male (___) and female (---) *G. f.* ***fuscipes*** on (a) the mainland and (b) Rusinga Island, estimated from Moran plots.

Table 2. Reproductive abnormalities in *G. f. fuscipes* samples from Rusinga Island and the mainland from February 1988 to January 1989.

| Abnormality | Rusinga | Mainland |
|---|---|---|
| Follicular degeneration | 2/331 (0.6%) | 1/341 (0.3%) |
| Egg retention | 0/331 (0%) | 1/341 (0.3%) |
| Abortions (Ovarian age cat. 2-7) | 5/246 (2.05) | 5/247 (2.05) |

Denominator=number of flies dissected. In brackets = percentage.

Table 3. The frequency of empty uteri and abortions recorded in *G. f. fuscipes* samples from Rusinga Island and the mainland from February 1988 to January 1989.

| | Rusinga Island | Mainland |
|---|---|---|
| No. dissected | 246 | 247 |
| Empty uteri: | | |
| No. in age category 1 | 2 (0.8%) | 3 (1.2%) |
| No. in age category 2-7 | 7 (2.8%) | 7 (2.8%) |
| Total | 9 (3.7%) | 10 (4.0%) |
| No. of abortions in age category 2-7 | 5 (2.0%) | 5 (2.0%) |

revealed three cases of follicular degenerations. These involved two of the 331 (0.6 %) dissected flies from Rusinga Island and one of the 341 (0.3 %) from the mainland. Only one case of egg retention was recorded out of a total of 672 flies dissected from both localities. Intra-uterine egg measurements of 61 flies gave a mean egg size of 1.65 ± 0.05 mm with a limiting value of 1.55 mm. Category 1 flies were not included because these are undersampled by biconical traps and the size of the sample was small as stated earlier. Nine of the 246 (3.7 %) females from Rusinga Island had empty uteri and 5 (2.0 %) were determined to have had abortions (Table 3). Ten of the 247 (4.0 %) females from the mainland had empty uteri but again only 5 (2.0 %) were determined to have had abortions. Nearly all the flies examined for insemination (total 700) were found to be inseminated except flies in the category OA in which 6 of the 14 (43 %) examined from the island and the mainland combined were not inseminated.

## Mark-release-recapture studies

### Feeding and pregnancy cycles

Corrected recapture rates (CRRs) from mark-release-recapture data for the first experiment shown in Appendix II (Table 2.3) indicated that there was no discernible pattern

of peaks when CRRs were plotted against time. In addition, the experiment was of a rather short duration to depict any cycles. CRRs from the second experiment, which ran for a longer period of time (Appendix II, Table 2.4), showed peaks at intervals of 5, 9, 14, 18, 22 and 25 days for female flies (Fig. 14b). This could reflect a pregnancy cycle of 8-9 days, with a hunger cycle superimposed at 4-5 days. There was no clear cut pattern in the peaks for male flies (Fig. 14a).

**Absolute population size**

The absolute population density for the Wakondo/Kakrigu area in the southern part of Rusinga Island (Fig. 2) was determined by regression lines drawn through CRRs plotted against time (Fig. 14). The regression lines were significant: for male flies the equation was Y=0.865-0.73X ($R^2$=0.7467, where Y=ln CRR, X=ln Day and standard error of b=0.089***). For female flies the equation was Y=0.245-0.086X ($R^2$=0.5074, F=27.8***, where Y=ln CRR, X=Day, standard error of b=0.016 and ***=P<0.001). Extrapolating the regression lines to day '0' the male and female populations on the day of marking were estimated at 4,211 and 7,872 in the estimated area of 14 hectares which was equivalent to 301 males and 559 females per hectare, respectively.

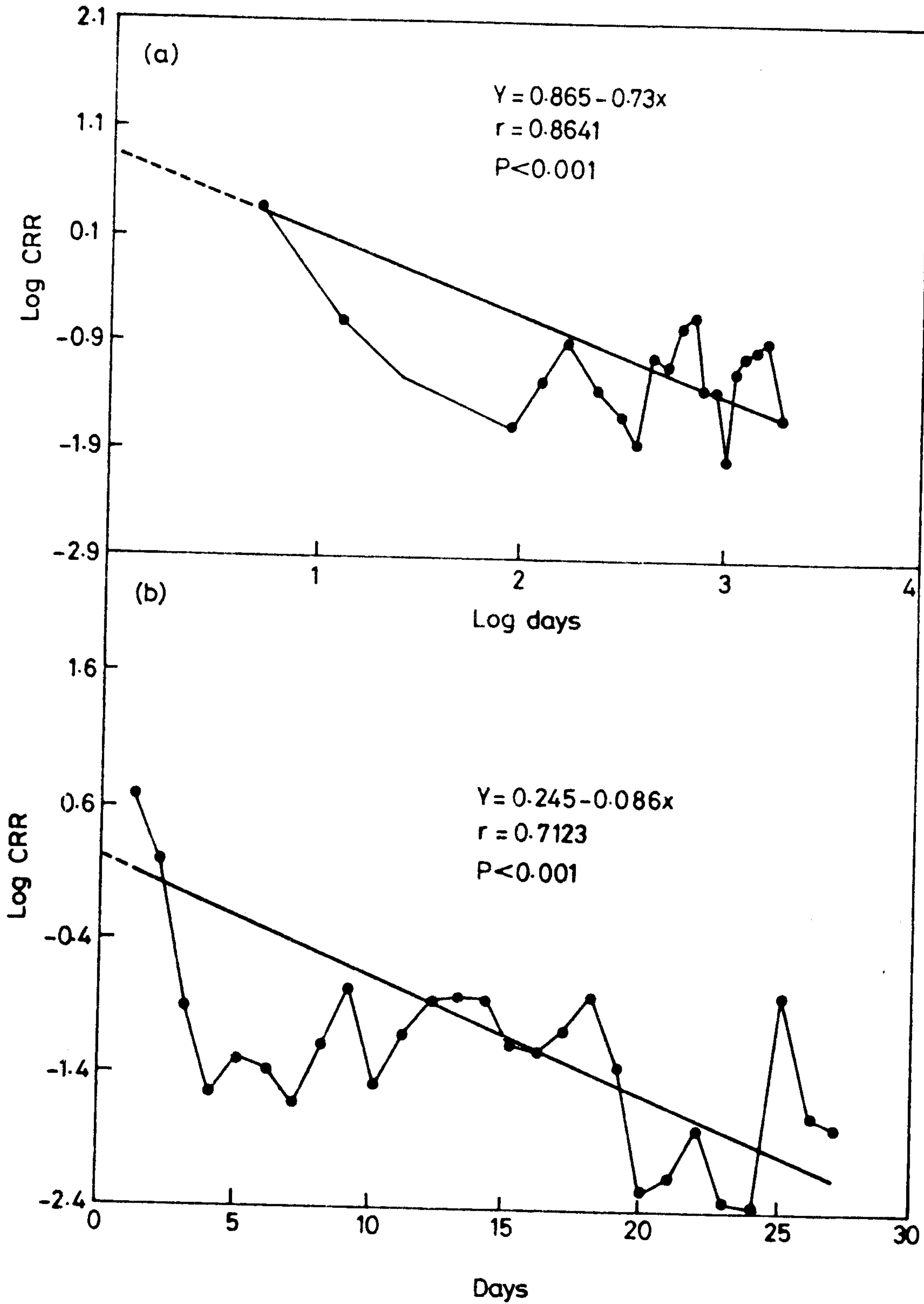



Fig. 14. Corrected recapture rates of (a) male and (b) female *G. f. fuscipes* on Rusinga island showing peaks for females at intervals of about 4 and 7-9 days following marking.

**Dispersal**

In the first experiment 1,027 flies (501 males and 526 females) were marked and released. Of the marked and released flies, 329 (140 males and 189 females or 32.0 % of the total number of flies released) were recaptured within eleven days Appendix II, Table 2.3. The distances at which flies were recaptured within seven hours following their release in one of the experiments is presented in Table 4. The farthest distance from the release point at which a fly was caught was 600 m in seven hours. Using the modified equation of Pielou (1977) described previously (section on mark-release-recapture experiments) the best fit at 120 m, was obtained when lambda ($\lambda$) was equated to 22 m for males and 32.5 m for females (Table 5). If fly activity is diurnal lasting six hours the distance travelled per day would be 54 m for males and 80 m for females. If fly activity is extended further to twelve hours the distance travelled is estimated at 76 m and 112 m for each sex, respectively. An attempt was made to include an escape response in the calculations but this did not improve the fit.

In the second mark-release-recapture experiment 2,199 flies comprising 802 male and 1,397 female *G. f. fuscipes*

Table 4. The distances from the release point at which *G. f. fuscipes* was recaptured and the time taken.

| Distance (m) | Time (hours) 1 | | 2 | | 3 | | 4 | | 5 | | 6 | | 7 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | M | F | M | F | M | F | M | F | M | F | M | F | M | F |
| 120 | 0 | 0 | 1 | 3 | 0 | 2 | 0 | 3 | 2 | 13 | 8 | 11 | 3 | 3 |
| 240 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 4 | 1 | 3 | 1 | 1 |
| 360 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 1 | 2 | 1 |
| 480 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 2 |
| 600 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| 720 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

Table 5 Best fit values of lambda to estimate root-mean-square displacement per hour for *G. f. fuscipes* on Rusinga island.

| Time (hours) | Observed | | Predicted | |
|---|---|---|---|---|
| | Male | Female | Male | Female |
| 1 | 0.000 | 0.000 | 0.000 | 0.001 |
| 2 | 0.007 | 0.024 | 0.000 | 0.014 |
| 3 | 0.000 | 0.016 | 0.003 | 0.034 |
| 4 | 0.000 | 0.025 | 0.010 | 0.053 |
| 5 | 0.014 | 0.110 | 0.019 | 0.066 |
| 6 | 0.056 | 0.112 | 0.028 | 0.076 |
| 7 | 0.022 | 0.038 | 0.038 | 0.083 |

Best fit value of lambda gives Root-mean-square displacement per hour of 22 m for males and 32.5 m for females.

were marked and released. Of these 422 (120 males and 302 females or 19.2 % of the marked and released flies) were recaptured (Appendix II, Table 2.4). From 12 November to 5 December 1988, after traps were increased in number and rearranged so as to determine distances moved by flies from the release point, 238 flies were recaptured. Of these 201 (84 %) were recaptured in trap W1 placed 0.5 km west of the release point, 18 (8 %) in trap E1 placed 0.5 km east of the release point and 6 (3 %) in trap W2 sited 1 km from the release point (Fig. 4). A few flies were also caught in traps W3 (4) and E2 (1) which were set 1.5 km west and 1 km east of the release point, respectively. None of the flies was caught beyond 1.5 km in 28 days.

## DISCUSSION

*G. f. fuscipes* population densities on Rusinga Island and the mainland showed remarkable stability. This may suggest an adaptation of this subspecies to equable and almost optimum environmental conditions offered by its habitat. The absence of human trypanosomiasis in the area for a long time may explain why there are no active tsetse fly control measures on Rusinga Island and in the Mbita area. The result is that the present tsetse habitat is largely undisturbed except for localized clearings of vegetation for cultivation of crops.

The fall in trap catches during the rainy seasons could be an artefact arising from the poor availability of flies to biconical traps at this time of the year. Dransfield *et al.* (1982) who used water traps and biconical traps to monitor changes in the populations of ***G. m. submorsitans*** and ***G. tachinoides*** in Nigeria observed that the effectiveness of these sampling tools varied over the year. Glasgow (1954) working in the same region where the present study was conducted employed fly rounds to monitor changes in populations of ***G. f. fuscipes*** and observed that population fluctuations were not related to seasons. Correlations between climatic factors and changes in fly populations have been reported by some workers, for example, Nash (1937). Rogers (1979) and Rogers and Randolph (1984; 1985) have, however, pointed out in separate studies that climatic factors do not act directly to reduce population size but will reduce populations indirectly through birth and death rates. There are other factors such as the availability of host animals of tsetse (see Chapter 7) and restricted mobility of flies that could also be responsible for the stability of the populations in addition to the climate being equable.

The factors that caused a drop in the female sex ratio after the rainy season are difficult to explain. It is possible that at this time of the year when floods were

usually observed, females could have moved a little farther inland to seek larviposition sites. However, it is unlikely that the movement of females could have been massive or taken place over long distances on the basis of evidence obtained from the mark-release-recapture studies.

Due to logistical problems it was not possible to carry out mark-release-recapture experiments monthly so as to determine changes in the absolute population densities of flies on Rusinga Island. There is, however, evidence that biconical trap catches are correlated with absolute population densities (Gouteux and Buckland, 1984; Dransfield ***et al.***, in press). The absolute population density estimates obtained tallies with Glasgow's (1963) study and showed that the tsetse fly infestation in thick vegetation on Rusinga Island was heavy. Glasgow's estimates were 22 and 243 tsetse flies per hectare in two localities of Central Nyanza region as compared to 301 male and 559 female flies per hectare in this study.

Mortality rates estimated by the ovarian age analysis methods were slightly higher during the rainy season but the calculations were based on the analysis of data pooled for two months due to the small size of the samples obtained. On Rusinga Island changes in mortality correlated with the amount of rainfall recorded but this trend was not observed on the mainland. However, mortality due to rainfall did not

appear to be the causal factor for the drop in the tsetse fly catches as rainfall is likely to act on the puparial stage which is burried in the soil rather than the adults whose mortality this method estimates.

There was no correlation between mortality rates derived by ovarian age analysis and by Moran plots after data for two months were pooled. Neither was there a significant correlation between mortality rates determined by the two methods and the environmental factors except rainfall for Rusinga Island as mentioned above. The seemingly lack of consistency in the effects of the environmental factors in the two study sites suggests that the size of the fly populations may not have actually changed during the rainy season. The two study sites were so close to each other that it is difficult to envisage how the effects of weather could have been different in the two areas. Flooding, however, would be an exception in this respect.

The short duration of this study and the small sample sizes obtained particurlary for the ovarian age dissections renders it difficult to draw conclusions on the suitability of each method from this study. However, there is evidence from the results using both methods that ***G. f. fuscipes*** populations on Rusinga Island and the mainland in Mbita did

not experience 'catastrophic' changes during the period of this study.

The difference in the age distribution of males and the fact that there was no correlation in mortality rates of females from Rusinga Island and those of the mainland probably indicated local factors, for example, competition for food, in the two areas which were about 7 km apart. Rogers ***et al.*** (1984) and Randolph ***et al.*** (1984) observed that the dynamics of two populations of ***G. p. palpalis*** in Ivory Coast showed marked differences although the populations were only about 2 km apart. They attributed this to be due to the influence of density-dependent factors, particulary, immigration of the flies into one of the areas. Whilst density-dependent factors may act differently on populations in close proximity to each other it is unlikely that weather, a density-independent factor, (flooding could be an exception) would act differently on populations which are so close. The estimates of mean wing fray age for male ***G. f. fuscipes*** calculated in this study were used with caution because these were based on the rate of fray of wings of the ***morsitans*** group of flies. If time allowed, better estimates would have been obtained by carrying out separate mark-release-recapture experiments to relate wing fray and calendar age for ***G. f. fuscipes.***

Reproductive abnormalities were rare in *G. f. fuscipes.* This supported earlier observations on another tsetse fly species, *G. pallidipes*, (Turner and Snow, 1984; Dransfield *et al.*, 1985). Abortions can be induced by confining flies in trap cages for a period of time (Turner and Snow, 1984) and it is not possible to distinguish such abortions from those caused by natural causes in the field. The low percentages of abortions recorded, however, indicate that even taking trap-induced abortions into consideration the figures were still low. This suggests that the populations were not under stress.

On the basis of random diffusion movement, *G. f. fuscipes* on Rusinga Island was estimated to move not more than 112 m per day at most. This estimate is less than half the estimate of 270 m given by Rogers (1977) for this subspecies in Uganda. Considering the patchy nature of the thickets inhabited by this fly on Rusinga Island, the estimated distance moved by flies in this study is reasonable and indeed indicates that this subspecies has restricted mobility. Inclusion of an escape response to the equation did not improve the fit suggesting that an escape response behaviour did not occur. The patchy nature of the tsetse fly habitat and the short distance moved by flies imply that immigration on a large scale probably does not take place. If this is the case, traps will have considerable effect in controlling the fly densities but

only over areas in the immediate vicinity of t.aps. Thus local suppression in small areas (for example, villages) will be easy but control of the flies from large areas would be very difficult.

# CHAPTER 5

# RESPONSES OF *GLOSSINA FUSCIPES FUSCIPES* TO ODOUR BAITS AND TRAP TYPES ON RUSINGA ISLAND, KENYA

## INTRODUCTION

The development of the biconical trap by Challier and Laveissiere (1973) and later its modification (Challier ***et al.***, 1977) led to widespread use of this trap for sampling and controlling tsetse fly populations, especially the ***palpalis*** group. Recently, the rediscovery of attractive substances and the identification of new compounds as chemical baits greatly improved the prospects of using odour-baited traps for sampling and controlling tsetse fly populations (Vale, 1980; Vale ***et al.***, 1988; Hall ***et al.***, 1984; Owaga, 1985; Owaga ***et al.***, 1988; Dransfield ***et al.***, 1986; Hassanali ***et al.***, 1986; Gough ***et al.***, 1987;). However, until very recently most of the chemical baits identified have been for the ***morsitans*** group of flies, specifically, ***G. morsitans*** and ***G. pallidipes.*** The potential of odour-baited traps for controlling tsetse flies has stimulated the search for chemical baits attractive to other tsetse fly species. One of the objectives of this study was ,therefore, to determine the responses of ***G. f. fuscipes*** to various chemical baits some of which have been reported to be successful for other tsetse fly species. In addition, to

determine the efficacy of various new trap designs which have been developed over recent years for this subspecies and other species (Flint, 1985; Green and Flint, 1986; Gouteux and Lancien, 1986; Laveissiere, 1989; Brightwell *et al.*, 1987, 1990) for use in control schemes.

## MATERIALS AND METHODS

### Chemical baits

Various chemical baits, some of which have been proven attractive for *G. morsitans* and *G. pallidipes* were tested for efficacy in the field against *G. f. fuscipes* either, singly or in combinations, using biconical traps (Challier *et al.*, 1977). These included the following:

i. Cow urine.

ii. Human urine.

iii. Acetone.

iv. 1-octen-3-ol.

v. A mixture of 8 parts p-cresol: 4 parts 1-octen-3-ol: 1 part 3-n-propylphenol designated as TF 841 obtained from the Overseas Development Natural Resources Institute (ODNRI) of the United Kingdom.

vi. A mixture of 1 part m-cresol: 1 part p-cresol: 2 parts 1-octen-3-ol designated as TF 89/4 obtained from ODNRI.

vii. A mixture of 3 parts m-cresol: 1 part 1-octen-3-ol designated as TF 89/1 obtained from ODNRI.

viii. Washings from a monitor lizard.

ix. Washings from a goat.

Cow urine was obtained from zebu cattle belonging to farmers on Rusinga Island. It was from different sources but was mixed in a 20-litre container before being separated into 2.5 litre glass bottles and stored at room temperature. Human urine was collected from the author and, like cow urine, was kept in 2.5-litre glass bottles stored at room temperature. The urine was stored for two to four weeks before use. Earlier studies (Dransfield *et al.*, 1986) indicated that cow urine kept for this period was more effective than fresh urine for *G. pallidipes* in Nguruman, Kenya. 1-octen-3-ol, TF/841, TF 89/1 and TF 89/4 were obtained from the Overseas Development Natural Resources Institute, United Kingdom. These were provided in 120 um thick polythene sachets with a nominal area of 70 $cm^2$ (Dr. D. R. Hall, personal communication) and were kept in air tight glass bottles at room temperature before use. Washings from a monitor lizard were obtained by scraping the skin of this animal that was trapped on Rusinga Island in water using a dissecting scapel (Fig. 15). The same procedure was used to obtain goat washings. The washings were stored at 4 °C to prevent fermentation before use.

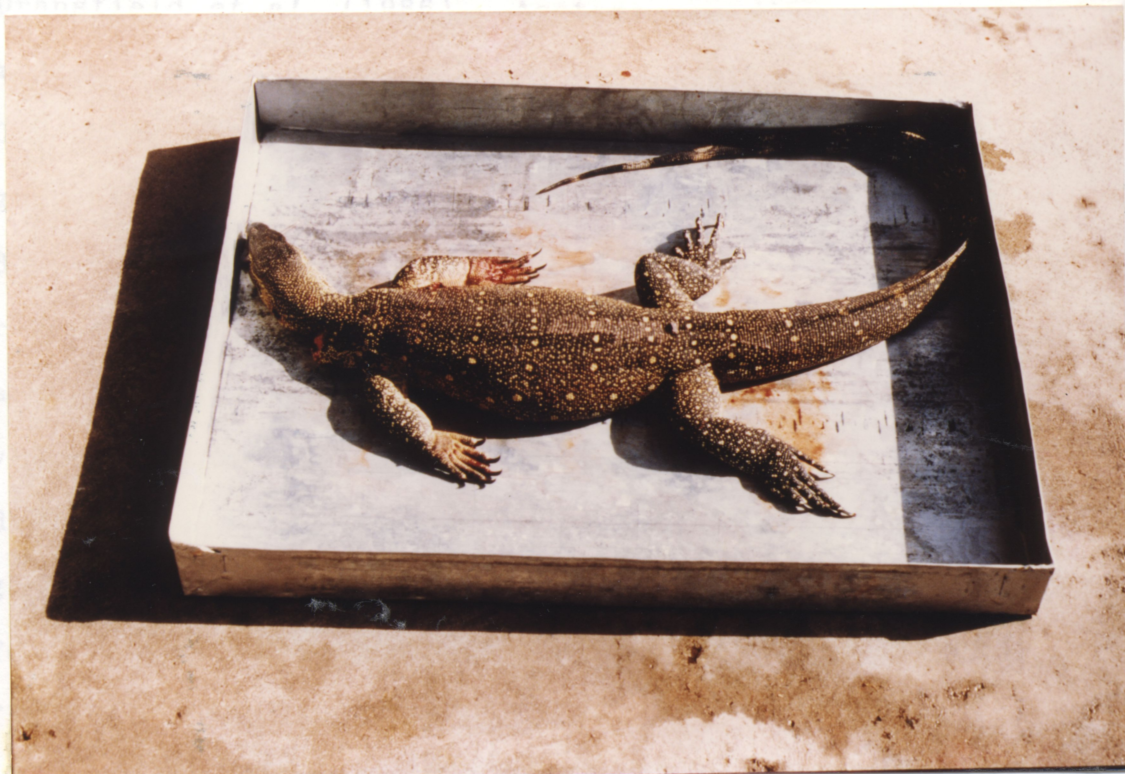


Fig. 15. Monitor lizard from which skin scrapings and body washings baits were derived.

**Dispensers**

Cow and human urine were dispensed in 560-ml open-top cans with an aperture diameter of 8.3 cm as reported by Dransfield *et al.* (1986). Acetone was dispensed at low, medium and high dose rates in 216-ml glass bottles with a 0.8 cm diameter hole drilled in the lids; in 185-ml GIBCO glass bottles with an aperture diameter of 2.2 cm, and in 330-ml glass bottles with an aperture diameter of 5.2 cm, respectively. Except where stated, the medium dose rate of acetone was used in all the trials. 1-octen-3-ol and the various phenolic compounds were dispensed in sachets as described above. All the dispensers were placed on the ground 30 cm from the base of the trap (see Figs. 16 and 17) for maximum concentration of odours near the point where flies were focussed by the trap (Vale, 1982a, 1983). Rain water was kept out by covers constructed from tin cans placed over the dispensers.

**Dose rates**

Acetone, cow and human urine dose rates were determined by estimating the volume of the bait that evaporated from each dispenser over the duration of the experiments. The experiments on odour baits were run for 12 hours, from 6.00-18.00 hours, this being the time *G. f. fuscipes* was caught

Fig. 16. Some of the dispensers used for 1-octen-3-ol, acetone and cow urine baits in trapping trials for *G. f. fuscipes* on Rusinga Island and the mainland.

in traps (see Chapter 3). This study was conducted from February 1988 to July 1989. By taking the means of the volume of baits dispensed over 12 hours with a known weight per millilitre it was possible to estimate the amount of bait in milligrammes that was dispensed during each trial. The dose rates for phenolic mixtures used were as reported by Dr. D. R. Hall (personal communication) (Table 6 and Appendix III, Table 3.1).

**Trap types**

The trap types that were compared included the biconical trap (Challier, *et al.*, 1977); NG2B trap (Brightwell *et al.*, 1987); NG2G trap (Brightwell *et al.*, 1990); F3 trap (Flint, 1985 and Green and Flint, 1986); Vavoua trap (Laveissiere, 1989) and the pyramidal trap (Gouteux and Lancien, 1986 ). The biconical trap (Fig. 17), NG2B (Fig. 18) and NG2G (Fig. 19) were made from the same types of material consisting of blue and black cloth with white netting. The F3 trap (Fig. 20), Vavoua trap (Fig. 21) and pyramidal trap (Fig. 22) were all made from different materials which were of a similar shade of blue colour as the biconical trap and the NG models. Slight modifications were made to the collecting cages of the F3 and pyramidal traps by adding a central pole to support the collecting cages. This modification was necessary to standardise the

Table 6. Dose rate of odour baits determined in a series of experiments on Rusinga Island from February 1988 to July 1989.

| Odour bait | Dose rate |
|---|---|
| Cow urine | 253.3-1425.0 mg/h |
| Human urine | 726.0-1457.0 mg/h |
| Acetone | |
| Low dose | 414.2-415.8 mg/h |
| Medium dose | 841.6-844.8 mg/h* |
| High dose | 9205.0-9240.0 mg/h |
| Phenol/1-octen-3-ol** | |
| p-cresol | 9.1 mg/day |
| 1-octen-3-ol | 3.0 mg/day |
| 3-n-propyl phenol | 0.5 mg/day |

* This dose rate was obtained from one experiment (see Table 7 Experiment iii). Throughout the study the medium dose rate varied from 440.5-914.4 mg/h.

** Provided by Hall (personal communication).

Fig. 17. The biconical trap used in the trapping studies.

Fig. 18. The NG2B trap used in the trapping studies.

Fig. 20. The F3 trap used in the trapping studies.

Fig. 21. The Vavoua trap used in the trapping studies.

Fig.22. The pyramidal trap used in the trapping studies.

size of the collecting cages for comparative purposes. The original collecting cage of the pyramidal trap consisted of a plastic container to which detergent serving as a killing and preserving agent was added. The plastic cage was fixed inside the upper cone of the trap, while that of the F3 trap consisted of a system f plastic containers fixed at the top of the cone which served as the cage. Experiments to compare traps were conducted from 6.30-14.00 hours to give allowance for transfering traps from one site to another for comparisons the next day.

**Experimental design of trials.**

In all trials except where stated, experiments were arranged in a randomised 4X4 latin square design replicated twice in different positions with traps and treatments placed at least 200 m apart to eliminate the influence of each other. The following comparisons were made:

i. Control (unbaited biconical trap) versus acetone versus cow urine versus acetone plus cow urine. Inter-trap distance=100 m, three replicates.

ii. As above. Inter-trap distance=500 m, one replicate.

iii. Control versus low, medium and high dose rates of acetone.

iv. Control versus acetone versus 1-octen-3-ol versus TF 841.

v. Control versus TF 89/1 versus TF 841 versus TF 89/4.

vi. Control versus acetone plus cow urine versus cow urine plus 1-octen-3-ol versus acetone plus cow urine plus TF 841.

vii. Control versus cow urine versus human urine versus cow urine plus human urine.

viii. Control versus washing from a goat versus washing a from a monitor lizard (***Varanus niloticus niloticus***) (Fig. 15). 3x3 latin square design replicated twice.

ix. Biconical trap versus NG2B trap versus NG2G trap versus F3 trap.

x. Biconical trap versus pyramidal trap versus NG2B trap versus Vavoua trap.

Catches of male and female ***G. f. fuscipes*** were analysed separately. An analysis of variance was carried out on the data, after a log (x+1) transformation in order standardise the data thereby avoiding the problem that would be caused by zero catches in the calculations. The Student-Newman-Keuls test was used to determine differences between treatment means.

# RESULTS

Catches of *G. f. fuscipes* using cow urine show that when traps were placed 100 m apart, whether baited with or without acetone, caught significantly ($P<0.05$) more females than the control (Table 7a). When the experiment was repeated with traps placed 500 m apart, there was no significant difference in fly catches between traps with and without cow urine, and in fact all baited traps caught fewer flies (Table 7b). Further tests carried out to investigate the effect of three different dose rates of acetone revealed no significant differences in increases in the catch at any dose rate (Table 7c). The series of trials involving combinations of acetone, 1-octen-3-ol, phenols and urine conducted with traps 200 m apart also showed no significant differences in increases in the catches of females (Tables 8a, 8b and 9a). However, the combination of acetone, cow urine, 1-octen-3-ol and phenols revealed a reduction in the catch (Table 8c) at the 1 % level of significance. The effect of human urine was not significantly different from that of cow urine in increasing the catch (Table 9a). Washings from a goat and a monitor lizard did not enhance trap catches (Table 9b). A summary of all these results is presented in Table 10.

Results for the comparison of the six trap types show that the biconical trap caught significantly more flies than

Table 7. The effect oı acetone and cow urine on cathes of *G. f. fuscipes* on Rusinga Island.

| | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | Total | Detrans. mean | Catch index | Total | Detrans. mean | Catch index |
| **(a) Treatments** | | | | | | |
| Control | 379 | 20.6a | 1.00 | 821 | 55.1a | 1.00 |
| Acetone | 455 | 29.6a | 1.44 | 978 | 62.3ab | 1.13 |
| Cow urine | 390 | 25.9a | 1.25 | 928 | 72.8b | 1.31 |
| Acetone + cow urine | 414 | 28.0a | 1.34 | 1067 | 72.9b | 1.32 |
| | F=2.43 ns; df=(3,18) $R^2$=0.95 CV=9.05 | | | F=4.32* ; df=(3,18) $R^2$=0.95 CV=5.30 | | |
| **(b) Treatments** | | | | | | |
| Control | 123 | 25.1a | 1.00 | 227 | 52.5a | 1.00 |
| Acetone | 107 | 25.5a | 1.02 | 185 | 43.8ab | 0.83 |
| Cow urine | 91 | 20.9a | 0.83 | 183 | 42.9ab | 0.82 |
| Acetone + cow urine | 83 | 13.5a | 0.54 | 157 | 36.7b | 0.70 |
| | F=1.05 ns; df=(3,6) $R^2$=0.76 CV=17.9 | | | F=7.06* ; df=(3,6) $R^2$=0.97 CV=2.84 | | |
| **(c) Treatments** | | | | | | |
| Control | 160 | 17.2a | 1.00 | 272 | 30.4a | 1.00 |
| High rate | 191 | 18.8a | 1.09 | 239 | 22.2a | 0.74 |
| Medium rate | 149 | 15.1a | 0.89 | 205 | 20.2a | 0.67 |
| Low rate | 159 | 15.9a | 0.93 | 223 | 21.5a | 0.71 |
| | F=0.46 ns; df=(3,12) $R^2$=0.89 CV=13.0 | | | F=1.76 ns; df=(3,12) $R^2$=0.90 CV=11.9 | | |

Means in the same column with the same letter are not significantly different. ns=not significant; *=P<0.05;

Table 8. The effect of acetone, 1-octen-3-ol, cow urine, TF 841, TF 89/1 and TF 89/4 applied singly or in combinations on the catches of *G. f. fuscipes* on Rusinga Island.

| | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | Total | Detrans. mean | Catch index | Total | Detrans. mean | Catch index |
| **(a) Treatments** | | | | | | |
| Control | 101 | 8.46a | 1.00 | 189 | 16.5a | 1.00 |
| Acetone | 130 | 8.64a | 1.02 | 169 | 18.9a | 1.14 |
| 1-octen-3-ol | 138 | 11.7a | 1.35 | 174 | 15.6a | 0.95 |
| TF 841 | 134 | 9.19a | 1.08 | 170 | 14.3a | 0.88 |
| | F=0.61 ns; df=(3,12) $R^2$=0.91 CV=21.3 | | | F=0.71 ns; df=(3,12) $R^2$=0.96 CV=9.02 | | |
| **(b) Treatments** | | | | | | |
| Control | 330 | 34.4a | 1.00 | 301 | 34.1a | 1.00 |
| TF 89/1 | 368 | 39.0a | 1.13 | 365 | 40.6a | 1.18 |
| TF 841 | 366 | 42.8a | 1.24 | 354 | 37.3a | 1.09 |
| TF 89/4 | 461 | 49.6a | 1.43 | 431 | 47.5a | 1.38 |
| | F=2.18 ns; df=(3,12) $R^2$=0.90 CV=7.75 | | | F=1.56 ns; df=(3,12) $R^2$=0.87 CV=8.38 | | |
| **(c) Treatments** | | | | | | |
| Control | 122 | 12.7a | 1.00 | 273 | 25.2a | 1.00 |
| Acetone + cow urine | 177 | 12.7a | 1.00 | 223 | 25.0a | 0.99 |
| Cow urine + octenol | 107 | 11.2a | 0.89 | 93 | 11.3b | 0.50 |
| Acetone + cow urine + TF 841 | 65 | 5.82a | 0.50 | 77 | 7.59b | 0.33 |
| | F=0.36 ns; df=(3,12) $R^2$=0.78 CV=20.9 | | | F=13.1***; df=(3,12) $R^2$=0.88 CV=15.6 | | |

Means in the same column with the same letter are not significantly different. ns=not significant; ***=P<0.001

Table 9. The effect of cow and human urine and washings from a monitor lizard and a goat on catches of *G. f. fuscipes* on Rusinga Island.

| | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | Total | Detrans. mean | Catch index | Total | Detrans. mean | Catch index |
| (a) Treatments | | | | | | |
| Control | 122 | 11.1a | 1.00 | 207 | 19.4a | 1.00 |
| Cow urine | 143 | 13.9a | 1.23 | 184 | 18.9a | 0.98 |
| Human urine | 117 | 11.0a | 0.99 | 211 | 22.2a | 1.15 |
| Cow urine + human urine | 116 | 11.8a | 1.06 | 150 | 16.5a | 0.86 |
| | F=0.70 ns; df=(3,12) $R^2$=0.93 CV=13.2 | | | F=0.84 ns; d=(3,12) $R^2$=0.89 CV=11.9 | | |
| (b) Treatments | | | | | | |
| Control | 280 | 38.0a | 1.00 | 371 | 53.6a | 1.00 |
| Goat | 273 | 43.7a | 1.14 | 360 | 53.5a | 0.99 |
| Lizard | 259 | 36.1a | 0.95 | 370 | 50.1a | 0.93 |
| | F=0.80 ns; df=(2,4) $R^2$=0.95 CV=7.11 | | | F=1.00 ns; df=(2,4) $R^2$=0.99 CV=2.37 | | |

Means in the same column with the same letter are not significantly different. ns=not significant.

Table 10. Summary of odour baits used in various experiments on Rusinga Island on *G. f. fuscipes*.

| Odour | Index of increase Male | Female |
|---|---|---|
| Control | 1.00 | 1.00 |
| Experiment 1 | | |
| Acetone | 1.44 | 1.13 |
| Cow urine | 1.25 | 1.31 |
| Acetone + cow urine | 1.34 | 1.32 |
| Experiment 2 | | |
| Acetone | 0.87 | 0.82 |
| Cow urine | 0.74 | 0.81 |
| Acetone + cow urine | 0.67 | 0.69 |
| Experiment 3 | | |
| High dose rate acetone | 1.09 | 0.74 |
| Medium dose rate acetone | 0.89 | 0.67 |
| Low dose rate acetone | 0.93 | 0.71 |
| Experiment 4 | | |
| Acetone | 1.02 | 1.14 |
| 1-octenol-3-ol | 1.35 | 0.95 |
| TF 841 | 1.08 | 0.88 |
| Experiment 5 | | |
| TF 89/1 | 1.13 | 1.18 |
| TF 89/4 | 1.43 | 1.38 |
| TF 841 | 1.24 | 1.38 |
| Experiment 6 | | |
| Acetone + cow urine | 1.00 | 0.99 |
| Cow urine + 1-octen-3-ol | 0.89 | 0.50 |
| Acetone + cow urine + TF 841 | 0.50 | 0.33 |
| Experiment 7 | | |
| Cow urine | 1.23 | 0.98 |
| Human urine | 0.99 | 1.15 |
| Cow urine + human urine | 1.06 | 0.86 |
| Experiment 8 | | |
| Goat washings | 1.14 | 0.99 |
| Monitor Lizard washings | 0.95 | 0.93 |

Table 11. Analysis of numbers of *G. f. fuscipes* caught in different types of traps on Rusinga Island.

| | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | Total | Detrans. mean | Catch index | Total | Detrans. mean | Catch index |
| **(a) Trap type** | | | | | | |
| Biconical | 413 | 43.9a | 1.00 | 451 | 44.8a | 1.00 |
| NG2B | 125 | 13.7b | 0.31 | 145 | 14.1b | 0.31 |
| NG2G | 150 | 14.9b | 0.34 | 108 | 11.1b | 0.25 |
| F3 | 46 | 5.33c | 0.12 | 35 | 3.56c | 0.00 |
| | F=38.1***; df=(3,12) $R^2$=0.93 CV=13.1 | | | F=31.1***; df=(3,12) $R^2$=0.93 CV=18.2 | | |
| **(b) Trap type** | | | | | | |
| Biconical | 186 | 20.2a | 1.00 | 403 | 44.8a | 1.00 |
| Pyramidal | 74 | 18.0a | 0.89 | 244 | 38.4a | 0.86 |
| NG2B | 150 | 16.3a | 0.81 | 273 | 30.8a | 0.69 |
| Vavoua | 71 | 6.71b | 0.33 | 180 | 20.6b | 0.46 |
| | F=23.4***; df=(3,10) $R^2$=0.96 CV=0.96 | | | F=11.3**; df=(3,10) $R^2$=0.90 CV=7.89 | | |

Means in the same column with the same letter are not significantly different. **=P<0.01; ***=P<0.001

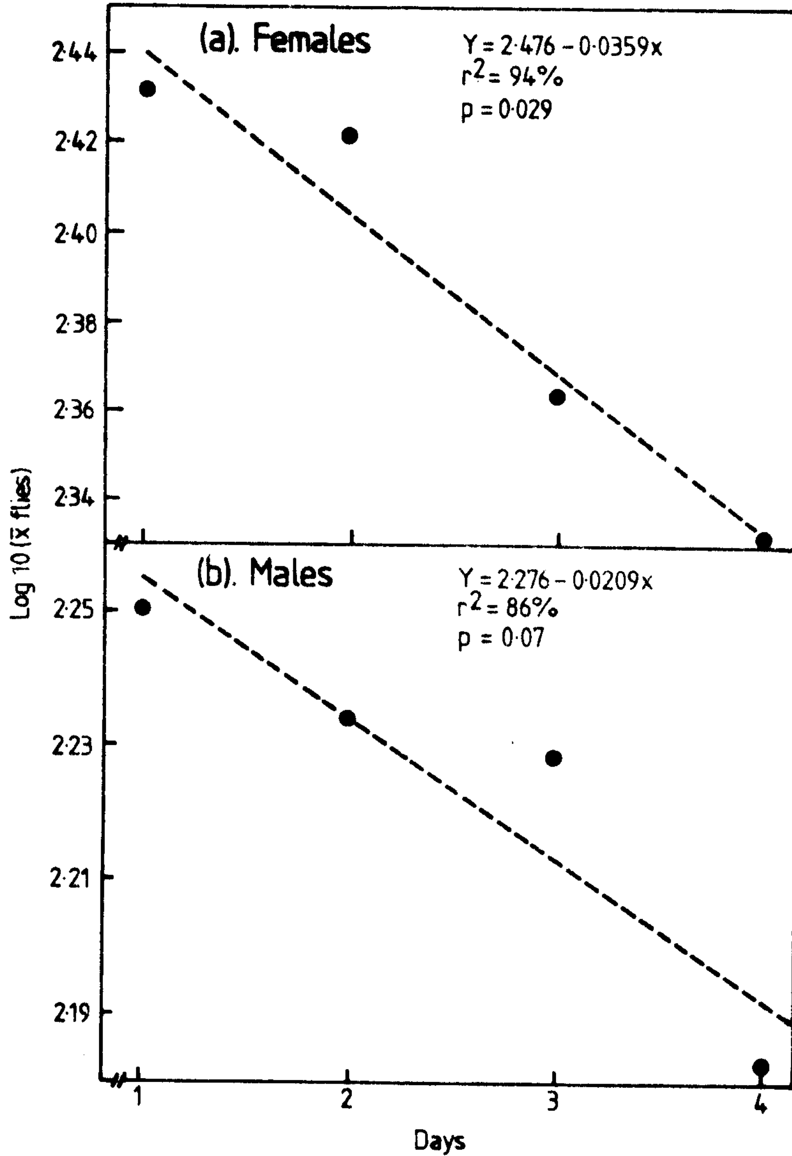



Fig. **23.** The decline in the catches of ***G. f. fuscipes*** over the four days of testing various odour baits in latin-square designed experiments on Rusinga Island.

the NG traps, which in turn caught significantly more flies than the F3 trap (Table 11a). In the second trial (Table 11b), there was no significant difference in the catches between the biconical, pyramidal and NG2B traps (although the biconical trap still caught the most flies) while the Vavoua trap caught significantly fewer flies. There was a tendency for catches to decline from the first to the last day of trapping for both sexes although the differences between the daily catches were only significant at the 10 % level (Fig. 23).

## DISCUSSION

The inter-trap spacing used was considered suitable taking into consideration the area of dense vegetation where the study was undertaken. The range of attraction of the unbaited biconical trap was estimated by Dransfield (1984) to be 15-20 m for ***G. pallidipes*** and 10-15 m for ***G. brevipalpis***. In other insect groups, for example moths, Perry ***et al.*** (1980) who studied their responses to sex attractants reported that the distance at which the attractants were placed from each other influenced the response of the moths. Vale (1977) observed that a single ox attracted tsetse flies from a distance of up to 90 m.

There is little evidence from these data that any of the compounds tested increased the trap catches of ***G. f. fuscipes***. To the contrary, in some instances there was evidence that some substances were repellent (for example, acetone plus cow urine, cow urine plus 1-octen-3-ol, and acetone, cow urine plus TF 841). The R-square values from analysis of variance of the data were generally high (above 90%) suggesting that the experimental design accounted for most of the variability of the data.

This did not tally with earlier findings, for example, Chorley (1933) who reported that the catch of ***G. f. fuscipes*** increased when he smeared extracts of animal glands and the fat of birds (cormorants) and crocodiles to his traps. Persoons (1966) also reported to have improved the catches of ***G. pallidipes*** and ***G. f. fuscipes*** by applying hot- water washings of pigs treated with petroleum spirit to tsetse traps. The results obtained in this study also differed from those of Frezil and Carnavale (1976) who increased the catch of ***G. f. quanzensis*** by applying carbon dioxide as dry ice to traps. Furthermore, the results in this study did not corroborate earlier findings on other tsetse fly species of the ***palpalis*** group which were attracted to odour baits. For instance, Galey ***et al.*** (1986) used carbon dioxide to increase the catch of ***G. tachinoides*** to traps and Merot ***et al.*** (1986) also increased the catch of the same species by applying ox odour near traps. Cheke and Garms (1988)

doubled the catch of ***G. p. palpalis*** by adding acetone and 1-octen-3-ol to traps and Spath and Kupper (1989) employed a mixture of 3-methylphenol, 4-methylphenol and 1-octen-3-ol to raise the catch of ***G. tachinoides***. Laveissiere (personal communication) who recently conducted studies on a related subspecies, ***G. f. quanzensis***, also reported negative results for the various odour baits that he tested. Since testing of washings from a goat and a monitor lizard which in the wild is swarmed by ***G. f. fuscipes*** did not enhance the catch of flies, it is probable that the water medium used for the washings did not dissolve any attractive odours.

There are three possible explanations that may account for the results obtained in this study, especially the apparent variability in response to acetone and cow urine. First, responsiveness may vary seasonally. Kupper (1988) reported that the attractiveness of 1-octen-3-ol to ***G. tachinoides*** varied over time and attributed this variation to the influence of temperature, wind and humidity. Merot (1989) also observed that the use of 1-octen-3-ol and m-cresol against ***G. tachinoides*** gave inconsistent results throughout the year and suggested that the effectiveness of odour baits could change seasonally.

Secondly, there was evidence that ***G. f. fuscipes*** on Rusinga Island had restricted mobility and that this could have lead to a trapping out effect. The effect of trapping

out could have come in two ways. Traps could have had a general effect on the tsetse population in a given area or each individual trap could have brought about such an effect in the immediate area surrounding it. In such a situation it would be difficult to determine the effectiveness of strong odour baits in latin square designs as treatments were changed each day.

Thirdly, it still remains to be elucidated whether ***G. f. fuscipes*** uses more of the visual rather than the olfactory cues to locate its hosts. It was occasionally observed, using a telephoto lens of a 135 mm camera that flies alighted on monitor lizards and sometimes swarms of flies even formed on these animals as Fiske (1920) reported. It was, however, surprising that of the 12 blood meal samples, mostly collected from the mainland which has almost the same environmental setting as on Rusinga Island, 11 blood meals were from goats and one was from cattle. Although the number of blood meals examined was small the preponderance of goat blood meals over these other hosts available in the area is difficult to explain. How then did the flies locate the monitor lizards? It is suggested that for future work host animals of tsetse flies be tested in pits, as the attractive components may not be from the skin but the animals' breath. This will also rule out the possibilty of visual detection of hosts by the flies. Studies using pits have been successfully carried out on ***G.***

***pallidipes*** and ***G. m. morsitans*** in Zimbabwe (Vale, 1974a, 1974b).

The biconical trap was found to be the most effective trap for ***G. f. fuscipes***. Ryan ***et al.*** (1982) who compared the relative effectiveness of older trap designs for ***G. p. palpalis*** and ***G. m. centralis*** found that the biconical trap caught at least twice as many tsetse flies as any other trap they tested. Although the biconical trap was designed mainly for the riverine species of tsetse flies, it has proved to be relatively more effective than many other older trap designs for the other groups of tsetse fly species too (for example, Hargrove, 1977; Owaga, 1981; Takken, 1984). However, in recent years a number of new trap designs have been developed for various tsetse fly species. For example, Gouteux and Lancien (1986) found that their pyramidal trap was two to five times more effective than the biconical trap for ***G. f. quanzensis***. Flint (1985) and Brightwell ***et al.*** (1987, 1990) developed the F3 and NG traps, respectively, which they reported to be more effective than the biconical trap for ***G. pallidipes***. In this study it was however found that the biconical trap was the most effective trap for ***G. f. fuscipes***. The small modifications made to the pyramidal, F3 and Vavoua traps in order to standardise the collecting cages for comparative purposes of this study were not expected to cause significant variations in the fly catches. However, it was shown by Laveissiere ***et al.*** (1987) and Green

(1988) that the material and the shade of blue used to construct screens could influence the number of flies attracted to such screens. All the traps used in this study were made from cloth of the same colour.

# CHAPTER 6

# REARING *G. F. FUSCIPES* FOR VECTORIAL CAPACITY STUDIES

## INTRODUCTION

Tsetse flies of uniform age were required to carry out comparative studies on the vectorial role of ***G. f. fuscipes*** in transmitting trypanosomes. Furthermore, there was need to determine whether ***G. f. fuscipes*** could be reared at the ICIPE Mbita Point Field Station. This chapter is devoted to the procedures which were followed and the results obtained when rearing this subspecies for this purpose. Studies on vectorial capacity are covered in chapter 7.

Methods of rearing tsetse flies in the laboratory have been reviewed by Nash and Jordan (1970), Itard and Jordan (1977) and Wetzel (1977). Colonies of tsetse flies are initiated either from wild collected adults which are brought to the laboratory for production of pupae or pupae are searched for in the field. It is easier to start a colony with adults than pupae as these are easily caught with traps. While notable advances have been made in colonising a number of tsetse fly species in the laboratory in the last two decades, it has not always been easy to rear

and maintain in the laboratory some tsetse fly species in order to provide sufficient material for research (Itard and Jordan, 1977). This is due to a number of factors. Tsetse flies have a low reproductive rate. Females are larviparous, depositing the first larva on the eighteenth to the twentieth day after emergence. Subsequently, larvae are produced at intervals of about 8-10 days. Under optimum conditions the mean life span in the laboratory is about 100-150 days during which period 10-15 larvae are produced (Itard and Jordan, 1977). Tsetse flies are very sensitive to contamination with chemicals and bacteria which can lead to very high mortality rates in insectaries. The cost of rearing is high because both sexes are exclusively haematophagous. Besides the colony of tsetse flies, there is need for a regular supply of blood from mammals such as goats, guinea pigs and rabbits so these animals have also to be reared. Alternatively, flies may be fed ***in vitro*** through a synthetic membrane on blood obtained from an abattoir which is defibrinated or blood to which preservatives such as heparine have been added to stop coagulation. Finally, the most favourable climatic conditions for rearing tsetse flies are, depending on species, when the temperature is between 24-26 °C and relative humidity 60-85 % (Itard and Jordan, 1977). Regulation of climatic conditions at these levels in insectaries is relatively expensive.

Successful colonisation of tsetse flies has been achieved by using live animals (for example, Geigy, 1948; Nash *et al.*, 1966, 1968; Mews *et al.*, 1972; Moloo *et al.*, 1985) and *in vitro* techniques (Bauer and Wetzel, 1976; Mews *et al.*, 1977; Vloedt *et al.*, 1987). Recently, Ochieng *et al.* (1987) reported successful colonization of *G. pallidipes* reared under relatively simple conditions. These conditions were tested for *G. f. fuscipes* in this study.

## MATERIALS AND METHODS

### Tsetse insectary

The ICIPE Mbita Point Field Station tsetse insectary has been described in detail by Ochieng *et al.* (1987). The construction is such that the section between the roof and walls is covered only with grass and wire gauze to allow a continous flow of air. As a result it is cooler inside the insectary than outside. During this study, conducted between April 1988 and December 1989, minimum temperatures in the insectary ranged from 18.5-24.0 °C and maximum temperatures from 21.5-30.0 °C. Relative humidity recorded at 9.00 h ranged from 53-91 %. The surrounding climatic conditions outside the insectary were similar to those presented in Fig. 5.

Tsetse fly collection

Using biconical traps *G. f. fuscipes* were caught on Rusinga Island and transfered to the Mbita Point Field Station in cages. Fly cages were made of polyvinyl chloride tube sections which were elliptically shaped and covered with black terylene netting glued to the periphery of the tube suitable for feeding tsetse flies on rabbits' ears (Mews *et al.*, 1972). Flies were kept in batches of about 10-30 per cage and the cages were placed on trays covered with wire mesh to allow larvae to pass through the terylene netting of the cage and the wire mesh to the collecting tray underneath. The flies were initially fed daily on defibrinated ox-blood. This blood was collected from the local abattoir at the time animals were slaughtered for sale and was defibrinated using stirrers before being stored at 4 °C. The blood was first thawed and warmed up to 37 °C and then offered to flies through a silicone synthetic membrane as recommended by Bauer and Wetzel (1976). Due to failure in achieving sterile conditions at the abattoir this method was later discontinued because a number of flies were dying with fully engorged guts showing undigested blood several days after the initial blood meal. It was suspected that these flies were contaminated with bacteria which could have been the source of mortality. Mortality due to bacterial contamination has been reported by Wetzel (1977) and Kaaya

and Darji (1989). To avoid this problem flies were switched to feeding on rabbits' ears following a procedure described by Nash *et al.* (1966). Several rabbits of mixed breeds obtained locally (see Chapter 7) were set aside for this purpose and were examined at monthly intervals for trypanosome infection by examination of wet blood smears under the light microscope.

Pupae deposited by flies were collected daily in the morning. The pupae were weighed individually and each weight was entered into one of the following classes; less than 21, 21-25, 26-30, 31-35, 36-40 and over 40 mg. Pupae of all weight classes except those considered to have been aborted (weighing less than 21 mg and still whitish in colour) were placed in emergence boxes (26 cm x 26 cm x 26 cm) made of wood and wire mesh, according to the month in which they were deposited. Collection of wild tsetse flies started in April 1988 and was carried out at irregular intervals thereafter to reinforce the colony whenever there was a great demand for flies.

**Tsetse fly rearing**

Flies emerging from pupae in the insectary were kept under identical environmental conditions as reported earlier for wild collected flies, but in separate batches of 10-15

flies per cage according to sex. They were fed daily on rabbits' ears. When females were two days old batches of 15-20 flies were placed in cages together with an equal number of 7-day-old males for 7 days after which the sexes were separated. Due to a high number of flies dying while in copula the age of females at mating was raised from two to four days and the mating period reduced from 7 to 2 days. The pupae produced by these flies were classified according to weight classes as previously mentioned. The total number of mated females, the mean number of females producing pupae, percent daily mortality, mean number of pupae per female, mean weight of pupae and emergence rates of flies were calculated to ass ss the performance of the colony.

## RESULTS

The mean number of mated females per month was 273 by November 1988, this mumber dropped to 147 in January 1989 and increased to 1,138 in April 1989 (Table 12). Thereafter the number remained at around a thousand. Daily female mortality averaged about 0.64 %. The mean number of pupae produced per female per month was 2.1. From April to December 1989 an average of 182 males and 185 females per month were used for experiments. In July and December 1989, 241 and 673 pupae, respectively were used for experiments. Low pupal weights were recorded from December 1988 to

Table 12. Performance of the *Glossina fuscipes fuscipes* colony at the ICIPE Mbita Point Field Station from November 1988-September 1989

| Parameter/Month | Nov 1988 | Dec | Jan 1989 | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Mean total females | 273 | 255 | 147 | 163 | 592 | 1138 | 1662 | 1406 | 1358 | 1172 | 1036 |
| Mean producing females | 23[illegible] | 213 | 91 | 104 | 334 | 871 | 1125 | 988 | 1017 | 927 | 867 |
| Mean daily female mortality (%) | 0.50 | 0.48 | 0.30 | 0.93 | 0.50 | 0.50 | 0.68 | 0.92 | 0.88 | 0.57 | 0.67 |
| Mean pupae per female per month | 2.02 | 1.81 | 2.59 | 2.19 | 1.81 | 1.99 | 2.07 | 2.44 | 2.29 | 1.86 | 1.98 |
| Mean weight of pupae (mg) | 28.56 | 22.44 | 23.47 | 23.24 | 25.73 | 26.47 | 27.13 | 27.36 | 26.99 | 27.41 | 25.93 |
| No. pupae produced | 472 | 386 | 236 | 228 | 606 | 1730 | 2334 | 2412 | 2328 | 1728 | 1714 |
| Estimated emergence (%) (live flies only) | 33 | 54 | 39 | 46 | 72 | 65 | 64 | 81 | 82 | 65 | 72 |
| Pupae used for research | - | - | - | - | - | - | - | - | 241 | - | 673 |
| Female flies used for research | - | - | - | - | - | 74 | 120 | 338 | 111 | 220 | 247 |
| Male flies used for research | - | - | - | - | - | 139 | 140 | 304 | 123 | 185 | 196 |

Table 13 Weight of pupae produced by wild and laboratory reared *G. f. fuscipes* collected from the field from April 1988-August 1989 arranged in class weights. In brackets are percentages of total weight for each class weight.

| Weight class (mg) | <21 | 21-25 | 26-30 | 31-35 | 36-40 | >40 | Total |
|---|---|---|---|---|---|---|---|
| Wild flies | 1035 (10.7) | 2777 (28.7) | 3808 (39.4) | 1864 (19.3) | 172 (1.8) | 7 (0.07) | 9663 |
| Laboratory flies | 1357 (10.5) | 4085 (31.5) | 5592 (43.1) | 1783 (13.8) | 149 (1.1) | 1 (0.007) | 12967 |
| Total | 2392 | 6862 | 9400 | 3647 | 321 | 8 | 22630 |

February 1989 as shown by the monthly means (Table 12). The majority of pupae deposited by both wild and laboratory flies weighed between 26-30 mg (Table 13) and comparison of pupae produced by these two groups of flies (excluding pupae less than 21 mg) using the paired-sample test indicated no significant difference between them (t=-2.58 ns, df=4, P>0.05).

## DISCUSSION

In assessing the performance of the colony there were some difficulties. Flies had to be continously brought in from the field to replenish the colony whenever the need for flies for use was too high. The total number of females and pupae produced was actually a product of the number of flies brought in from the field and the productivity of the colony. The mean number of pupae per female per month of 2.1 was higher than the figure reported for the same subspecies by Moloo ***et al.*** (1985) and was close to the figure of 2.0 reported by Ochieng ***et al.*** (1987) for ***G. pallidipes***. The mean pupal weight of between 26-30 mg was, however, lower than the mean of 34.9 mg obtained by Moloo and his team for the same subspecies. The observation that there was no significant difference between the weights of pupae produced by wild-collected and laboratory-reared females in this study indicated that the feeding regime

adopted was not nutritionally poor. However, Moloo and his team working with the same subspecies recorded a higher mean pupal weight. The difference between the mean pupal weight recorded in this study and their figure could be due to the different strains of *G. f. fuscipes* used. Their colony originated from tsetse flies obtained from the Central African Republic. The low pupal weight recorded from December 1988 to February 1989 were not related to any physical factor recorded and probably these were a result of the feeding responses of the female tsetse to rabbits.

The estimated monthly emergence rates were low mainly because pupae of all weight classes were put together in one emergence box. It is probable that pupae under 21 mg contributed to the number that did not emerge from the puparia or emerged but soon after died. The exclusion of these under weight pupae from the emergence box would probably have raised the emergence rates.

There is very little information available in literature on the performance of *G. f. fuscipes* colonies in the laboratory to make any detailed comparisons and, such comparisons with other tsetse fly species may not strictly be justified due to inherent differences within the tsetse species. Invaluable information, however, has been reported on other tsetse fly species for example, on *G. austeni* (Nash *et al.*, 1966, 1968), on *G. p. palpalis* (van der Vloedt *et*

*al.*, unpublished), several species including ***G. m. morsitans, G. austeni, G. p. palpalis, G. p. gambiensis, G, tachinoides*** and ***G. brevipalpis*** (Moloo, ***et al.***, 1985). Results obtained in this study did not show any major deviations from the general trends of colony productivity of other tsetse fly species.

Although the primary objective of establishing and maintaining the colony was to provide specimens for vectorial capacity studies, it was demonstrated that with care it would be possible to expand the ***G. f. fuscipes*** colony under the simple conditions initially designed for ***G. pallidipes.***

# CHAPTER 7

# STUDIES ON VECTORIAL CAPACITY OF *G. F. FUSCIPES*

## INTRODUCTION

Knowledge of the vectorial capacity of any vector is important to understand the epidemiology of the disease as well as for control strategies. In general the various factors involved in disease transmission should be investigated for a proper control programme to be done. In the case of tsetse flies there are many factors that would influence the development of trypanosomes in the fly and these have been reviewed in detail by Jordan (1974, 1976) and Molyneux (1977, 1980). Molyneux grouped all the factors involved under three headings: (a) endogenous factors associated with the fly, (b) ecological factors and (c) factors associated with the parasite and the host. Because of the many factors involved and the bias inherent in sampling techniques for tsetse flies (Glasgow and Phelps, 1970), conflicting results of trypanosome infection rates of flies in the field have often been reported by various workers. Laboratory studies on trypanosome infection rates attempt to resolve the above variations. However, laboratory studies alone should also be considered with caution as they have the limitation of oversimplifying natural conditions. In this study both approaches were

taken to investigate the vectorial capacity of *G. f. fuscipes* collected from Rusinga Island.

## MATERIALS AND METHODS

### Field collected tsetse flies

*G. f. fuscipes* were caught using biconical traps on Rusinga Island and the mainland of Mbita, South Nyanza District, Kenya, during tsetse surveys and routinely each month (see Chapter 4). Each month, 30 males and 30 females were picked randomly from fly cages containing flies caught from each study site for dissection and examination for trypanosome infection.

Flies were dissected using the method of Lloyd and Johnson (1924). The midgut, labrum, hypopharynx and both salivary glands of each fly were dissected on microscopic slides to which drops of 0.9 % physiological saline had been added. These were then examined for trypanosome infection in separate drops of saline under the light microscope. This study was conducted from February 1988 to June 1989.

## Host determination

An attempt was made to determine the animal source of bloodmeals for the flies in the study area. Fed flies caught in traps at various marked sites were dissected and a smear of the gut made onto a sector of a filter paper provided by the International Laboratory Research for Animal Diseases (ILRAD). The smear was allowed to dry in the air before being placed in a desiccator over calcium chloride. To avoid contamination blank filter papers were placed between smears. A record was kept of the smear numbers, subspecies of fly, sexes, study sites, dates and types of animals seen near the places where the tsetse flies were caught. All the filter paper smears were sent to ILRAD for bloodmeal analysis.

## Laboratory studies

### Laboratory animals

1. **Trypanosome stocks:**

   An attempt was made to isolate trypanosomes from flies and cattle on Rusinga Island and the area within the vicinity of Mbita Point Field Station on the mainland. However, this failed because only one fly was found infected with *T. congolense* type trypanosomes. The midgut, labrum,

hypopharynx and salivary glands of this fly were macerated and inoculated separately into mice. The mice were examined for trypanosome infection for eight weeks but none picked up the infection. Some stocks of *T. congolense* and ***T. simiae***, which is closely related to it, fail to develop in laboratory animals (Nyeko, personal communication). Collaborative observations were carried out with Drs A. Latif, D. Punyua and M. Hassan (Resident Research Scientists of the Livestock Ticks Research Programme based at Mbita Point Field Station) to determine the incidence of trypanosomiasis in cattle in the study area with the intention of isolating trypanosome strains for use in this study. During routine examinations of cattle on the island initiated by complaints lodged by cattle owners that their livestock were diseased, animals suspected to have been suffering from trypanosomiasis were bled from the ears and blood collected in heparinised tubes. Thin, thick and wet blood smears were prepared and examined for the presence of trypanosomes. In addition, 0.2 ml of blood from each animal source was inoculated into mice. The mice were checked for trypanosome infection for eight weeks.

Of the four animals found infected with trypanosomes three were found to be infected with *T. vivax* as revealed by thin blood smears examined. The infected animals all came from the island. The fourth animal was infected with *T. congolense* and came from the mainland. Unfortunately this animal was treated with Berenil before blood was collected for mouse inoculation (Latif, personal communication). It was not surprising therefore, that mice did not pick up the infection. Because of scarcity of trypanosomes from the study area trypanosome stocks used in this study were collected from Lambwe Valley by the Tsetse Research Programme Scientists (Darji, personal communication):

i) F1 - A *T. congolense* stock isolated from a female *G. pallidipes* caught in Ruma thicket, Lambwe Valley, on 31/5/88. It was passaged once into mice.

ii) F2 - A *T. congolense* stock isolated from a female *G. pallidipes* caught in Ruma thicket, Lambwe Valley, on 6/6/88. It was passaged once into mice.

iii) Maruma - A *T. congolense* stock isolated from a cow in the Coast Province of Kenya on 6/7/83. It was passaged many times in mice and rats before use in this study.

It was found to be resitant to normal curative doses of samorin (Nyeko, personal communication).

iv) F4 - A ***T. brucei*** stock isolated from a female ***G. pallidipes*** in Ruma thicket, Lambwe Valley on 3/2/87. It was passaged once into mice. It caused chronic infection in mice (Darji, personal communication).

v) F6 - A ***T. brucei*** stock isolated from a male ***G. pallidipes*** caught in Ruma thicket, Lambwe Valley on 7/3/87. It was passaged once into mice. It was found to be a virulent stock (Darji, personal communication).

vi) F27 - A ***T. brucei*** stock isolated from ***G. pallipides*** in Ruma thicket, Lambwe Valley, in January 1988.

**2. Tsetse flies:**

***G. f. fuscipes***

A colony of ***G. f. fuscipes*** was raised from flies caught on Rusinga Island. For details and history of this colony see Chapter 6. Only teneral ***G. f. fuscipes*** were used.

*G. pallidipes*

Male and female ***G. pallidipes*** were obtained from the Tsetse Insectary at Mbita Point Field Station. This colony was raised from flies caught in Lambwe Valley (Ochieng ***et al.***, 1987). At the time this study was carried out serious rearing problems were experienced with the ***G. pallidipes*** colony in the insectary. There was a significant drop in insemination rates with a subsequent corresponding drop in pupal production rates. For this reason only teneral and non-teneral males up to 4 weeks old were made available for this study. The females were strictly reserved for the expansion of the colony.

**3. Mice and rats:**

Balb C mice and Wistar rats were obtained from the Animal rearing Unit of the ICIPE in Nairobi. Mice and rats were kept in plastic cages with steel wire tops and were fed on commercial rodent pellets and water ***ad libitum***. They were kept at room temperature ranging from 18 to 30 °C.

**4. Rabbits:**

These were of mixed breeds which included; New Zealand white, Californian white, French lobe and Kenyan white. They were reared at the ICIPE, Nairobi and Mbita Point Field Station Animal Units. They were

kept at room temperature as recommended for mice and were fed on commercial rabbit pellets, green vegetables and water *ad libitum*.

**Infection of rats and tsetse flies**

Each stock of trypanosomes was innoculated into a group of six rats at a dosage of 0.2 ml of diluted blood per animal. For each stock a rat was selected at peak parasiteamia to feed batches of teneral *G. f. fuscipes* and teneral and non-teneral *G. pallidipes*. Each rat was anaesthetized with sodium pentabarbitone (Sagatal) before flies fed on its belly through the cage netting. The flies were left to feed for 30 minutes. One rat was usually enough to feed both groups of *G. f. fuscipes* and *G. pallidipes*, one batch after another, with flies numbering up to 100. If an infected rat died in the process it was replaced with another.

Flies were offered the infective blood meal twice, on the first and second day after emergence.
This was to increase the number of flies feeding since not all the flies fed on the first day. Old flies were initially starved for two days prior to being given the infective bloodmeal. After taking the infective meals

flies were maintained for 30 days on separate groups of clean rabbits according to trypanosome stocks innoculated in them. Flies which died during this period were removed from the cages at least twice in a week. On the 31 st day post-infected feed, flies were not offered a bloodmeal and were dissected and examined for trypanosome infection the next day. The Chi-square test was used to compare the proportions of flies with infection at the midgut (immature), hypopharynx and salivary gland (mature) levels. Comparisons were done between males and females of ***G. f. fuscipes*** and between males of ***G. f. fuscipes*** and ***G. pallidipes***. The Yates Correction factor was applied if degrees of freedom equaled one (Clarke, 1969).

## RESULTS

### Field studies

One thousand and six ***G. f. fuscipes*** comprising 509 males and 497 females from Rusinga Island were dissected and examined for trypanosome infection. None of these was found to be infected with trypanosomes (Table 14). A total of 477 male and 526 female flies from the mainland were dissected and examined for trypanosome infection. Of these only one female fly (age category 5b, that is, about 50-54 days old)

Table 14 The number of ***G. f. fuscipes*** dissected and examined for trypanosome infection. The flies were obtained from Rusinga Island and the mainland in Mbita, South Nyanza District, Kenya.

| Locality | *G. f. fuscipes* | | |
|---|---|---|---|
| | Male | Female | Total |
| Rusinga Island | 509 | 497 | 1006 |
| Mainland: | | | |
| Kisui/Kombe | 421 | 455* | 876 |
| Mbita Mission | 56 | 71 | 127 |
| subtotal | 477 | 526 | 1003 |
| Total | 986 | 1023 | 2009 |

* Of these one female fly was infected with ***T. congolense*** type trypanosomes.

Table 15 Results of tsetse blood meal analysis of *G. f. fuscipes* caught on Rusinga Island and mainland.

| Smear No. | Species | Sex | Details | Results |
|---|---|---|---|---|
| 1. A1/K/R | *G.f.f.* | F | Wanyama area, Rusinga Island, trap 1, 12/5/88 | Cow |
| 2. A2/K/R | *G.f.f.* | M | Wanyama area, Rusinga Island, trap2, 12/5/88 | Goat |
| 3. A3/K/R | *G.f.f.* | F | Wanyama area, Rusinga Island, trap1, 12/5/89 | Goat |
| 4. A4/K/M | *G.f.f.* | M | Kisui, mainland, trap 1 14/5/88 | Goat |
| 5. A5/K/M | *G.f.f.* | M | Kisui, mainland, trap 1, 14/5/88 | Not suitable |
| 6. A6/K/M | *G.f.f.* | F | Kisui, mainland, trap 1 14/5/88 | Goat |
| 7. A7/K/M | *G.f.f.* | M | Kisui, mainland, trap 3 14/5/88 | Goat |
| 8. A8/K/M | *G.f.f.* | F | Kisui, mainland, trap 3 14/5/88 | Goat |
| 9. B1/K/M | *G.f.f.* | F | Kisui, mainland, trap 3 14/5/88 | Not suitable |
| 10.B2/K/M | *G.f.f.* | M | Kisui, mainland, trap 3 14/5/88 | Not suitable |
| 11.B3/K/M | *G.f.f.* | M | Kisui, mainland, trap 1 14/5/88 | Goat |
| 12.B4/K/M | *G.f.f.* | F | Kisui, mainland, trap 1 12/5/88 | Not suistable |
| 13.B5/K/M | *G.f.f.* | F | Kisui, mainland, trap 3 12/5/88 | Goat |
| 14.B6/K/M | *G.f.f.* | F | Kisui, mainland, trap 1 29/7/88 | Goat |
| 15.B7/K/M | *G.f.f.* | F | Kisui, mainland, trap 1 29/7/88 | Goat |
| 16.B8/K/M | *G.f.f.* | F | Kisui, mainland, trap 1 18/8/88 | Goat |

was found to be infected. The infection was observed in the midgut, labrum and hypopharynx which suggested a *T. congolense* type of infection. This gave an infection rate of 0.10 %.

## Host determination

Sixteen bloodmeals were analysed. Of these 11 indicated feeds obtained from a goat and one from a cow (Table 15). Four bloodmeals were found not to be suitable for analysis.

## Laboratory studies

### Trypanosome infection in flies

Of the three *T. congolense* stocks two (stocks F1 and F2) showed males of *G. f. fuscipes* to be more infected in the midgut than females ($N=385$, $X^2=8.37$, $df=1$, $P<0.01$ and $N=412$, $X^2=11.69$, $df=1$, $P<0.001$), respectively (Tables 16 and 17). The third *T. congolense* stock (Maruma) gave a different result. There was no significant difference between the two sexes of *G. f. fuscipes* ($N=275$, $X^2=0.38$, $df=1$, $P>0.05$) (Table 18). In all the three strains comparison of midgut (immature) infections between male *G.*

Table 16 Trypanosome infection rates in ***G. f. fuscipes*** and ***G. pallidipes*** infected with a ***T. congolense*** stock F1. In brackets are percentages of infected flies.

| Number | *G. f. fuscipes* | | *G. pallidipes* |
|---|---|---|---|
| | Male | Female | Male* |
| Dissected | 183 | 202 | 158 |
| Infected in midgut | 31 (16.9) | 14 (6.9) | 18 (11.4) |
| Infected in the labrum | 1 (0.5) | 1 (0.5) | 6 (3.8) |
| Infected in the hypopharynx | [illegible] (0.5) | 0 (0) | 7 (4.4) |

*Male ***G. pallidipes*** included teneral and non-teneral flies.

Male vs. female ***G. f. fuscipes*** (immature infections):
$N=385$, $X^2=8.37$, $df=1$, $P<0.01$**

Male ***G. f. fuscipes*** vs. male ***G. pallidipes*** (immature infections):
$N=341$, $X^2=1.69$, $df=1$, $P>0.05$ ns.

Male ***G. f. fuscipes*** vs. male ***G.pallidipes*** (mature infections):
$N=341$, $X^2=4.02$, $df=1$, $P<0.05$

Table 17. Trypanosome infection rates in ***G. f. fuscipes*** and ***G. pallidipes*** infected with a ***T. congolense*** stock F2. In brackets are percentages of infected flies.

| Number | *G. f. fuscipes* | | *G. pallidipes* |
|---|---|---|---|
| | Male | Female | Male* |
| Dissected | 175 | 237 | 15 |
| Infected in the midgut | 50 (28.6) | 34 (14.4) | 3 (20.0) |
| Infected in the labrum | 0 (0) | 0 (0) | 1 (6.7) |
| Infected in the hypopharynx | 0 (0) | 0 (0) | 1 (6.7) |

*Male ***G. pallidipes*** included teneral and non-teneral flies

Male vs. female ***G. f. fuscipes*** (immature infections):
N=412, $X^2$=11.69, df=1, P<0.001 ***

Male ***G. f. fuscipes*** vs. male ***G. pallidipes*** (immature infections):
N=190, $X^2$=0.17, df=1, P>0.05 ns

Male ***G. f. fuscipes*** vs. male ***G. pallidipes*** (mature infections):

N=190, $X^2$=2.45, df=1, P>0.05 ns

Table 18. Trypanosome infection rates in *G. f. fuscipes* and *G. pallidipes* infected with a *T. congolense* stock Maruma. In brackets are percentages of infected flies.

| Number | *G. f. fuscipes* | | *G. pallidipes* |
|---|---|---|---|
| | Male | Female | Male* |
| Dissected | 155 | 120 | 60 |
| Infected in the midgut | 19 (12.3) | 11 (9.2) | 5 (8.3) |
| Infected in the labrum | 1 (0.6) | 0 (0) | 3 (5.0) |
| Infected in the hypopharynx | 0 (0) | 0 (0) | 2 (3.3) |

*Male *G. pallidipes* included teneral and non-teneral flies.

Male vs female *G. f. fuscipes* (immature infections):
$N=275$, $X^2=0.39$, $df=1$, $P>0.05$ ns

Male *G. f. fuscipes* vs. male *G. pallidipes* (immature infections):
$N=215$, $X^2=0.33$, $df=1$, $P>0.05$ ns

Male *G. f. fuscipes* vs. male *G. f. fuscipes* (mature infections):
$N=215$, $X^2=2.22$, $df=1$, $P>0.05$ ns

Table 19. Trypanosome infection rates in *G. f. fuscipes* and *G. pallidipes* infected with a *T. brucei* stock F4. In brackets are percentages of infected flies.

| Number | *G. f. fuscipes* | | *G. pallidipes* |
|---|---|---|---|
| | Male | Female | Male* |
| Dissected | 220 | 188 | 77 |
| Infected the midgut | 26 (11.8) | 29 (15.4) | 5 (6.5) |
| Infected in the labrum | 0 (0) | 0 (0) | 2 (2.6) |
| Infected in the hypopharynx | 0 (0) | 0 (0) | 2 (2.6) |
| Infected in the salivary glands | 0 (0) | 1 (0.5) | 5 (6.5) |

*Male *G. pallidipes* included teneral and non-teneral flies.

Male vs. female *G. f. fuscipes* (immature infection):
$N=408$, $X^2=0.84$, $df=1$, $P>0.05$ ns

Male *G. f. fuscipes* vs. male *G. pallidipes* (immature infection):
$N=297$, $X^2=1.20$, $df=1$, $P>0.05$ ns

Male *G. f. fuscipes* vs. male *G. pallidipes* (mature infection):
$N=297$, $X^2=10.87$, $df=1$, $P<0.01$ **

Table 20. Trypanosome infection rates in ***G. f. fuscipes*** and ***G. pallidipes*** infected with a ***T. brucei*** stock F6. In brackets are percentages of infected flies.

| Number | *G. f. fuscipes* | | *G. pallidipes* |
|---|---|---|---|
| | Male | Female | Male* |
| Dissected | 169 | 213 | 154 |
| Infected in the midgut | 25 (14.8) | 24 (1.3) | 22 (14.3) |
| Infected in the labrum | 0 (0) | 0 (0) | 0 (0) |
| Infected in the hypopharynx | 0 (0) | 0 (0) | 4 (2.6) |
| Infected in the salivary glands | 1 (0.6) | 1 (0.5) | 14 (9.1) |

*Male ***G. pallidipes*** included teneral and non-teneral flies.

Male vs. female ***G. f. fuscipes*** (immature infections):
N=382, $X^2$=0.76, df=1, P>0.05 ns

Male ***G. f. fuscipes*** vs. male ***G. Pallidipes*** (immature infections):
N=323, $X^2$=0.00, df=1, P>0.05 ns

Male ***G. f. fuscipes*** vs. ***G. pallidipes*** (mature infections)
N=323, $X^2$=11.29, df=1, P<0.001 ***

Table 21. Trypanosome infection rates in *G. f. fuscipes* and *G. pallidipes* infected with a *T. brucei* stock F 27. In brackets are percentages of infected flies.

| Number | *G. f. fuscipes* | | *G. pallidipes* |
|---|---|---|---|
| | Male | Female | Male* |
| Dissected | 163 | 118 | 127 |
| Infected in the midgut | 20 (12.3) | 16 (13.6) | 37 ( 29.1) |
| Infected in the labrum | 0 (0) | 0 (0) | 8 (6.3) |
| Infected in the hypopharynx | 0 (0) | 0 (0) | 12 (9.4) |
| Infected in the salivary glands | 1 (0.6) | 0 (0) | 23 (18.1) |

*Male *G. pallidipes* included teneral and non-teneral flies.

Male vs. female *G. f. fuscipes* (immature infections):
N=281, $X^2$=0.24, df=1, P>0.05 ns

Male *G. f. fuscipes* vs. male *G. pallidipes* (immature infections):
N=290, $X^2$=11.80, df=1, P<0.001 ***

Male *G. f. fuscipes* vs. male *G. pallidipes* (mature infections):
N=290, $X^2$=26.53, df=1, P<0.001 ***

*f. fuscipes* and male *G. pallidipes* were not significantly different at P=0.05. Only the F1 stock showed that male *G. pallidipes* developed significantly more hypopharyngeal (mature) infections than male *G. f. fuscipes* (N=341, $X^2$=4.02, df=1, P<0.05) (Table 16).

Different results were obtained when *T. brucei* stocks were compared. In all the stocks immature infections in male and female flies were not significantly different (Tables 19, 20 and 21). Comparison of immature infections between male *G. f. fuscipes* and male *G. pallidipes* indicated that in two of the three stocks (stocks F4 and F6) there was no significant difference. In all cases of mature infections male *G. pallidipes* were significantly more infected than male *G. f. fuscipes*.

## DISCUSSION

Field results indicated that none of the *G. f. fuscipes* from Rusinga Island were infected with trypanosomes and only one of the flies from the mainland was infected with a *T. congolense* type of trypanosomes. It appears that the main factor responsible for the absence of trypanosomiasis in the area is the lack of animal reservoir hosts for this disease and/or the lack of contact between infected hosts and the flies. There were few species of game animals in the study

area (see Chapter 2) and these existed in low numbers. In *addition, most of these animals were found inland on hills* so that there was littl or no contact between them and ***G. f. fuscipes*** along the lake shore. Of the animals that were present in the study area it appeared as if there was more contact between the flies and goats as shown by the bloodmeal analysis. Eleven of the 12 bloodmeals analysed were classified as having been derived from goats and one from a cow. However, the number of bloodmeals analysed was too small to draw conclusions. Of the twelve bloodmeals analysed only three were collected from Rusinga Island, the rest were from the mainland. Early studies by Weitz (1970) showed that ***G. f. fuscipes*** was an opportunistic feeder utilizing available hosts and that a significant proportion of its bloodmeals were derived from reptiles. This observation has since been corroborated by other workers who conducted similar studies on the same subspecies in the neighbourhood of the present study area, in south eastern Uganda (van Vegten, 1971b) and Mfangano Island (Wijers, 1974a). It was probable that on Rusinga Island and the mainland monitor lizards also formed a major source of feeds because on many occassions it was observed that flies formed swarms on these animals while they basked in the sun on the lake shore.

Ashcroft (1959) and Ashcroft ***et al.*** (1959) showed that different game animals vary in their reservoir potential as

hosts of trypanosomes. Several workers (for example, Jordan, 1965; Harley, 1966a; Moloo, 1980) also showed that the origin of bloodmeals of different species of tsetse flies is an important factor that determined their trypanosome infection rates. Infection rates were observed to be higher in tsetse species which derived most of their feeds from bovids than any other hosts. There was no evidence that at the time of this study goats and cattle (and monitor lizards) which were the likely major hosts of the flies in the study area constituted a major reservoir of trypanosomiasis. During the course of this study three cases of trypanosomiasis in cattle were diagnosed on the island and a fourth one on the mainland. The cattle diagnosed to have had trypanosomiasis on the island were imported from endemic areas on the mainland. Monitor lizards are not reservoirs of salivarian trypanosomes which affect mammals (Hoare, 1970, 1972). However, Onyango *et al.* (1966) observed that cattle under certain circumstances can be reservoirs of human trypanosomiasis. This situation is reported to have occurred in Alego and Samia, Kenya, when following the rise of the water level of Lake Victoria game animals came into proximity with *G. f. fuscipes* which passed the infection to cattle and in turn to man.

There was no significant difference between male *G. f. fuscipes* and male *G. pallidipes* when immature (gut forms) *T. congolense* infections were compared. While immature

infections were fairly high, mature infections (hypopharyngeal) were very low in both species, particulary in ***G. f. fuscipes***. Duke (1933a, 1933b) observed that ***G. morsitans*** was a more efficient vector of trypanosomes than ***G. palpalis*** (presently referred to as ***G. f. fuscipes***). Various workers have since showed that different tsetse fly species vary in their vectorial capacity as transmitters of trypanosomes. For example, Harley and Wilson (1968) compared ***G. morsitans, G. pallidipes*** and ***G. f. fuscipes*** as vectors of ***T. congolense***. They found that ***G. f. fuscipes*** was a poor vector of this stock of trypanosomes with an infection rate of 2.9 % compared to ***G. morsitans*** with 11.6 % and ***G. pallidipes*** with 13.2 %. In another comparative study Harley (1971) found that salivary gland infection rates due to ***T. b. rhodesiense*** were 10.3 % and 2.6 % in male and female ***G. morsitans***, 24.1 % and 9.5 % in ***G. pallidipes***, 20.6 % and 14.6 % in ***G. f. fuscipes*** and none in the 202 ***G. brevipalpis*** dissected. Similar results were obtained in other comparative studies reported by van Vegten (1971a), Roberts and Gray (1972), Moloo and Kutuza (1988) and Moloo ***et al***. (1985, 1988).

Genetic differences in vectorial capacity of tsetse species were elucidated by Maudlin (1982) who showed that susceptibility of ***G. morsitans*** to ***T. congolense*** and later to ***T. brucei*** (Maudlin, 1985) was inherited through the female fly. Subsequent studies (Maudlin and Ellis, 1985) indicated

that the rickettsia-like organisms (RLOs) which had been observed in several wild tsetse fly species and also thought to be maternally inherited were closely associated with trypanosome infections. Maudlin and Ellis suggested that RLOs affected the digestion of serum in the susceptible fly which in turn appeared to be very important in killing trypanosomes. They observed that the reduction of levels of serum in the flies' bloodmeals increased midgut infection rates of *T. b. rhodesiense* which suggested that proteinases were involved. However, they noted that the process was much more complex because they could not detect any differences in the rate of serum digestion between susceptible and refractory flies. Furthermore, removal of lipids from bloodmeal serum mimicked the removal of all the serum from the bloodmeal. Later, Maudlin (1985) suggested that in the flies that were refractory to trypanosome infection, trypanosomes were killed by products of serum digestion, probably by the lysis of trypanosomes by lipids. In susceptible flies the RLOs affected the midgut/mycetome metabolism in some way which inhibited trypanocidal activity. Trypanosomes which survived either circumnavigated or penetrated the peritrophic membrane which enclosed the bloodmeal and then entered into the ectoperitrophic space where they transformed into dividing midgut forms. Further development of trypanosomes or maturation took place after a certain interval of time. This process took place in the presence of bloodmeal serum

and it was also probably stimulated by serum products resulting from fly digestion. Trypanosomes with a competent genotype then migrated to either the proboscis in the case of ***T. congolense*** or the salivary glands in the case of ***T. brucei***.

More recently Maudlin and Welburn (1988) concluded that lectin secreted in the fly midgut in response to bloodmeal serum was responsible for killing trypanosomes that entered the guts of refractory flies. Susceptible flies did not secrete enough lectin to kill the trypanosomes because RLOs which infected them produced the enzyme chitinase which hydrolysed chitin in the midgut to form Glucosamine during the larval/pupal stage. Glucosamine was responsible for the increased susceptibility to trypanosome infection because it inhibited midgut lectin. Maudlin and Welburn (1988) suggested that lectins provided a signal to trypanosomes established in the midgut which stimulated their maturation process. They also suggested that different trypanosome stocks might have different numbers of lectin binding sites and therefore those with few binding sites would mature even when lectin levels were very low. Flies with many lectin binding sites required high levels of lectin to mature.

In this study immature infections due ***T. congolense*** stocks used were lower in the female than in male ***G. f. fuscipes***. Immature infections in male ***G. f. fuscipes*** and

male *G. pallidipes* were not significantly different but mature infections with the *T. brucei* stocks were higher in the former than the latter group. It would, therefore, appear that female *G. f. fuscipes* had higher levels of lectins relative to the males and that male *G. f. fuscipes* had more lectins than male *G. pallidipes.* Various workers (Burtt, 1946b; Fairbairn and Culwick, 1950; Clarke, 1969; Otieno *et al*, 1983; Mwangelwa *et al.*, 1987) reported higher infection rates in males than females of other tsetse fly species in laboratory controlled studies. Harley and Wilson (1968), van Vegten (1971a) and Moloo *et al.* (1985, 1988) reported that *G. pallidipes* developed higher trypanosome infections due to *T. congolense* and *T. brucei* than *G. f. fuscipes* in studies conducted in the laboratory. However, it still remains to be shown what levels of lectins are produced by different tsetse fly species and how these levels are affected by other factors that influence the development of trypanosomes in the fly such as temperature, the source of the bloodmeal, age of the fly at the time of infective bloodmeal, etc.

Laboratory studies indicated that *G. f. fuscipes* developed lower trypanosome infection rates than *G. pallidipes.* Infection rates in the field were also low. However, although *G. f. fuscipes* is less likely to develop a mature infection than *G. pallidipes* it is more likely to bite man and, therefore, transmit human trypanosomiasis

because of its feeding patterns. This appears to be the case in Busia (Kenya) and Busoga (Uganda) where cases of this disease, transmitted by ***G. f. fuscipes***, are presently being reported. It would appear that since there were no reservoir hosts in the dense vegetation along the lake shore in the study area which interacted intimately with the tsetse flies, and that the distribution of flies remained as it was at the time, the likelihood of infection of flies, livestock and people would be low.

# CHAPTER 8

## GENERAL DISCUSSION

The knowledge of the distribution of tsetse flies is important in relation to the epidemiology of the disease. ***G. f. fuscipes*** on Rusinga Island and the mainland in the Mbita Division of South Nyanza District of Kenya was confined to the thick vegetation along the shores of the lake. These thickets were probably more extensive in the past than they appear to be today, having been reduced to isolated clusters because of interference by the local people.

The central part of Rusinga Island is hilly and so is the area further inland on the mainland. As a result of this, these areas are sparsely populated and most of the human settlements and cultivation of crops occur on a strip of flat land near the lake shore. Clearings of vegetation for cultivation of crops have influenced the distribution of ***G. f. fuscipes*** which as reported in Chapter 3 is usually a subspecies associated with water courses along which dense vegetation occurs.

***G. f. fuscipes*** was caught in thick vegetation within 100 m from the lake shore. Since the area in which this fly was caught coincided with thickets it was considered that

vegetation cover was the main factor limiting its distribution inland. However, in situations where the dense vegetation extends further inland the distribution of the fly could also be more extensive providing conditions are suitable for its survival. Such situations have been reported by various workers (Chorley, 1944; Willett, 1965; Langridge and Mgutu, 1971; Okoth, 1985, 1986a).

Mainly due to increased human settlement in the study area it will be unlikely that the distribution of ***G. f. fuscipes*** would extend much further inland than is presently reported here. With time, and as the human population increases the need for more land for cultivation of crops will mean that much of the vegetation fringing the lake shore will be reduced in size and hence the distribution of this fly will likely to be reduced too.

Studies of population dynamics of tsetse flies are very relevant to tsetse control strategies to be adopted. If it is established that density indepedent factors are mainly operational in a tsetse population, for example, as is the case at the edge of the fly belt like in South Africa (Rogers, 1979) the population will take a long time to resurge following a tsetse control method. If density dependent factors are mainly in operation, for example, in the Lambwe Valley of Kenya (Turner, 1984) there will be a tendency for the tsetse population to resurge rather rapidly

after a tsetse control measure. This is because the introduced 'artificial' mortality say, from the use of insecticides, will tend to suppress natural mortality factors. With the latter having been reduced tsetse flies would then multiply faster than they would have in the absence of insecticides.

The use of traps to control tsetse flies actually means adding trap mortality to already existing natural mortality. Studies on population dynamics make it possible to estimate the density of traps that would be required to reduce a population of tsetse flies in a given period of time providing there is no reinvasion in the control area.

In Chapter 4 the size of the populations of ***G. f. fuscipes*** on both Rusinga Island and the mainland were reported to be remarkably stable. However, there was a consistent drop in catches during the rainy seasons. In the absence of estimates indicating changes in monthly absolute population sizes of the flies and more convincing evidence to show seasonality in mortality rates that were recorded, it would appear that the fall in trap catches may have resulted from the poor availability of flies to the biconical traps at this time of the year rather than an actual decline in the population size. Dransfield ***et al.*** (1982) who sampled ***G. m. morsitans*** in Nigeria throughout the

year observed that the effectiveness of biconical and water traps varied according to season.

It may be concluded that the stability of the populations of ***G. f. fuscipes*** on Rusinga Island and the mainland means that these would be resilient following tsetse control methods. The restricted mobility of the flies also means it would be difficult to control flies in large areas because many traps would be required per given area. However, it would be relatively easy to control this fly over small areas because there would be limited reinvasion.

In Chapter 5 it was reported that none of the odour baits tested for effectiveness against this subspecies (i.e. cow and human urine, acetone, 1-octen-3-ol, mixtures of phenolic fractions and washings from a monitor lizard and a goat) using randomised latin square designs in the setting up of baited traps in the field were found effective. It still remains to be determined whether this fly uses visual rather than olfactory cues to locate its hosts. It is therefore suggested that ***G. f. fuscipes***'s preference for goats in the presence of other hosts observed in this study should be further investigated. Further studies should also be conducted to determine the effectiveness of various odours emanating from the breaths of different animal hosts as ***G. f. fuscipes*** may be responding to these odours in its

host finding responses. Odour attractants have recently been used for other ***palpalis*** group of flies like ***G. tachinoides***.

Of the six different types of traps compared, the biconical trap was the most effective for ***G. f. fuscipes***. However, the cost of the variants of this trap (i.e. the pyramidal and Vavoua traps) should be studied to determine whether these would be cheaper if used in a control campaign against ***G. f. fuscipes***. Further experiments should be conducted to determine why the biconical trap was the most effective..

A colony of ***G. f. fuscipes*** was raised from adult flies collected in the field and successfully reared under simple conditions designed earlier for ***G. pallidipes*** to provide specimens for studies on vectorial capacity of the subspecies. The rearing conditions were found to be cheaper and suitable for small scale production of ***G. f. fuscipes***.

Trypanosome infection rates of ***G. f. fuscipes*** in the field were found to be very low. Infection rates were 0 % and 0.10 % on Rusinga Island and the mainland, respectively. In the laboratory ***G. f. fuscipes*** was found to be less susceptible to mature trypanosome infection with ***T. congolense*** and ***T. brucei*** than ***G. pallidipes***. However, there were no significant differences between the two fly species

when immature infections were compared. It seems reasonable to suggest that there could be a substance or substances in the gut of ***G. f. fuscipes*** that inhibited further development of the trypanosomes. Further studies should be carried out to compare the levels of lectins in ***G. pallidipes*** and ***G. f. fuscipes*** with the aim of finding out what amounts are required to inhibit the development of trypanosomes. However, in nature ***G. f. fuscipes*** would appear to be a more efficient vector of human trypanosomiasis than ***G. pallidipes*** because it comes into contact with man more frequently.

In the study area *G. f. fuscipes* was found to feed mostly on goats. This probably accounts for the observed low trypanosome infection rates in the flies as goats are not a major natural reservoirs of trypanosomes that cause the human disease. The absence of natural reservoirs of *trypanosomes in the study area implied that* it was unlikely that an epidemic of trypanosomiasis would occur among the human inhabitants. This could also explain why in some parts of Kenya this fly occurs without the disease. The situation in Busia near the Uganda/Kenya border could be chosen as an example of areas where there had been no cases of the disease until the disease flared up in Uganda and was reintroduced in the area.

## SUMMARY

1. The ecology and vectorial capacity of ***G. f. fuscipes*** were studied on Rusinga Island and the mainland in Mbita Division, South Nyanza District of Kenya from November 1987 to December 1989.

2. The distribution of ***G. f. fuscipes*** was confined to thick vegetation along the lake shores formed mainly by the following plant species: ***S. sesban, A. elaphroxylon, Phragmites*** species and several creepers of the family Nyctaginacea.

3. These thickets were probably more extensive in the past and have become less extensive today because of clearings made for cultivation of crops. This has in turn influenced the distribution of ***G. f. fuscipes.***

4. Results showed that ***G. f. fuscipes*** was diurnal in activity with peak activity occurring from 8.00-9.00 h for females and 9.00-10.00 h for males, respectively.

5. Solar radiation intensity was the main factor influencing activity patterns of ***G. f. fuscipes.***

6. The population size of ***G. f. fuscipes*** on Rusinga Island and the mainland was remarkably stable varying by a factor of 5 on the island and 7 on the mainland.

7. There was a drop in trap catches soon after the rainy seasons. This fall in catches may have been associated with the poor visibility of flies to biconical traps during the rainy season rather than a decline in the actual population size.

8. The age of male flies on Rusinga Island and the mainland was estimated using the wingfray method at 24 and 21 days, respectively. This gave mortality rates of about 4.2 and 4.8 % per day.

9. The age distribution of the females from the two localities was not significantly different.

10. Mortality rates estimated using the ovarian age analysis were higher on Rusinga Island than on the mainland. There was a positive correlation between mortality rates and amount of rainfall on Rusinga Island.

11. Estimates of mortality rates obtained using the Moran curve technique showed no clear trends.

12. There was no correlation between mortality rates obtained by the ovarian age analysis method and the Moran curve technique.

13. Reproductive abnormalities in fly samples from Rusinga Island and the mainland were rare, not exceeding 2 %. This implied that the populations of ***G. f. fuscipes*** were not under stress.

14. Corrected recapture rates (CRRs) showed peaks at intervals of 5, 9, 14, 18, 22 and 25 days for female flies. This could reflect a pregnancy cycle of 8-9 days, with the hunger cycle superimposed at 4-5 days.

15. The absolute population density of ***G. f. fuscipes*** on Rusinga Island was estimated at 301 males and 559 females per hectare in November/December 1988. This was considered a heavy infestation of this subspecies compared to other studies in literature.

16. Using the random diffusion equation first described by Pileou (1977) and modified by Dr. B. Williams for this study the distance moved by ***G. f. fuscipes*** was estimated at 76 m for males and 112 m for females in 12 hours, respectively.

17. The restricted mobility of this fly implied that control of this subspecies using traps would be difficult in large areas because many traps would be required per unit area. However, substantial reductions could be achieved in small areas.

18. None of the odour baits tested (i.e. cow and human urine, acetone, 1-octen-3-ol, mixtures of phenolic fractions, washings from a goat and a monitor lizard) were found effective for ***G. f. fuscipes***. The combination of acetone and cow urine produced variable responses especially for female flies. It was considered that such variable responses may have been partly due to a trapping out effect on this fly.

19. The biconical trap was the most effective trap for ***G. f. fuscipes***. The superiority of this trap over other trap designs tested in this study should be further investigated.

20. ***G. f. fuscipes*** was succeessfully reared under simple conditions earlier designed for ***G. pallidipes***. This was found to be cheap and ideal for small scale production of flies for various studies.

21. Studies on vectorial capacity showed that ***G. f. fuscipes*** developed significantly fewer mature

trypanosome infection due to ***T. congolense*** and ***T. brucei*** than ***G. pallidipes***. Further studies are required to determine the factors involved in inhibiting further development of trypanosomes in ***G. f. fuscipes***.

22. Human trypanosomiasis was unlikely to occur in the study area because of the confinement of the distribution of the fly to the lake shore and the absence of reservoir hosts of the disease.

# REFERENCES

Abaru D. E. (1985). Sleeping sickness in Busoga, Uganda, 1976-1983. *Trop. med. Parasit.*, **36**: 72-76.

Abaru D. E. and Matovu F. S. (1981). Sleeping sickness in south eastern Uganda. *In International Scientific Council for Trypanosomiasis Research and Control, Seventh Meeting, Arusha, Tanzania*, pp. 183-186.

Allsopp R. and Baldry D. A. T. (1972). A general description of the Lambwe Valley area of South Nyanza District, Kenya. *Bull. Wld. Hlth Org.*, **47**: 691-697.

Ashcroft M. T. (1959). The importance of African wild animals as reservoirs of trypanosomiasis. *E. Afri. med. J.*, 36: 289-297.

Ashcroft M. T., Burtt E. and Fairbairn H. (1959). The experimental infection of some African wild animals with ***Trypanosoma rhodesiense, T. brucei*** and ***T. congolense***. *Ann. trop. Med. Parasit.*, **53**: 147-161.

Ayot H. O. (1979). *A history of the Luo-Abasuba of Western Kenya from A. D. 1760-1940.* Kenya Literature Bureau, Nairobi, 214 pp.

Baldry D. A. T. (1964). Observations on a close association between ***Glossina tachinoides*** and domestic pigs near Nsukka, Eastern Nigeria II. Ecology and trypanosome infection rates in ***G. tachinoides***. *Ann. trop. Med. Parasit.*, 58: 32-44.

Baldry D. A. T. (1980). Local distribution and ecology of ***Glossina palpalis*** and ***G. tachinoides*** in forest foci of West African human trypanosomiasis, with special reference to associations between peri-domestic tsetse and their hosts. *Insect Sci. Applic.*, 1: 85-93.

Barrass R. (1960). The settling of tsetse flies ***Glossina morsitans*** Westwood (Diptera; Muscidae) on cloth screens. *Ent. Exp. Appl.*, 3: 59-67.

Bauer B. and Wetzel H. (1976). A new membrane for feeding ***Glossina morsitans*** Westw (Diptera, Glossinidae). *Bull. ent Res.*, 65: 563-565.

Bax S. N. (1937). The senses of smell and sight in ***Glossina swynnertoni***. *Bull. ent. Res.*, 28: 539-586.

Bell H. (1909). Report on the measures adopted for suppression of sleeping sickness in Uganda. *Colonial Reports- Miscellaneous*, 65: 3-27

Brightwell R., Dransfield R. D. and Kyorku C. (1990). Development of a low cost trapping technology for the tsetse flies ***Glossina pallidipes*** and ***G. longipennis***. *Med. Vet. Entomol.*, (in press).

Brightwell R., Dransfield R. D., Kyorku C., Golder T. K., Tarimo S. A. and Mungai D. (1987). A new trap for ***Glossina pallidipes***. *Tropical Pest Management*, **33**: 151-159.

Brues C. T., Melander A. L. and Carpenter F. M. (1954). *Classification of insects*. Cambridge, Mass., Harvard University Press, 917 pp.

Bursell E. (1977). Chemosterilisation of tsetse flies using a pressurised metepa aerosol. *Trans. Rhod. scient. Ass.*, 58: 43-47

Bursell E. and Glasgow J. P. (1960). Further observations on lake-side and riverine communities of ***Glossina palpalis fuscipes*** Newst. *Bull. ent. Res.*, **51**: 47-56.

Burtt E. (1946a). Incubation of tsetse pupae; increased transmission rate of ***Trypanosoma rhodisiense*** in ***Glossina*** morsitans. *Ann. trop. Med. Parasit.*, **40**: 18-28.

Burtt E. (1946b). The sex ratio of infected flies found in transmission experiments with ***Glossina morsitans morsitans*** and ***Trypanosoma rhodesiense***. *Ann. trop. Med. Parasit.*, **40**: 74-79.

Buxton P. A. (1955). The natural history of tsetse flies: an account of the biology of the genus ***Glossina*** (Diptera). *Lond. Schl. Hyg. Trop. Med. Mem. no.* 10. London, 816 pp.

Carter R. M. (1906). Tsetse fly in Arabia. *Brit. Med. J.*, **2**: 1393.

Challier A. (1965). Amelioration de la method de determination de l'age physioloque des glossines. Etudes faites sur ***Glossina palpalis gambiensis*** Vanderplank 1949. *Bull. ent. Res.*, **57**: 985-991.

Challier A. (1973). Ecologie de ***Glossina palpalis gambiensis*** Vanderplank, 1949 (Diptera-Muscidae) en savane d'Afrique occidentale. *Memoires O.R.S.T.O.M.* No. 64, 274 pp.

Challier A. (1982). The ecology of tsetse (***Glossina*** spp.) (Diptera; Glossinidae): a review (1970-1981). *Insect Sci. Applic.*, 3: 97-143.

Challier A. and Laveissiere C. (1973). Un nouveau piege pour la capture des glossines (**Glossina**: Diptera Muscidae): description et essais sur le terrain. *Cah. O.R.S.T.O.M. ser. Ent. med. Parasitol.*, 11: 251-262.

Challier A., Eyraud M., Lafaye A. and Laveissiere C. (1977). Amelioration du rendement piege biconique pour glossines (Diptera, Glossinidae) par l'emploi d'um cone inferieur blue. *Cah. O.R.S.T.O.M. ser. Ent. med. Parasitol.*, 15: 283-286.

Cheke R. A. and Garms R. (1988). Trials of compounds to enhance trap catches of ***Glossina palpalis palpalis*** in Liberia. *Med. Vet. Entomol.*, 2: 199-200.

Chorley C. W. (1933). Traps for tsetse-flies of the "crinoline" and "ventilator" forms. *Bull. ent. Res.*, 24: 315-320.

Chorley T. W. (1944). ***Glossina palpalis fuscipes*** breeding away from water (Diptera). *Proc. R. Soc. Lond. (A)*, 19: 1-4.

Chorley T. W. (1948). ***Glossina pallidipes*** Austen attracted by the scent of cattle-dung and urine. *Proc. R. Ent. Soc. Lond. (A)*, 23: 9-11,.

Clarke G. M. (1969). *Statistics and experimental design.* Edward Arnold, London, 161 pp.

Clarke J. E. (1966). Trypanosome infection in the mouthparts of ***Glossina morsitans*** Westwood: variations in frequency and extent of labral infections with age. *Ann. trop. Med. Parasit.*, **60**: 223-229.

Clarke J. E. (1969). Trypanosome infection in the mouthparts of Zambian tsetse. *Ann. trop. Med. Parasit.*, **63**: 15-34.

Dipeolu O. O. and Adam K. M. G. (1974). On the use of membrane feeding to study the development of ***Trypanosoma brucei*** in ***Glossina***. *Acta trop.*, **31**: 185-201.

Distelmans W., D'haeselear F., Kaufman L. and Rousseuw P. (1982). The susceptibility of ***Glossina palpalis palpalis*** at different ages to infection with ***Trypanosoma congolense***. *Ann. Soc. belge Med. trop.*, **62**: 41-47.

Dransfield R. D. (1984). The range of attraction of the biconical trap for ***Glossina pallidipes*** and ***G. brevipalpis***. *Insect Sci. Applic.*, **5**: 363-368.

Dransfield R. D., Brightwell R., Onah J. and Okolo C. J. (1982). Population dynamics of ***Glossina morsitans submorsitans*** Newstead and ***G. tachinoides*** Westwood (Diptera: Glossinidae) in sub-Sudan savanna in northern Nigeria I. sampling methodolgy for adults and seasonal changes in numbers caught in different vegetation types. *Bull. ent. Res.*, **72**: 175-192.

Dransfield R. D., Brightwell R., Kyorku C. and Williams B. (in press). Control of tsetse (Diptera: Glosinidae) populations using traps at Nguruman, South-West Kenya. *Bull. ent. Res.*

Dransfield R. D., Chaudhry M. F. B., Tarimo S. A., Golder T. K and Brightwell R. (1985). Population dynamics of ***Glossina pallidipes*** under drought conditions at Nguruman, Kenya. *In International Scientific Council for Trypanosome Research and Control. Fightneeth meeting, Harare, Zimbabwe, pp.* 284-292.

Dransfield R. D., Brightwell R., Chaudhury M. F., Golder T. K. and Tarimo S. A. R. (1986). The use of odour attractants for sampling ***Glossina pallidipes*** Austen (Diptera: Glossinidae) at Nguruman, Kenya. *Bull. ent. Res.*, **76**: 607-619.

Duke H. L. (1933a). Studies on the factors that may influence the transmission of the polymorphic trypanosomes by tsetse. I. A review of existing knowledge on this subject, with some general observations. *Ann. trop. Med. Parasit.*, 27: 99-118.

Duke H. L. (1933b). Studies on the factors that may influence the transmission of the polymorphic trypanosomes III. ***Glossina morsitans*** versus ***G. palpalis*** as a transmitter of the polymorphic group of typanosomes. *Ann. trop. Med. Parasit.*, **27**: 123-130.

Duke H. L. (1933c). Relative susceptibility of the sexes of ***Glossina*** to infection with trypanosomes. *Ann. trop. Med. Parasit.*, 27: 355-356.

Duke H. L. (1933d). Studies on the factors that may influence the transmission of the polymorphic trypanosomes by tsetse V. On the effect of temperature. *Ann. trop. Med. Parasit.*, **27**: 437-450.

Duke H.L. (1936). On the power of ***Glossina morsitans*** and ***Glossina palpalis*** to transmit the trypanosomes of the ***brucei*** group. *Ann. trop. Med. Parasit.*, **30**: 37-38.

Elce B. J. (1974). The development of salivarian trypanosomes in ***Glossina morsitans*** and small laboratory mammals. *Trans. R. Soc. trop. Med. Hyg.*, **68**: 162.

Eouzan J-P. (1977). Distribution and bionomics. In Laird M. (ed.). *Tsetse: the future for Biological Methods in Integrated Control* pp. 99-107, IDRC, Ottawa.

Eouzan J-P., Lancien J. and Frezil J-L. (1981). Analyse critique d'une method de lutte adapte a deux especes de glosines riveraines en Republique Populaire du Congo. *Cah. O.R.S.T.O.M ser. Ent. med Parasitol.*, 19: 75-80.

Fairbairn H. and Culwick A. T. (1950). The transmission of the polymorphic trypanosomes. ***Acta trop.***, 7: 19-44.

Fairbairn H. and Watson H. J. C. (1955). The transmission of ***Trypanosoma vivax*** by ***Glossina palpalis.*** *Ann. trop. Med. Parasit.*, **49**: 250-259.

Fairclough R. and Thompson W. E. F. (1957). The effect of insecticidal spraying against ***Glossina fuscipes fuscipes*** (Newst.) in the Nyando River Basin of Kenya. *E. A. Agric. J.*, **23**: 186-189.

FAO (1979). Report of the second consultation on the programme for the control of African animal trypanosomiasis held from 5-7 December 1978, Lusaka, Zambia, 75 pp., Rome.

Fiske W. F. (1920). Investigations into the bionomics of *Glossina palpalis*. *Bull. ent. Res.*, **10**: 347-446.

Flint S. (1985). A comparison of various traps for *Glossina* spp. (Glossinidae) and other Diptera. *Bull. ent. Res.*, **75**: 529-534.

Ford J. (1970). The geographical distribution of *Glossina*. In Mulligan H. W. (ed.). *The African trypanosomiases*. Allen and Unwin, London, pp. 274-297.

Ford J. (1971). *The role of the trypanosomiases in African ecology: a study of the tsetse fly problem*. Clarendon, Oxford, 529 pp.

Ford J. and Katondo K. M. (1977a). Revision of the *Glossina* distribution map of Africa. *In International Scientific Council for Trypanosomiasis Research. Fourteenth meeting, Dakar, Senegal*, pp. 252-256,

Ford J. and Katondo K. M. (1977b). Maps of tsetse flies (*Glossina*) distribution in Africa, 1973: according to subgeneric groups on scale of 1:5,000,000. *Bull. Anim. Hlth Prodn.*, **25**: 187-193.

Frezil J. L. and Carnervale P. (1976). Utilisation de la carboglace pour la capture de ***Glossina fuscipes quanzensis*** Pires, 1948 avec le piege Challier-Laveisseire consequences epidemilogiques. *Cah. O.R.S.T.O.M. ser. Ent. med. Parasitol.*, **14**: 225-233.

Galey J. B., Merot P., Mitteault A., Filledier J. and Politzar H. (1986). Efficate du dioxyde carbone comme attractif pour ***Glossina tachinoides*** en savane humide d'Afrique de l'Ouest. *Rev d'elev. Med. vet. Pays trop.*, **39**: 351-354.

Geigy R. (1948). Elevage de ***Glossina palpalis***. *Acta trop.*, **5**: 201-218.

Gibbins E. G. (1941). Studies on the bionomics, control and natural infectivity of the riverine ***Glossina palpalis*** subspecies ***fuscipes*** Newstead in the West Nile District of Uganda. *Ann. trop. med. Parasit.*, **35**: 195-217.

Gingrich J. B., Ward R. A., Macken L. M.and Ester K. M. (1982). *African sleeping sickness: new evidence that mature tsetse flies (**Glossina morsitans morsitans**) can become potent vectors.* *Trans. R. Soc. trop. Med. Hyg.*, **76**: 479-481.

Glasgow J. P. (1954). ***Glossina palpalis fuscipes*** Newst. in the Lake-side and in riverine forest. *Bull. ent. Res.*, **45**: 563-574.

Glasgow J. P. (1963). *The distribution and abundance of tsetse.* Pergamon Press, London, 241 pp.

Glasgow J. P. (1970a). The genus ***Glossina.*** Introduction. *In Mulligan H. W. (ed). The African trypanosomiases.* Allen and Unwin, London, pp. 225-242.

Glasgow J. P. (1970b). The ***Glossina*** community. *In Mulligan H. W. (ed.). The African trypanosomiases.* Allen and Unwin, London, pp, 348-381.

Glasgow J. P. and Duffy B. J. (1917). The extermination of *Glossina palpalis fuscipes*, Newstead, by hand-catching. *Bull. ent. Res.*, **38**: 465-477.

Glasgow J. P. and Duffy B. J. (1951). Further observations on the extermination of ***Glossina palpalis fuscipes***, Newstead, by hand-catching. *Bull. ent. Res.*, 42, 55-63.

Glasgow J. P. and Phelps R. J. (1970). Methods for the collecting and sampling of ***Glossina***. *In Mulligan H. W. (ed.). The African trypanosomiasis.* Allen and Unwin, London, pp. 395-415.

Glover P. E., Le Roux J. G. and Parker D. F. (1958). The extermination of ***Glossina palpalis*** on Kuja-Migori river systems with the use of insecticides. In *International Scientific Committee for trypanosomiasis Research. Seventh Meeting*, pp. 331-342. (Commission for Technical Cooperation in Africa, publ. no. 41).

Godfrey D. G. (1966). Diagnosis of trypanosome infections in the tsetse flies- *In Corradetti A. (ed.). Proceedings of the first international congress of parasitology.* pp. 990-992.

Gough A. J. E., Hall D. R., Beevor P., Cork A. Bursell E. and Vale G. A. (1987). Attractants for tsetse from cattle urine. *In International Scientific Council for Trypanosomiasis Research and Control, Nineteenth Meeting, Lome, Togo, pp.* 493-499.

Gouteux J-P. and Buckland S. T. (1984). Ecologie des glossines en secteur pre-forestier de Cote d'Ivoire 8. Dynamique des populations. *Cah. O.R.S.T.O.M. ser. Ent. med. Parasitol.*, 22: 19-34.

Gouteux J-P. and Challier A. (1978) Essai de lutte anti-glossines en foret par utilisation d'ecrans de tissu impregnes d'insecticides I. Resultats obtenus en saison des pluies. Mission O.R.S.T.O.M. aupres de l'OCCGE, no. 25/Ent. 78.

Gouteux J-P. and Lancien J. (1986). Le piege pyramidal a' tsetse' (Diptera: Glossinidae) pour la capture et la lutte Essais comparatifs et description de nouveax systemes de captire. *Trop. med. Parasit.*, 37: 61-66.

Gouteux J-P. and Laveissiere C. (1982). Ecologie des glossines en secteur pre-forestier de Cote d'Ivoire 4. Dynamic de l'ecodistribution en terroir villageois. *Cah. O.R.S.T.O.M. ser. Ent. med. Parasitol.*, 20: 199-229.

Gouteux J-P. and Monteny B. (1986). Ecologie des glossines en secteur pre-forestier de Cote d'Ivoire. 10. *Cah. O.R.S.T.O.M. ser. Ent. med. Parasitol.*, 24: 83-97.

Gouteux J-P., Noireau F., Sinda D. and Frezil J-L. (1986). Essais du piege Pyramidal contre ***Glossina palpalis palpalis*** (R-D) dans le foyer du Niari (Region de la Bouenza, Republique poplaire du Congo). *Cah. O.R.S.T.O.M. ser. Ent. med. Parasitol.*, **24**: 181-190.

Green C. H. (1988). The effect of colour on trap- and screen-orientated responses in ***Glossina palpalis palpalis*** (Robineau-Desvoidy) (Diptera: Glossinidae). *Bull. ent. Res.*, **78**: 591-604.

Green C. H. and Flint S. (1986). An analysis of colour effects in the performance of the F2 trap against ***Glossina pallidipes*** Austen and *G.* ***morsitans morsitans*** Westwood (Diptera: Glossinidae). *Bull. ent. Res.*, **76**: 409-418.

Haeselbarth E. Segerman J. and Zumpt F. (1966). The arthropod parasites of vertebrates in Africa south of the Sahara (Ethiopian Region), Vol III (insects excl. Phithiraptera). *Publs S. Afr. Inst. med Res.*, **13**: (52), 283 pp.

Hall D. R., Beevor P. S., Cork A, Nesbitt B. F. and Vale G. A. (1984). A potent olfactory stimulant and attractant for tsetse isolated from cattle odours. *Insect Sci. Applic.*, **5**: 335-339.

Hargrove J. W. (1976). The effect of human presence on the behaviour of tsetse flies (*Glossina* spp.) (Diptera; Glossinidae) near a stationary ox. *Bull. ent. Res.*, **66**: 173-178.

Hargrove J. W. (1977). Some advances in the trappping of tsetse (*Glossina* spp.) and other flies. *Ecol. Entomol.*, **2**: 123-137.

Hargrove J. W. and Vale G. A. (1978). The effect of host odour concentration on catches of tsetse flies (Glossinidae) and other Diptera in the field. *Bull. ent. Res.*, **68**: 607-612.

Hargrove J. W. and Vale G. A. (1979). Aspects of the feasibility of employing odour-baited traps for controlling tsetse flies (Diptera: Glossinidae). *Bull. ent. Res.*, **69**: 283-290.

Hargrove J. W. (1989). Age-dependent changes in the probabilities of survival and capture of an island population of tsetse flies: implications for the determination of the population dynamics of ***Glossina*** spp. International Study Workshop on tsetse population and Behaviour held at Duduville, Nairobi, Kenya from 6-1? August 1989.

Harley J. M. B. (1965). Activity cycles of ***Glossina pallidipes*** Aust., ***G. palpalis fuscipes*** Newst., and ***G. brevipalpis*** Newst. *Bull. ent. Res.*, **56**: 141-160.

Harley J. M. B. (1966a). Studies on age and trypanosome infection rates in females of ***Glossina pallidipes*** Aust., ***G. palpalis fuscipes*** Newst., and ***G. brevipalpis*** Newst in Uganda. *Bull. ent. Res.*, **57**: 23-37.

Harley J. M. B. (1966b). Further studies on age and trypanosome infection rates in ***Glossina pallidipes*** Aust., ***G. pallidipes*** Aust., ***G. palpalis fuscipes*** Newst. and ***C. brevipalpis*** Newst. in Uganda. *Bull. ent. Res.*, **57**: 459-477.

Harley J. M. B. (1971). Comparison of the susceptibility to infection with ***Trypanosoma rhodesiense*** of ***Glossina pallidipes, G. morsitans, G. fuscipes*** and ***G. brevipalpis.*** *Ann. trop. Med. Parasit.*, **65**: 185-189.

Harley J. M. B. and Wilson A. J. (1968). Comparison between ***Glossina morsitans, G. pallidipes*** and ***G. fuscipes*** as vectors of trypanosmes of the ***Trypanosoma congolense*** group: the proportions of infected experimentally and the number of infective organisms extruded during feeding. *Ann. trop. Med. Parasit.*, **62**: 178-187.

Harris R. H. T. P. (1930). Report on the bionomics of tsetse fly (***Glossina pallidipes*** Aust), and a preliminary report of a new method of control, presented by the provincial administration of Natal. Fol. 75 pp. Pietermaritzburg.

Hassanali A., McDonwell P. G., Owaga M. L. A. and Saini R. K. (1986). Identification of tsetse attractants from excretory products of a wild host animal, ***Syncerus caffer***. *Insect Sci. Applic.*, 7: 5-9.

Harternorth T. and Diller H. (1980). *A guide to the mammmals of Africa including Madascar*. Collins, London, 400 pp.

Hoare C. A. (1970). The mammalian trypanosomes of Africa and systematic description of mammalian trypanosomes of Africa. In Mulligan H. W. (ed.). *The African Trypanosomiases*. Allen and Unwin, London, pp. 3-59.

Hoare C. A. (1972). *The trypanosomes of mammals. A zoological monograph*. Oxford, Edinburgh, 749 pp.

Hughes J. C. (1957a). Olfactory stimulation of tsetse flies and blowflies. *Bull. ent. Res.*, **48**: 561-579.

Hughes J. C. (1957b). Olfactory stimulation of ***Glossina palpalis*** (R-D) by combustion products from petrol engines. *Bull. ent. Res.*, **48**: 581-583.

International Centre of Insect Physiology and Ecology (ICIPE). Thirteenth Annual Report 1985.

Itard J. and Jordan A. M. (1977). Mass rearing using animals for feeding. In Laird M. (ed.). *Tsetse the future for biological methods in integrated control. pp. 125-140, IDRC, Ottawa.*

Jack R. W. (1941). Notes on the behaviour of ***Glossina pallidipes*** and ***G. brevipalpis*** and some comparisons with ***G. morsitans***. *Bull. ent. Res.*, **31**: 407-430.

Jackson C. H. N. (1946). An artificially isolated generation of tsetse flies (Diptera). *Bull. ent. Res.*, **37**: 291-299.

Jackson C. H. N. (1948). The analysis of a tsetse-fly population III. *Annals of Eugenics, Cambridge*, **14**: 91-108.

Jackson C. H. N. (1953). A mixed population of ***Glossina morsitans*** and ***G. swynnertoni***. *J. Anim. Ecol.*, **22**: 78-86.

Jordan A.M. (1965). The hosts of ***Glossina*** as the main factor affecting trypanosome infection rates of tsetse flies in Nigeria. *Trans. R. Soc. Med. Hyg.*, 59: 423-431.

Jordan A. M. (1974). Recent development in the ecology and methods of control of tsetse flies (***Glossina*** spp.) (Diptera, Glossinidae) - a review. *Bull. ent. Res.*, 63: 361-399.

Jordan A. M. (1976). Tsetse flies as vectors of trypanosomes. *Vet. Parasit.*, 2: 143-152.

Jordan A. M. (1986). *Trypanosomiasis control and African rural development.* Longman, 357 pp.

Kaaya G. P. and Darji N. (1989). Mortality in adult tsetse, ***Glossina morsitans morsitans***, caused by entomopathogenic bacteria. *J. Invertebr. Pathol.*, 54: 32-38.

Kangwagye T. N. (1975). Control of ***Glossina fuscipes*** in the 1971 sleeping sickness outbreak at Busesa, South Busoga, Uganda. *In International Scientific Council for Trypanosomiasis Research and Control, Fourteenth Meeting, Dakar, Senegal, pp.* 365-370.

Katabazi B. K. (1983). The tsetse fly ***Glossina fuscipes*** in the sleeping sickness epidemic area of Busoga, Uganda. *E. Afric. Med. J.*, **60**: 397-401.

Katondo K. M. (1984). Revision of second edition of tsetse distribution maps an entrim report. *Insect Sci. Applic.*, **5**: 381-388.

Kenya Population Census Volume I. (1979). Central Bureau of Statistics. Ministry of Economic Planning and Development, June, 1981.

Kinghorn A., Yorke W. and Lloyd L. (191-). Final report of the Luangwa sleeping sickness commission of the British South African Company. *Ann. trop. Med. Parasit.*, **7**: 183-302.

Kupper W. (1988). The efficiency of various odours in attracting ***G. tachinoides*** Westwood. Results of 2 years' experiment in northern Cote d'lvoire. *In International Scientific Council for Trypanosomiasis Research and Control. Nineth Meeting, Lome, Togo, pp.* 107.

Kupper W., Manno A. Douati A. and Koulibali S. (1984). Impact des pieges biconiques impregnes sur les populations de ***Glossina palpalis gambiensis*** et ***Glossina tachinoides*** de lutte a granade echelle contre la trypanosomose animale au nord de la Cote-d'Ivoire. *Rev. Elev. Med. vet Pays trop.*, **37**: (no. special), 176-185.

Kupper W., Manno A., Clair M. and Kotia K. (1985). The large-scale control of ***Glossina palpalis s. l., G. fusca fusca*** and ***G. longipalpis*** in the southern guinean zone of the Ivory Coast by deltamethrin impregnated biconical traps. *Cah. .O.R.S.T.O.M., ser. Ent. med. parasitol.*, **23**: 9-16.

Lamborn W. A. (1915). A preliminary report on the problem of controlling ***Glossina*** in Nyasaland. *Bull. ent. Res.*, **6**: 59-65.

Lancien J. (1981). Description du piege monoconique utilise pour l'elimination des glossines en Republique Populaire du Congo. *Cah. O.R.S.T.O.M. ser. Ent. med. Parasitol.*, **29**: 235-238.

Lancien J., Eozan J-P., Frezil J-L. and Mouchet J. (1981). Elimination des glossines par piegeage dans deux foyers de trypanosomiase en Republique Populaire du Congo. *Cah. O.R.S.T.O.M. ser. Ent. med. Parasitol.*, 19: 239-246.

Langley P. A. and Hall M. J. R. (1986). Tsetse control by autosterilization. *Parasitology Today*, 2: 125-126.

Langley P. A. and Weidhass D. (1986). Trapping as a means of controlling tsetse, ***Glossina*** spp. (Diptera: Glosinidae): the relative merits of killing and of sterilization. *Bull. ent. Res.*, 76: 89-95.

Langridge W. P. (1960). Scent attractants for tsetse. *In International Scientific Council for Trypanosomiasis Research and Control, Eighth Meeting, Jos, Nigeria, pp.* 235-241.

Langridge W. P. (1975). Design and operation of the 'Langridge' tsetse fly trap. *In the International Scientific Council for Trypanosomiasis Research and Control, Fourteenth Meeting, Dakar, Senegal, pp.* 277-281.

Langridge W. P. and Mgutu S. P. (1971). A training manual for tsetse field officers. WHO/UNDP/SF Project operational research on human and animal trypanosomiasis in Nyanza and Western Provinces of Kenya-Tsetse entomology and related subjects, Sindo, Kenya.

Laveissiere C. (1987). Trapping committed to rural communities for the control of sleeping sickness. In Cavalloro R. (ed.) pp. 67-70. Intergrated tsetse fly control methods and strategies. Proceedings of the CEC International Symposium, Ispra, 4-6 March 1986. Rotterdam, Netherlands and Brookfield, USA, A. A. Bakema, 203 pp.

Laveissiere C. (1989). Sleeping sickness: peasants in charge of vector control. *In International Scientific Council for Trypanosomiasis Research and Control, Twentieth Meeting, Mombasa, Kenya.*

Laveissiere C. and Couret D. (1981). Essai de lutte contre les glossines riveraines a l'aide d'ecrans impregnes d'insecticide. *Cah. O.R.S.T.O.M. ser. Ent. med. Parasitol.*, 19: 271-283.

Laveisseire C. and Couret D. (1983a) Dieldrine et ecrans pour la lutte contre les glossines riveraines. *Cah. O.R.S.T.O.M., ser. Ent. med. Parasitol.*, 21: 57-62.

Laveissiere C. and Couret D. (1983b). Consequences d'essais de lutte repetes sur les proportions des especes de glossines riveraines. *Cah. O.R.S.T.O.M. ser. Ent. med. Parasitol.*, 21: 63-67.

Laveissiere C., Couret D. and Eouzan J-L. (1986). La campagne pilote de lutte contre la trypanosomiase humaine dans le foyer de Vavoua (Cote d'Ivoire) 3. Resultats des evaluations entomoloques. *Cah. O.R.S.T.O.M., ser. Ent. med. Parasitol.*, 24: 7-20.

Laveisseire C., Couret D. and Grebaut P. (1987). Recherche sur les ecrans pour la lutte contre les glossines en region forestiere de Cote d'Ivoire. Misc au point d'un nouvel ecran. *Cah. O.R.S.T.O.M. ser. Ent. med. Parasitol.*, 25: 145-164.

Laveissiere C., Hervout J-P, Meouze F. and Cattand P. (1986). La campagne pilote de lutte contre la trypanosomiase humaine dans le foyer de Vavoua (Cote d'Ivoire) 4. Bilan de la campagne: les prospections medicales et la participation de la population. *Cah. O.S.R.T.O.M., ser Ent. med. Parasitol.*, 24: 111-120.

Lewillon R. (1945). Le piegeage experimental de *Glossina palpalis* a la Mission Medi.ale du Kwango. *Recl. Trans. Sci.med. Congo belge*, **4**: 45-57.

Lloyd LL. and Johnson W. B. (1921). The trypanosome infections of tsetse flies in Northern Nigeria and a new method of estimation. *Bull. ent. Res.*, **14**: 265-288.

Lloyd LL., Johnson W. B., Young W. A. and Morrison H. (1924). Second report of the tsetse-fly investigation in the northern provinces of Nigeria. *Bull. ent. Res.*, **15**: 1-27.

Lloyd C. W. (1933). Traps for tsetse flies of the "crinoline" and "ventilator" forms. *Bull. ent. Res.*, **24**: 315-317.

Lloyd H. M. (1935). Notes on the bionomics of *Glossina swynnertoni* Austen. *Bull. ent. Res.*, **26**: 439-468.

Machado A de B. (1954). Revision systematique des glosines du groupe *palpalis* (Diptera). *Publ. Cult. Co. Diamantes de Angola* **22**: 1-189.

Machado A de B. (1959). Nouvelles contributions a l'etude systematics et biogeographique des glossines (Diptera). *Publ. Cult. Co. Diamantes de Angola* 46: 15-90.

Mackichan I. W. (1944). Rhodesian sleeping sickness in Eastern Uganda. *Trans. roy. Soc. trop. Med. Hyg.*, 38: 49-60.

Madubunyi L. C. (1975). A technique for detecting abortions in wild populations of ***Glossina*** species. *In Sterility Principles for Insect Control or Eradication. IAEA/FAO, Innsbruck 22-26 July 1974*, pp. 477-485, Vienna (SRI/PUB/377).

Madubunyi L. C. (1986). Aspects of the ecology and epizootiological/epidemiological importance of ***Glossina*** species inhabiting a peridomestic agroecosystem in the Nsukka area, Anambra State, Nigeria. *Insect Sci. Applic.*, 7: 515-520.

Maina A. (1977). The need for joint tsetse control programmes across national borders. *In the Internatonal Scientific Council for Trypanosomiasis Research and Control. Fifteenth Meeting, Banjul, Gambia*, pp. 581-584.

Maina A. (1979). Review of the present situation regarding human and animal trypanosomiasis in Kenya. *In the International Scientific Council for Trypanosomiasis Research and Control. Sixteenth Meeting, Yaounde, Cameroun, pp.* 193-195.

Maldonado B. (1910). (English abstract of Portuguese texts of 1906 and 1909), *Sleeping Sickness Bureau Bull.*, 2: 26

Matovu F. S. (1982). Rhodesian sleeping sickness in south-eastern Uganda: the present problems. *E. Afric. Med. J.*, **59**: 390-393.

Maudlin I. (1982). Inheritance of susceptibility to ***Trypanosoma congolense*** infection in ***Glossina morsitans***. *Ann. trop. Med. Parasit.*, **76**: 225-227.

Maudlin I. (1985). Inheritance of susceptibility to trypanosomes in tsetse flies. *Parasitology Today*, 1: 59-60.

Maudlin I. and Ellis D. S. (1985). Association between intracellular rickettsial-like infections of midgut cells and susceptibility to trypanosome infection in ***Glossina*** spp. *Z. Parasitenk.*, **71**: 683-687.

Maudlin I and Welburn S. C. (1987). Lectin mediated establishment of midgut infections of *Trypanosoma congolense* infections and *Trypanosoma brucei* in *Glossina morsitans*. *Trop. Med. Parasit.*, 38: 167-170.

Maudlin I and Welburn S. C. (1988). Tsetse immunity and the transmission of trypanosomiasis. *Parasitology Today*, 4: 109-111.

Mbulamberi D. B. (1989). Recent epidemic of human trypanosomiasis in Uganda. International study Workshop on tsetse population and behaviour held at the International Centre of Insect Physiology and Ecology, Nairobi, Kenyam, from 6-11 August 1989.

McConnell R. E. (1912). Notes on the occurence and habits of *Glossina fuscipes* in Uganda. *Bull. ent. Res.*, 3: 55-59.

Merot P. (1989). Olfactory attractants of riverine tsetse. International Study Workshop on tsetse population and behaviour held at the International Centre of Insect Physiology and Ecology, Nairobi, Kenya, from 6-11 August 1989.

Merot P., Galey J. B., Politzar H., Filledier J. and Mitteault A. (1986). Pouvoir attractif de l'odeur des hotes nourriciers pour ***Glossina tachinoides*** en zone soudano-guineenne (Burkina Faso). *Rev. d'elev. Med. vet. Pays trop.*, 39: 345-350.

Mews A. R., Offeri E., Baumgarter H., and Luger D. (1972). Techniques used at the IAEA laboratory for rearing the tsetse fly, ***Glossina moristans*** Westwood. *In Internatinal Scientific Council for Trypanosome Research and Control, Thirteenieth Meeting, Lagos, Nigeria, pp.* 243-254.

Mews A. R., Langley P. A., Pimley R. W. and Flood M. E. T. (1977). Large-scale rearing of tsetse flies (***Glossina*** spp.) in the absence of a living host. *Bull. ent. Res.*, 67: 119-128.

Moloo S. K. (1973). A new trap for ***Glossina pallidipes*** Aust. and ***G. fuscipes*** Newst. (Diptera. Glossinidae). *Bull. ent. Res.*, 63: 231-236.

Moloo S. K. (1980). Interacting factors in the epidemiology of trypanosomiasis in an endemic/enzootic region of Uganda and its contigous area of Kenya. *Insect Sci. Applic.*, 1: 117-121.

Moloo S. K. and Kutuza S. B. (1988). Comparative study on the infection rates of different laboratory strains of ***Glossina*** species by ***Trypanosoma congolense***. *Med. Vet. Entomol.*, 2: 253-257.

Moloo S. K., Kutuza S. B. and Desai J. (1988). Infection rates in sterile males of ***morsitans, palpalis*** and ***fusca*** groups ***Glossina*** for pathogenic ***Trypanosoma*** species from East and West Africa. *Acta trop.*, **45**: 145-152.

Moloo S. K., Steiger R. F. and Brun R. (1973). Trypanosome infection rates in ***Glossina swynnertoni*** and ***G. pallidipes*** in Ikoma, Musoma District, Tanzania. *Parasitology*, 66: 257-267.

Moloo S. K., Kutuza S. B., Bakakimpa I., Kamunya G. W., Desai J. and Pereira H. (1985). Colonisation of ***Glossina*** species and studies on some aspects of their vector role. *In the Internatinal Council for Trypanosomiasis Research and Control. Eighteenth Meeting, Harare, Zimbabwe, pp.* 314-321.

Molyneux D. H. (1977). Vector relationships in the Trypanosomatidae. *Adv. Parasit.*, **15**: 1-82.

Molyneux D. H. (1980). Host-trypanosome interactions in ***Glossina***. *Insect Sci. Applic.*, 1: 39-46.

Morris K. R. S. (1960). Trapping as a means of studying the game tsetse, *Glossina pallidipes*. *Bull. ent. Res.*, **51**: 533-557.

Morris K. R. S. and Morris M. G. (1949). The use of traps against tsetse in West Africa. *Bull. ent. Res.*, **39**: 491-528.

Mwangelwa M. I., Otieno L. H. and Reid G. D. F. (1987). Some barriers to *Trypanosoma congolense* development in *Glossina morsitans morsitans*. *Insect Sci. Applic.*, 8: 33-37.

Nash T. A. M. (1937). Climate, the vital factors in the ecology of *Glossina*. *Bull. ent Res.*, **28**: 75-127.

Nash T. A. M. and Jordan A. M. (1970). Methods for rearing and maintaining *Glossina* in the laboratory. In Mulligan H. W. (ed.). *The African trypanosomiases*. Allen and Unwin, pp. 441-455.

Nash T. A. M., Jordan A. M. and Boyle J. A. (1966). A promising method for rearing *Glossina austen* (Newst.) on a small scale, based on the use of rabbits' ears for feeding. *Trans. R. Soc. trop. Med. Hyg.*, **60**: 183-188.

Nash T. A. M., Jordan A. M. and Boyle J. A. (1968). The large-scale rearing of ***Glossina austeni*** Newst. in the laboratory IV. The final technique. *Ann. Trop. Med. Parasit.*, **62**: 336-341.

National Atlas of Kenya (1970), Third Edition, Kenya Government, 103 pp.

Newstead R. (1911). A revision of the tsetse flies (***Glossina***) based on a study of the male genitalia. *Bull. ent. Res.*, **2**: 9-36.

Newstead R., Evans A. M. and Potts W. H. (1924). Guide to the study of tsetse flies. *Mem. Lpool Sch. trop. Med.* (new series) no. 1, 332 pp.

OAU/STRC (1980). Tsetse and trypanosomiasis control: a strategy for the future in Africa. Based on the deliberations of an International Task Force under the auspices of IBAR and sponsred by USAID 51 pp.

Ochieng R. S., Otieno L. H. and Banda H. K. (1987). Performance of the tsetse fly ***Glossina pallidipes*** reared under simple laboratory conditions. *Entomol. exp. appl.*, **45**: 265-270.

Okiwelu S. N. (1982). Diurnal and seasonal flight activity cycles of ***Glossina palpalis gambiensis*** Vanderplank and ***Glossina morsitans submorsitans*** Newstead in Mali. *Cah. O.R.S.T.O.M. ser. Ent. med. Parasitol.*, **20**: 99-107.

Okoth J. O. (1980). Observations on the composition of ***Glossina*** population at Lugala, South Busoga District, Uganda. *E. Afric. Med. J.*, **57**: 332-335.

Okoth J. O. (1982). Further observations on the composition of ***Glossina*** populations at Lugala, South Busoga, Uganda. *E. Afric. Med. J.*, **59**: 582-584.

Okoth J. O. (1985). The resting and breeding sites of ***Glossina fuscipes fuscipes*** (Newstead) in relation to ***Lantana camara*** thickets and coffee and banana plantations. *E. Afric. Med. J.*, **62**: 686-688.

Okoth J. O. (1986a). Peridomestic breeding sites of ***Glossina fuscipes fuscipes*** Newst. in Uganda, and epidemiological implications for trypanosomiasis. *Acta trop.*, **43**: 283-286.

Okoth J. O. (1986b). Community participation in tsetse control. *Parasitology Today*, **2**: 88.

Okoth J. O. and Kapaata R. (1987). A study of the resting sites of ***Glossina fuscipes fuscipes*** (Newstead) in relation to ***Lantana camara*** thickets and coffee and banana plantations in a sleeping sickness epidemic focus, Busoga, Uganda. *Insect Sci. Applic.*, 8: 57-60.

Oloo F. P. (1983). Ecology of ***Glossina fuscipes*** Newstead (Diptera: Glossinidae) along the shore of Lake Victoria. M. Sc thesis, University of Nairobi.

Onyango R. J. (1974). African human trypanosomiasis (sleeping sickness). Vogel L. C., Muller A. S., Odingo R. S., Onyango Z., and De Geus A. (ed.). *In Health and disease in Kenya*. p. 319-330. , 529 pp.

Onyango R. J., Van Hoeve K. and De Raadt P. (1966). Epidemiolgy of ***Trypanosoma rhodesiense*** sleeping sickness in Alego location, Central Nyanza, Kenya I. Evidence that cattle may act as reservoir hosts of tryapnosomes infective to man. *Trans. R. soc. Trop. Med. Hyg.*, 60: 175.

Otieno L. H., Darji N., Onyango P. and Mpanga E. (1983). Some observations on factors associated with the development of ***Trypanosoma brucei brucei*** infections in ***Glossina morsitans morsitans***. *Acta trop.*, 40: 113-120.

Owaga M. L. A. (1981). Relative efficiency of some mechanical traps used in the study of tsetse flies, ***Glossina pallidipes*** Austen. *Insect Sci. Applic.*, 1: 197-201.

Owaga M. L. A. (1984). Preliminary observations on the efficacy of olfactory attractants derived from wild hosts of tsetse. *Insect Sci. Applic.*, **5**: 87-90.

Owaga M. L. A. (1985). Observations on the efficacy of buffalo urine as a potent olfactory attractant for ***Glossina pallidipes*** Austen. *Insect Sci. Applic.*, 5: 561-566.

Owaga M. L. A., Hassanali A. and McDowell P. G. (1988). The role of 4-cresol and 3-n-propyphenol in the attraction of tsetse flies to buffalo urine. *Insect Sci. Applic.*, **9**: 95-100.

Perry J. N., Wall C. and Greenway A. R. (1980). Latin square designs in field experiments involving insect attractants. *Ecol. ent.*, **5**: 385-396.

Persoons C. J. (1966). Trapping ***Glossina pallidipes*** and ***G. palpalis fuscipes*** in scented traps. *In International Council for Trypanosomiasis Research and Control. Eleventh Meeting, Nairobi, Kenya, pp.* 127-132.

Pielou E. C. (1977). *Mathematical ecology*. John Willey, New York.

Pollock J. N. (1980) (ed.). FAO training manual for tsetse control personnel, Vol. 1-3, FAO, Rome.

Potts W. H. (1970a). Systematics and identification of ***Glossina***. In Mulligan H. W. (ed). *The African trypanosomiases*, Allen and Unwin, London, pp. 243-273.

Potts W. H. (1970b). Miscellaneous techniques used in the study of ***Glossina***. In Mulligan H. W. (ed.). *The African Trypanosomiases*, Allen and Unwin, London, pp. 424-440.

Randolph S. E., Rogers D. J. and Kuzoe F. A. S. (1984). Local variation in the population dynamics of ***Glossina palpalis palpalis*** (Robineau-Desvoidy) (Diptera: Glossinidae) I. The effect of insecticidal spray programmes. *Bull. ent. Res.*, 74: 425-438.

Roberts C. J. and Gray A. R. (1972). A comparison of ***Glossina morsitans submorsitans*** Newst. and ***G. tachinoides*** Westw. collected and maintained under similar conditions as vectors of ***Trypanosoma (Nannomonas) congolense, T. (N.) simiae*** and ***T. (Duttonella) vivax***. *Ann. trop. Med. Parasit.*, **66**: 41-53.

Rogers D. (1977). Study of a natural population of ***Glossina fuscipes fuscipes*** Newstead and a model of fly movement. *J. Anim. Ecol.*, **46**: 389-330.

Rogers D. (1979). Tsetse populations dynamics and distribution: a new analytical approach. *J. Anim. Ecol.*, **48**: 825-849.

Rogers D. J. and Randolph S. E. (1984). A review of density-dependent process in tsetse populations. *Insect Sci. Applic.*, **5**: 397-402.

Rogers D. J. and Randolph S. E. (1985). Population ecology of tsetse. *Ann. Rev. Entomol.*, **30**: 197-216.

Rogers D. J. and Randolph S. E. (1986a). Distribution and abundance of tsetse flies (***Glossina*** spp.). *J. Anim. Ecol.*, **55**: 1007-1025.

Rogers D. J. and Randolph S. E. (1986b). Detection of activity cycles of tsetse from capture-recapture data. *Ecol. Entomol.*, **11**: 95-109.

Rogers D. J., Randolph S. E. and Kuzoe F. A. S. (1984). Local variation in the population dynamics of ***Glossina palpalis palpalis*** (Robineau-Desvoidy) (Diptera: Glossinidae) I. Natural population regulation. *Bull. ent. Res.*, **74**: 403-423.

Ruttledge W. (1928). Tsetse fly (***Glossina morsitans***) in the Koalib Hills, Nuba mountains Province, Sudan. *Bull., ent. Res.*, **19**: 309-315.

Ryan L. and Molyneux D. H. (1982). Observations on and comparisons of various traps for the collection of Glossinidae and other Diptera in Africa. *Rev. Elev. Med. vet. Pays trop*, **35**: 165-172.

Ryan L., Kupper W., Croft S. L., Molyneux D. H. and Clair M. (1982). Differences in rates of acquisitions of trypanosme infections between ***Glossina*** species in the field. *Ann. Soc. belge Med. trop.*, **62**: 291-300.

Saunders D. S. (1960). The ovulation cycle in ***Glossina morsitans*** Westwood (Diptera: Muscidae) and a possible method of age determination of their ovaries. *Trans. R. ent. soc. Lond.*, 112: 221-238.

Saunders D. S. (1962). Age determination for female tsetse flies and the age composition of samples of ***G. pallidipes*** Aust., ***G. palpalis fuscipes*** Newst. and ***G. brevipalpis*** Newst. *Bull. ent. Res.*, 53: 579-595.

van Sickle J. and Phelps R. J. (1988). Age distribution and reproductive status of declining and stationary populations of ***Glossina pallidipes*** Austen (Diptera: Glossinidae) in Zimbabwe. *Bull. ent. Res.*, 78: 51-61.

Spath J. and Kupper W. (1989). Experiments on olfactory attractants for tsetse flies, ***Glossina*** spp. (Diptera: Glossinidae) in the Ivory Coast. *In International Scientific Council for Trypanosomiasis Research and Control, Twentieth Meeting, Mombasa, Kenya.*

Ssebalijja J. M. S. (1981). Observations on the ***Glossina*** populations and sleeping sickness in Busoga, eastern Uganda. *In International Scientific Council for Trypanosomiasis Research, Seventeenth Meeting, Arusha, Tanzania*, pp. 373-380.

Stephen L. E. (1986). *Trypanosomiasis a veterinary perpective*. Pergamon Press, 551 pp.

Swynnerton C. F. M. (1933). Some traps for tsetse flies. *Bull. ent. Res.*, **24**: 69-106.

Swynnerton C. F. M. (1936). The tsetse flies of East Africa: a first study of their ecology, with a view to their control. *Trans. R. Ent. Soc. Lond.*, **84**: 1-579.

Symes C. B. and Southby R. (1938). The eradication of ***Glossina palpalis*** in lake shore area by block method. Government Printer, Nairobi.

Symes C. B. and Vane R. T. (1937). The eradication of ***Glossina palpalis*** from river areas by block method. Government Printer, Nairobi.

Takken W. (1984). Studies on the biconical trap as a sampling device for tsetse (Diptera: Glossinidae) in Mozambique. *Insect Sci. Applic.*, **5**: 357-361.

Taylor A. W. (1932). The development of West African strains of ***Trypanosoma gambiense*** in ***Glossina tachinoides*** under normal laboratory conditions and at raised temperatures. *Parasitology*, **24**: 401-419.

Tenabe S. O. (1983). A study of the diurnal activity of *Glossina palpalis* R-D (Diptera, Glossinidae) in Niger State, Nigeria using the Challier and Laveissiere trap. *Nigeria J. Entomol.*, 4: 81-87.

Torr S. J. (1988). Behaviour of tsetse flies (Glossina) in host plumes in the field. *Physiol. Ent.*, 13: 467-478.

Turner D. A. (1984). A preliminary assessment of some immediate and long-term effects of aerial spraying of endosulfan on *Glossina pallidipes* (Austen) in the Lambwe Valley, Kenya. *Insect Sci. Applic.*, 5: 425-429.

Turner D. A. and Snow W. F. (1984). Reproductive abnormality and loss in natural populations of *Glossina pallidipes* Austen (Diptera: Glossinidae) in Kenya. *Bull. ent. Res.*, **70**: 563-570.

Turner D. A. and Golder T. K. (1986). Susceptibilty to topical applications of endosulfan and dieldrin in sprayed and unsprayed populations of *Glossina pallidipes* Austen (Diptera: Glossinidae) in Kenya. *Bull. ent. Res.*, 76: 519-527.

Vale G. A. (1974a). New field methods for studying the responses of tsetse flies (Diptera, Glossinidae) to hosts. *Bull. ent. Res.*, 64: 199-208.

Vale G. A. (1974b). The responses of tsetse flies (Diptera, Glossinidae) to mobile and stationary baits. *Bull. ent. Res.*, 64: 545-588.

Vale G. A. (1977). The flight of tsetse flies (Diptera: Glossinidae) to and from a stationary ox. *Bull. ent. Res.*, 67: 297-303.

Vale G. A. (1978). Changes in our understanding of the behaviour and distribution of tsetse flies. *Rhod. Sci. News*, 12: 144-146.

Vale G. A. (1979). Field responses of tsetse flies (Diptera: Glossinidae) to odours of men, lactic acid and carbon dioxide. *Bull. ent. Res.*, 69: 459-467.

Vale G. A. (1980). Field studies of the responses of tsetse flies (Glossinidae) and other Diptera to carbon dioxide, acetone and other chemicals. *Bull. ent. Res.*, 70: 563-570.

Vale G. A. (1982a). The trap-orientated behaviour of tsetse flies (Glossinidae) and other Diptera. *Bull. ent. Res.*, 72: 71-93.

Vale G. A. (1982b). The improvement of traps for tsetse flies (Diptera: Glossinidae). *Bull. ent. Res.*, 72: 95-106.

Vale G. A. (1983). The effect of odour baits, wind direction and speed on the distribution of ***Glossina*** (Diptera: Glossinidae) and other insects near stationary targets. *Bull. ent. Res.*, 73: 53-64.

Vale G. A and Hall D. R. (1985a). The role of 1-octen-3-ol, acetone and carbon dioxide in the attraction of tsetse flies, ***Glossina*** spp. (Diptera: Glossinidae), to ox odour. *Bull. ent Res.*, 75: 209-217.

Vale G. A. and Hall D. R. (1985b). The use of 1-octen-3-ol, acetone and carbon dioxide to improve baits for tsetse flies, ***Glossina*** spp. (Diptera: Glossinidae). *Bull. ent. Res.*, 75: 219-231.

Vale G. A. and Hargrove J. W. (1979). A method of studying the efficiency of traps for tsetse flies (Diptera: Glossinidae) and other insects. *Bull ent Res.*, 69: 183-193.

Vale G. A., Bursell E. and Hargrove J. W. (1985). Catching out the tsetse fly. *Parasitology Today*, 1: 106-110.

Vale G. A., Hall D. R. and Gough A. J. E. (1988). The olfactory responses of tsetse flies, ***Glossina*** spp. (Diptera: Glossinidae) to phenols and urine in the field. *Bull. ent. Res.* **78**: 293-300.

Vale G. A., Hargrowe J. W., Cockbill G. F., and Phelps R. J. (1986). Field trials of baits to control populations of ***Glossina morsitans morsitans*** Westwood and ***G. pallidipes*** Austen (Diptera: Glossinidae). *Bull. ent. Res.*, 76: 179-193.

van Hoof L. M. J. J., Henrard C. and Peel E. (1937). Influences modificarrices de la transmissibite cyclique du ***Trypanosoma gambiense*** par ***Glossina palpalis***. *Ann. Soc. belge Med. trop.*, 17: 249-263.

van Vegten J. A. (1971a). Experimental comparison of ***Glossina fuscipes fuscipes*** and ***G. pallidipes*** as vectors of ***Trypanosoma brucei***. *In the International Scientific Council for Trypanosomiasis Research and Control.* Thirteenth *Meeting, Lagos, Nigeria, pp.* 115-116.

van Vegten J. A. (1971b). Choice of food of ***Glossina fuscipes fuscipes*** living in thickets away from open water in south eastern Uganda. *In the International Scientific Council for Trypnosomiasis Research and Control. Thirteenth Meeting, Lagos, Nigeria, Publ. no.* 105.

Vloedt A. M. V. van der, Luger D., Kabayo J. P. and Offori E. D. (1987). Tsetse research and development at Seibersdorf: a review. In Cavalloro R. (ed.). *Intergrated tsetse fly control: methods and strategies. (Proceedings of the CEC International Symposium, Ispra, 4-6 March 1986, Rotterdam, Netherlands and Brookfield, USA, 203 pp.*

Ward R. A. (1968). The susceptibility of ***Glossina austeni*** to infection with ***Trypanosoma brucei***. *Trans. R. Soc. trop. Med. Hyg.*, **62**: 672-678.

Warnes M. L. (1989). Responses of ***Glossina morsitans morsitans*** and ***G. pallidipes*** to ox sebum. *In International Scientific Council for Trypanosomiasis Research and Control, Twentieth Meeting, Mombasa, Kenya.*

Weitz B. (1956). Identification of blood meals of blood sucking arthropods. *Bull. Wld. Hlth. Org.*, **15**: 473-490.

Weitz B. G. F. (1970). Hosts of ***Glossina***. In Mulligan H. W. (ed.). *The African trypanosomiases*, pp. 317-326, Allen and Unwin, 950 pp.

Welburn S. C., Maudlin I. and Ellis D. S. (1989). Rate of trypanosome killing by lectins in midguts of different species and strains of *Glossina*. *Med. Vet. Entomol.*, 3: 77-82.

Wetzel H. (1977). Mass production using in vitro feeding. In Laird M. (ed.). *Tsetse: the future for biological methods in integrated control. pp. 141-148, IDRC. Ottawa.*

WHO. (1987). Tropical Disease Research: A global partnership. Eigth programme report of the UNDP/World Bank/WHO Special programme for research and training in tropical diseases (TDR). Rome, 191 pp.

Wijers D. J. B. (1958). Factors that may influence the infection raete of *Glossina palpalis* with ***Trypanosoma gambiense*** I. The age of the fly at the time of the infected feed. *Ann. trop. Med. Parasit.*, 52: 385-390.

Wijers D. J. B. (1974a). The complex epidemilogy of Rhodesian sleeping sickness in Kenya and Uganda I. The absence of the disease on Mfangano island (Kenya). *Trop. geogr. Med.*, **26**: 58-64.

Wijers D. J. B. (1974b). The complex epidemiology of Rhodesian sleeping sickness in Kenya and Uganda III. The epidemiolgy in the endemic areas along the lake shore between the Nile and the Yala swamp. *Trop. geogr. Med.*, **26**: 307-318.

Wijers D. J. B. (1974c). The complex epidemilogy of Rhodesian sleeping sickness in Kenya and Uganda IV. Alego and other *f*[illegible]*scipes* areas north of the endemic belt. *Trop. geogr. Med.*, **26**: 341-351

Willett K. C. (1965). Some observations on the recent epidemiology of sleeping sleeping sickness in Nyanza region, Kenya, and its relation to the general epidemiology of Gambian and Rhodesian sleeping sickness in Africa. *Trans. roy. Soc. trop. Med. Hyg.*, **59**: 374-386.

Willett K. C. (1966). Development of the peritrophic membrane in ***Glossina*** (tsetse flies) and its relation to infection with trypanosomes. *Expl. Parasit.*, **18**: 290-295.

Wilson S. G. (1953). The control of ***Glossina palpalis fuscipes*** (Newst.) in Kenya colony. *Bull. ent. Res.*, **44**: 711-728.

Wilson S. G., Morris K. R. S., Lewis I. J. and Krog E. (1963). The effect of trypanosomiasis on rural economy with special reference to the Sudan, Bechuanaland and West Africa. *Bull. Wld. Hlth. Org.*, **28**: 595-613.

## ACKNOWLEDGEMENTS

This work could not have been completed without the supervision of Drs. R. D. Dransfield, L. H. Otieno and K. J. Mbata and the assistance rendered by many people in various ways. I am greatly indebted to my supervisors for their support, suggestions, criticism and advice. Dr. L. H. Otieno suggested the research topic to me and made arrangements that enabled me to work and use the facilities of the Tsetse Research Programme at the ICIPE Mbita Point Field Station. Dr. R. D. Dransfield actually introduced me to the field of Tsetse Ecology and to the various methods of statistical analysis. Dr. K. J. Mbata provided immeasurable support and suggestions in conducting the research work. He suggested the format adopted in writing this thesis. I am indeed very grateful to all of them.

Several scientists assisted me in various ways. Prof. J. O. Kokwaro of the Botany Department, University of Nairobi, kindly identified all the plant specimens mentioned in the text. Drs. J. Lancien of the Department of Tsetse Control (Uganda), C. Laveissiere of IPR (Cote d'Ivoire) and Mr. R. Brightwell of ICIPE (Kenya) provided me with their designs of tsetse traps which were used in this work. Dr. D. R. Hall of ODNRI (UK) generously supplied the phenolic fractions that were tested for ***G. f. fuscipes*** in this study.

I am very grateful to the following people who willingly assisted me with the laborious tasks in the field and the Tsetse Insectary at Mbita Point Field Station: Messers S. Amayo, B. Ochieng, J. Ogosa, S. O. Maramba, J. O. Opere, J. K. Gitegi, H. K. Banda and the late B. Ogal. The Technical staff of the Tsetse Research Programme: Messers P. O. Agutu, E. Mpanga, J. Likhanga and J. Muchiri were very helpful in many ways.

In preparing the manuscripts I benefited from the lessons on the use of Microsoft Word given to me by Messers O. Okelo, J. O. Omwa and J. Ngoya. Drs. H. F. Magarit, R. D. Dransfield, B. G. Williams and D. Munyinyi assisted me greatly in statistical analysis and the running of several statistical programmes using IBM personal computers. I particulary wish to thank Dr. B. G. Williams for modifying the random diffusion equation and its application for this study to estimate the dispersal of ***G. f. fuscipes*** on Rusinga island. I am thankful to Mr. N. M. Komeri who prepared the maps and graphs presented in this thesis and to Dr. J. Zdarek (currently Visiting Scientist at ICIPE) who read through the manuscripts.

I am grateful to the ARPPIS Academic Coordinators, Dr. M. E. Smalley and his successor, Prof. Z. T. Dabrowski, for all the arrangements that made the research work easier. I also wish to thank my internal and external examiners whose

comments contributed very much to the improvemt of this thesis.

This work could not have been carried out without the research facilities provided by the Director of ICIPE, Prof. T. R. Odhiambo and the study leave granted to me by the Director of Tropical Diseases Research Centre (TDRC), Ndola Zambia, Dr. M. Mukunyandela. Finally, I wish to thank the Ford Foundation for granting me the scholarship that enabled me carry out this work under the ARPPIS Programme at ICIPE, Nairobi, Kenya.

# LIST OF ABBREVATIONS

| | |
|---|---|
| FAO | Food and Agricultural Organization of the United Nations |
| h | hour |
| ICIPE | International Centre of Insect Physiology and Ecology |
| ILRAD | International Laboratory for Research on Animal Diseases |
| IPR | Institut Pierre Richet |
| km | kilometre |
| m | metre |
| ml | millitre |
| mg | milligram |
| OAU | Organisation of African Unity |
| °C | Degrees Centrigrade (or Celsius) |
| ODNRI | Overseas Development Natural Resources Institute |
| RLOs | Rickettisia-like Organisms |
| STRC | Scientific, Technical and Research Commission |
| TDRC | Tropical Diseases Research Centre |
| WHO | World Health Organisation |
| µm | micrometre |

# APPENDIX I

Table 1.1. Catches of *G. f. fuscipes* in a survey carried out on Rusinga island. T=Teneral, N/T=Non-teneral.

| | Males | | | Females | | |
|---|---|---|---|---|---|---|
| Trap No. | T | N/T | % T | T | N/T | % T |
| 1 | 0 | 2 | 0 | 0 | 0 | 0 |
| 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| 3 | 0 | 1 | 0 | 0 | 0 | 0 |
| 4 | 0 | 0 | 0 | 0 | 0 | 0 |
| 5 | 0 | 0 | 0 | 0 | 0 | 0 |
| 6 | 0 | 0 | 0 | 0 | 0 | 0 |
| 7 | 0 | 2 | 0 | 1 | 6 | 16.7 |
| 8 | 0 | 0 | 0 | 0 | 1 | 0 |
| 9 | 0 | 0 | 0 | 0 | 0 | 0 |
| 10 | 0 | 3 | 0 | 0 | 4 | 0 |
| 11 | 0 | 0 | 0 | 0 | 0 | 0 |
| 12 | 0 | 0 | 0 | 0 | 0 | 0 |
| 13 | 0 | 0 | 0 | 0 | 0 | 0 |
| 14 | 0 | 0 | 0 | 0 | 1 | 0 |
| 15 | 0 | 0 | 0 | 0 | 1 | 0 |
| 16 | 0 | 0 | 0 | 0 | 0 | 0 |
| 17 | 0 | 0 | 0 | 0 | 0 | 0 |
| 18 | 1 | 26 | 3.7 | 4 | 51 | 7.2 |
| 19 | 1 | 15 | 6.3 | 1 | 26 | 3.7 |
| 20 | 0 | 0 | 0 | 0 | 0 | 0 |
| 21 | 0 | 0 | 0 | 0 | 0 | 0 |
| 22 | 0 | 0 | 0 | 0 | 0 | 0 |
| 23 | 1 | 13 | 7.1 | 2 | 86 | 2.3 |
| 24 | 11 | 118 | 9.3 | 13 | 65 | 16.7 |
| 25 | 8 | 111 | 7.2 | 16 | 307 | 5.0 |
| 26 | 8 | 72 | 10.0 | 11 | 307 | 3.5 |
| 27 | 11 | 88 | 11.1 | 7 | 239 | 2.8 |
| 28 | 6 | 56 | 10.7 | 12 | 95 | 12.6 |
| 29 | 0 | 0 | 0 | 0 | 0 | 0 |
| 30 | 1 | 43 | 2.3 | 1 | 44 | 2.2 |
| 31 | 0 | 19 | 0 | 2 | 83 | 2.4 |
| 32 | 0 | 0 | 0 | 0 | 0 | 0 |
| 33 | 0 | 0 | 0 | 0 | 0 | 0 |
| 34 | 0 | 3 | 0 | 5 | 11 | 45.5 |
| 35 | 7 | 42 | 13.0 | 5 | 15 | 33.3 |
| 36 | 0 | 0 | 0 | 0 | 0 | 0 |
| 37 | 7 | 28 | 20.0 | 12 | 63 | 19.0 |
| 38 | 0 | 4 | 0 | 3 | 9 | 33.3 |
| 39 | 0 | 1 | 0 | 0 | 1 | 0 |
| 40 | 0 | 1 | 0 | 0 | 0 | 0 |
| 41 | 0 | 27 | 0 | 1 | 8 | 11.1 |

Table 1.1 continued.

| Trap No. | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | T | N/T | % T | T | N/T | % T |
| 42 | 0 | 0 | 0 | 0 | 0 | 0 |
| 43 | 0 | 5 | 0 | 0 | 2 | 0 |
| 44 | 0 | 2 | 0 | 1 | 1 | 50 |
| 45 | 0 | 0 | 0 | 0 | 0 | 0 |
| 46 | 0 | 1 | 0 | 0 | 1 | 0 |

Table 1.2. Catches of *G. f. fuscipes* in a survey carried out on the mainland. T=Teneral, T/N=Non-teneral.

| Trap No. | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | T | N/T | % T | T | N/T | % T |
| 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| 3 | 0 | 0 | 0 | 0 | 0 | 0 |
| 4 | 0 | 0 | 0 | 0 | 0 | 0 |
| 5 | 0 | 4 | 0 | 0 | 8 | 0 |
| 6 | 0 | 7 | 0 | 0 | 4 | 0 |
| 7 | 12 | 99 | 12.1 | 9 | 119 | 3.9 |
| 8 | 4 | 161 | 2.5 | 7 | 345 | 2.0 |
| 9 | 2 | 26 | 7.7 | 3 | 47 | 6.4 |
| 10 | 0 | 0 | 0 | 0 | 0 | 0 |

# APPENDIX II

Table 2.1 Estimation of mean wing fray age for male *G. f. fuscipes* on Rusinga Island and the mainland caught in traps from February 1988 to June 1989.

| Locality | Wing fray | | | | | |
|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 |
| | | | Rusinga Island | | | |
| Total | 93 | 131 | 103 | 71 | 50 | 47 |
| Factor | 1.0 | 2.0 | 3.0 | 4.4 | 5.5 | 6.9 |
| Product | 93.0 | 262.0 | 309.0 | 312.4 | 275.0 | 324.3 |
| Product/Flies = 1575.7/495 = 3.2 = 24 days | | | | | | |
| | | | Mainland | | | |
| Total | 88 | 142 | 92 | 44 | 34 | 22 |
| Factor | 1.0 | 2.0 | 3.0 | 4.4 | 5.5 | 6.9 |
| Product | 88.0 | 284.0 | 276.0 | 193.6 | 187.0 | 151.8 |
| Product/Flies = 1180.4/422 = 2.8 = 21 days | | | | | | |

Table 2.2 Mortality rates of *G. f. fuscipes* read from Moran plots.

| Month | Mortality rates | | | |
|---|---|---|---|---|
| | Rusinga Island | | Mainland | |
| | Males | Females | Males | Females |
| March 1988 | 0.5 | 0.6 | 0.6 | 0.7 |
| May | 0 | ? | 0.1 | 0.3 |
| June | 0.5 | 0.7 | 0.8 | 0.8 |
| July | ? | 0.4 | ? | ? |
| August | 0.5 | 0.2 | 0.2 | 0.4 |
| September | 0.6 | 0.4 | 0.5 | 0.9 |
| October | 0.1 | 0 | 0.5 | 0 |
| November | 0.3 | 0.4 | ? | 0.1 |
| December | 0.3 | 0.4 | 0.6 | 0.5 |
| January 1989 | 0.3 | 0 | 0.1 | ? |
| February | 0.3 | 0.3 | 0.5 | 0.7 |
| March | 0.6 | 0.5 | 0.1 | 0.3 |
| April | 0.3 | 0.4 | 0.6 | 0.3 |
| May | 0 | 0.1 | 0.1 | 0.1 |
| June | 0.2 | 0.4 | 0.1 | 0.1 |

?=Mortality rate value lies outside expected tsetse reproductive rate (see text).

Table 2.3. Mark-release-recapture Experiment I for *G. f. fuscipes* carried out on Rusinga island from 22 June to 2 July 1988.

| | Marking days, n | No. marked (day 0) | | Recapture days 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 185 | Recapture | 6 | 10 | 9 | 5 | 5 | 5 | 3 | 4 | 4 | 5 |
| | | | Total | 170 | 146 | 197 | 229 | 149 | 128 | 85 | 135 | 127 | 132 |
| Males | 2 | 170 | Recapture | 3 | 7 | 12 | 6 | 1 | 4 | 4 | 2 | 3 | |
| | | | Total | 146 | 197 | 229 | 149 | 128 | 85 | 135 | 127 | 132 | |
| | 3 | 146 | Recapture | 1 | 12 | 4 | 10 | 3 | 6 | 4 | 2 | | |
| | | | Total | 197 | 229 | 149 | 128 | 85 | 135 | 127 | 132 | | |
| | | | Crr | 1.243 | 3.223 | 2.723 | 3.865 | 1.559 | 2.618 | 1.676 | 1.224 | 1.647 | 2.397 |
| | 1 | 182 | Recapture | 14 | 6 | 8 | 12 | 3 | 7 | 1 | 7 | 6 | 2 |
| | | | Total | 218 | 126 | 301 | 343 | 278 | 235 | 159 | 259 | 246 | 182 |
| Females | 2 | 218 | Recapture | 5 | 3 | 14 | 7 | 8 | 3 | 7 | 7 | 5 | |
| | | | Total | 126 | 301 | 343 | 278 | 235 | 159 | 259 | 246 | 182 | |
| | 3 | 126 | Recapture | 5 | 10 | 11 | 9 | 4 | 10 | 6 | 9 | | |
| | | | Total | 301 | 343 | 278 | 235 | 159 | 259 | 246 | 182 | | |
| | | | Crr | 2.284 | 1.442 | 2.005 | 2.229 | 1.231 | 1.817 | 1.203 | 1.859 | 1.303 | 0.604 |

Table 2.4. Mark-release-recapture Experiment II for *G. f. fuscipes* carried out on Rusinga island from 8 November to 12 December 1988.

| | Marking days, n | No. marked (day 0) | | Recapture days 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Males | 1 | 192 | Recaputure | 11 | 26 | 5 | 0 | 0 | 0 | 1 | 1 | 1 | 3 | 0 | 0 | 0 | 1 |
| | | | Total | 126 | 391 | 93 | 251 | 177 | 211 | 203 | 208 | 210 | 167 | 106 | 166 | 132 | 125 |
| | 2 | 126 | Recapture | 15 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | [illegible] | 0 | 0 | 1 | - |
| | | | Total | 391 | 93 | 251 | 177 | 211 | 203 | 208 | 210 | 167 | 106 | 166 | 132 | 125 | - |
| | 3 | 391 | Recapture | 14 | 1 | 2 | 2 | 1 | 1 | 2 | 3 | 3 | 3 | 0 | 2 | - | 3 |
| | | | Total | 93 | 251 | 177 | 211 | 203 | 208 | 210 | 167 | 106 | 166 | 132 | 125 | - | 225 |
| | 4 | 93 | Recapture | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | - | 0 | 1 |
| | | | Total | 251 | 177 | 211 | 203 | 208 | 210 | 167 | 106 | 166 | 132 | 125 | - | 225 | 213 |
| | | | CRR | 3.079 | 1.440 | 0.506 | 0.291 | 0.063 | 0.060 | 0.184 | 0.283 | 0.423 | 0.264 | 0 | 0.205 | 0.161 | 0.379 |
| Females | 1 | 369 | Recature | 29 | 31 | 7 | 5 | 3 | 1 | 1 | 2 | 4 | 1 | 1 | 2 | 2 | 1 |
| | | | Total | 298 | 559 | 171 | 257 | 210 | 324 | 247 | 257 | 287 | 158 | 94 | 128 | 103 | 107 |
| | 2 | 298 | Recapture | 12 | 8 | 1 | 0 | 2 | 2 | 3 | 2 | 2 | 1 | 3 | 3 | 2 | - |
| | | | Total | 559 | 171 | 257 | 210 | 324 | 247 | 257 | 287 | 158 | 94 | 128 | 103 | 107 | - |
| | 3 | 559 | Recapture | 37 | 13 | 5 | 2 | 2 | 7 | 3 | 4 | 4 | 2 | 1 | 1 | - | 8 |
| | | | Total | 171 | 257 | 210 | 324 | 247 | 257 | 287 | 158 | 94 | 128 | 103 | 107 | - | 249 |
| | 4 | 171 | Recapture | 6 | 1 | 0 | 1 | 3 | 0 | 0 | 1 | 1 | 0 | 0 | - | 1 | 1 |
| | | | Total | 257 | 210 | 324 | 247 | 257 | 287 | 158 | 94 | 128 | 103 | 107 | - | 249 | 267 |
| | | | CRR | 2.019 | 1.213 | 0.416 | 0.210 | 0.281 | 0.259 | 0.197 | 0.316 | 0.484 | 0.228 | 0.336 | 0.436 | 0.445 | 0.446 |

Table 2.4. Mark-release-recapture Experiment II for *G. f. fuscipes* carried out on Rusinga island from 8 November to 12 December 1988.

| | Marking days, n | No. marked (day 0) | | Recapture days 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Males | 1 | 192 | Recaputure | 11 | 26 | 5 | 0 | 0 | 0 | 1 | 1 | 1 | 3 | 0 | 0 | 0 | 1 |
| | | | Total | 126 | 391 | 93 | 251 | 177 | 211 | 203 | 208 | 210 | 167 | 106 | 166 | 132 | 125 |
| | 2 | 126 | Recapture | 15 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | [illegible] | 0 | 0 | 1 | - |
| | | | Total | 391 | 93 | 251 | 177 | 211 | 203 | 208 | 210 | 167 | 106 | 166 | 132 | 125 | - |
| | 3 | 391 | Recapture | 14 | 1 | 2 | 2 | 1 | 1 | 2 | 3 | 3 | 3 | 0 | 2 | - | 3 |
| | | | Total | 93 | 251 | 177 | 211 | 203 | 208 | 210 | 167 | 106 | 166 | 132 | 125 | - | 225 |
| | 4 | 93 | Recapture | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | - | 0 | 1 |
| | | | Total | 251 | 177 | 211 | 203 | 208 | 210 | 167 | 106 | 166 | 132 | 125 | - | 225 | 213 |
| | | | CRR | 3.079 | 1.440 | 0.506 | 0.291 | 0.063 | 0.060 | 0.184 | 0.283 | 0.423 | 0.264 | 0 | 0.205 | 0.161 | 0.379 |
| Females | 1 | 369 | Recature | 29 | 31 | 7 | 5 | 3 | 1 | 1 | 2 | 4 | 1 | 1 | 2 | 2 | 1 |
| | | | Total | 298 | 559 | 171 | 257 | 210 | 324 | 247 | 257 | 287 | 158 | 94 | 128 | 103 | 107 |
| | 2 | 298 | Recapture | 12 | 8 | 1 | 0 | 2 | 2 | 3 | 2 | 2 | 1 | 3 | 3 | 2 | - |
| | | | Total | 559 | 171 | 257 | 210 | 324 | 247 | 257 | 287 | 158 | 94 | 128 | 103 | 107 | - |
| | 3 | 559 | Recapture | 37 | 13 | 5 | 2 | 2 | 7 | 3 | 4 | 4 | 2 | 1 | 1 | - | 8 |
| | | | Total | 171 | 257 | 210 | 324 | 247 | 257 | 287 | 158 | 94 | 128 | 103 | 107 | - | 249 |
| | 4 | 171 | Recapture | 6 | 1 | 0 | 1 | 3 | 0 | 0 | 1 | 1 | 0 | 0 | - | 1 | 1 |
| | | | Total | 257 | 210 | 324 | 247 | 257 | 287 | 158 | 94 | 128 | 103 | 107 | - | 249 | 267 |
| | | | CRR | 2.019 | 1.213 | 0.416 | 0.210 | 0.281 | 0.259 | 0.197 | 0.316 | 0.484 | 0.228 | 0.336 | 0.436 | 0.445 | 0.446 |

Table 2.4 continued

| | Marking days, n | No. marked (day 0) | | Recapture days 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Males | 1 | 192 | Recapture | - | 1 | 3 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | | | Total | - | 225 | 213 | 151 | 179 | 203 | 177 | 182 | 144 | 104 | 126 | 119 | 112 |
| | 2 | 126 | Recapture | 1 | 3 | 1 | 1 | 2 | 1 | 2 | 1 | 0 | 1 | 0 | 0 | |
| | | | Total | 125 | 213 | 151 | 179 | 203 | 177 | 182 | 144 | 104 | 126 | 119 | 112 | |
| | 3 | 391 | Recapture | 3 | 2 | 4 | 1 | 1 | 1 | 2 | 2 | 4 | 3 | 0 | | |
| | | | Total | 213 | 151 | 179 | 203 | 177 | 182 | 144 | 104 | 126 | 119 | 112 | | |
| | 4 | 93 | Recapture | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | | | |
| | | | Total | 151 | 179 | 203 | 177 | 182 | 144 | 104 | 126 | 119 | 112 | | | |
| Females | 1 | 369 | Recapture | - | 3 | 7 | 2 | 2 | 0 | 1 | 1 | 2 | 1 | 1 | 1 | 1 |
| | | | Total | - | 249 | 267 | 165 | 212 | 206 | 216 | 208 | 149 | 161 | 137 | 160 | 154 |
| | 2 | 298 | Recapture | 2 | 4 | 1 | 2 | 3 | 1 | 0 | 0 | 0 | 1 | 3 | 1 | |
| | | | Total | 249 | 267 | 165 | 212 | 206 | 216 | 208 | 149 | 161 | 137 | 160 | 154 | |
| | 3 | 559 | Recapture | 6 | 2 | 2 | 7 | 2 | 1 | 2 | 3 | 0 | 0 | 5 | | |
| | | | Total | 267 | 165 | 212 | 206 | 216 | 208 | 149 | 161 | 137 | 160 | 154 | | |
| | 4 | 171 | Recapture | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | | | |
| | | | Total | 165 | 212 | 206 | 216 | 208 | 149 | 161 | 137 | 160 | 154 | | | |
| | | | CRR | 0.318 | 0.300 | 0.365 | 0.471 | 0.270 | 0.106 | 0.119 | 0.171 | 0.097 | 0.093 | 0.488 | 0.191 | 0.176 |

# APPENDIX III

Table 3.1 Amount of baits dispensed in millilitres over 12 hour periods showing means only from February 1988 to July 1989.

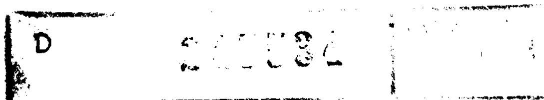
| Expt. no. | Day | Mean weight (ml/12 h) | | | | |
|---|---|---|---|---|---|---|
| | | cow urine | human urine | | | Acetone |
| 1 | 1 | 17.5 | | | | 14.5 |
| | 2 | 10.0 | | | | 10.0 |
| | 3 | 15.0 | | | | 12.0 |
| | 4 | 20.0 | | | | 18.5 |
| | x̄ | 15.8 | | | | 13.8 |
| 2 | 1 | 8.5 | | | | 7.2 |
| | 2 | 5.7 | | | | 5.3 |
| | 3 | 11.7 | | | | 7.7 |
| | 4 | 8.7 | | | | 6.4 |
| | x̄ | 8.7 | | | | 6.7 |
| 3 | 1 | | | | | 13.0 |
| | 2 | | | | | 13.0 |
| | 3 | | | | | 11.5 |
| | 4 | | | | | 18.0 |
| | x̄ | | | | | 13.9 |
| 4 | 1 | 4.0 | 5.0 | | | |
| | 2 | 12.5 | 14.5 | | | |
| | 3 | 20.3 | 23.0 | | | |
| | 4 | 22.5 | 21.7 | | | |
| | x̄ | 14.8 | 16.1 | | | |
| 5 | | | | L | M | H |
| | 1 | | | 4.0 | 10.0 | 14.0 |
| | 2 | | | 4.5 | 15.0 | 95.0 |
| | 3 | | | 7.5 | 12.0 | 165.0 |
| | 4 | | | 9.0 | 14.0 | 160.0 |
| | x̄ | | | 6.3 | 12.8 | 140.0 |

Table 3.1 continued.

L=Low dose rate of acetone.
M=Medium dose rate of acetone.
H=High dose rate of acetone.

*The acetone dose rate for Expt. 1-3 were taken over a longer period of time compared to the one shown in Expt. 5. Thus the range of the medium dose rate would be 440.5-914.4 mg/h

Weight of cow urine at 25°C=0.76 g/h.
Weight of human urine at 25°C=approx. 0.76 g/h.
Weight of acetone at 20°C=0.789-0.792 g/h.


UNIVERSITY OF ZAMBIA LIBRARY