I

TRAPPING STUDIES ON *GLOSSINA LONGIPENNIS* CORTI AT NGURUMAN, SOUTH-WESTERN KENYA.

A THESIS SUBMITTED TO THE DEPARTMENT OF ZOOLOGY, UNIVERSITY OF GHANA, IN FULFILLMENT OF THE REQUIREMENT FOR THE AWARD OF A DOCTOR OF PHILOSOPHY DEGREE.

BY

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DECLARATION

I THE UNDERSIGNED DECLARE THAT THIS THESIS IS MY OWN ORIGINAL WORK WHICH HAS NOT BEEN SUBMITTED FOR ANY DEGREE IN ANY UNIVERSITY AND ALL SOURCES OF MATERIAL HAS BEEN DULY ACHNOWLEDGED.

SIGNATURE

APPROVAL CERTIFICATE

THIS THESIS HAS BEEN APPROVED FOR SUBMISSION TO THE UNIVERSITY OF GHANA, LEGON, GHANA.

BY

MAJOR EXTERNAL SUPERVISOR

INTERNAL SUPERVISOR

DEDICATION

TO MY PARENTS, MY WIFE CHRISTY AND MY DAUGHTER ANATABA.

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ABSTRACT

Studies have been carried out at Nguruman, south-western Kenya, on *Glossina longipennis* Corti, a little known member of the fusca group of *Glossina*. The first objective was to develop an efficient trap suitable for both sampling and control purposes. Studies were then carried out on the population dynamics of *G. longipennis* using the newly developed sampling methods. Lastly the trap/odour bait system was tested in a control situation.

Replicated Latin square design experiments were used to compare the performance of various trap designs and odour attractants. The Zimbabwe F3 trap proved more effective than the widely used biconical trap, especially for females. A new trap developed at Nguruman, called the NG2B, was also very effective and had the advantage of being cheap and easy to construct. Acetone and cow urine together increased the catches by 4-5X over unbaited traps, but when dispensed alone neither of them was effective. There was no significant difference between the attractancy of cow urine and buffalo urine. Trap catches were further increased when 1-octen-3-ol was dispensed together with acetone and cow urine. A higher proportion of older flies was caught by the NG2B trap compared to the biconical but no significant difference was observed in the age structure of flies attracted by different odour baits. The effect of trap design on sample composition and the

potential for using odour baited traps for sampling the fusca group of tsetse flies are discussed.

An electric screen adjacent to a baited target was used to determine the precise activity pattern of *G. longipennis* which is known to be crepuscular in behaviour. Morning activity started at about 15 minutes before sunrise at 0630 h, peaked at about 0615 h and ceased by 0700 h. The species was more active in the evenings, when activity began at about 30 minutes before sunset at 1815 h, peaked at 1845 h and ended by 1900 h. Males were regularly active before females. Light intensity was found to be the most important factor influencing activity. The relationship between activity pattern and cattle-fly contact is discussed.

Changes in the apparent densities of *G. longipennis* were monitored simultaneously using biconical and NG2B traps in two areas located 7 km apart. Both trap types showed similar trends in population changes but higher apparent densities were recorded with the NG2B trap than with the biconical trap. Apparent densities in both sexes were regularly observed to increase during the rainy seasons and decrease during dry seasons. Peak catches in one area were observed to precede those in the other area by one month. Flies spread out to more open areas during the cool wet seasons and concentrated in the thicker woodland during the dry seasons. The factors influencing changes in population densities, including movement between the two areas and between vegetation types, are discussed.

Mortality rates estimated from ovarian age structure and from Moran curves were observed to be highest during the hot dry seasons and lower during the cool wet seasons. Adult mortality rates showed a significant positive correlation with maximum temperature and a negative correlation with minimum relative humidity. The effect of fly movement on mortality rate estimates and the reliability of the estimates by the two methods are discussed.

Dissections of female flies from NG2B traps showed that all non-teneral but nulliparous females and over 80% teneral females were inseminated. The average percentage distribution of the various pregnancy stages in trap samples were found to be very close to the values expected from the duration of the different stages, in contrast to the usual under-representation of flies with third instar larvae for other tsetse species. The average abortion rate was 6% but ranged from 0% in the rainy seasons to 60% in the hot dry season. A significant negative correlation was observed between abortion rate and minimum relative humidity. A significant positive correlation was also found between fly size and minimum relative humidity of the previous month but one. A discussion is given of the immediate causes of abortions and their effects on population levels and of the factors influencing fly size.

The absolute population size of *G. longipennis* was estimated through mark-release-recapture experiments. The mean population size was estimated at 17,300 males (range 10,471 - 25,703) and 16,900 females (range 14,125 - 20,892). The trend of changes in the absolute estimates corresponded with those in apparent estimates from trap catches. From the peaks in the recapture rate of marked flies, the feeding cycle of *G. longipennis* was found to be 2-3 days for males whilst for females the 9-10 day pregnancy cycle was the main factor affecting the recapture rate. There was a considerable amount of movement of marked flies between the two sampling areas but the movement was shown to be greater in one direction than the other.

A trial tsetse population suppression operation with baited NG2B traps was started during the course of the study. After 11 months of operation, the population levels of *G. longipennis* were reduced by about 60% for males and about 90% for females. Much greater reduction levels were obtained for *G. pallidipes*. A discussion is given of the factors influencing the lesser impact on the population of *G. longipennis* with suggestions on improving methods for the control of the species.

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CHAPTER ONE

GENERAL INTRODUCTION

Long before the importance of trypanosomiasis was realized, a stable system involving tsetse, the trypanosomes and the African game animal, had apparently been established in the African environment. It is believed that the occurrence of trypanosomes and trypanosomiases in man and his domestic animals is a more recent association. The pathological response by man and domestic animals to the trypanosome is evidence that the parasites (trypanosomes) are still maladapted to these hosts (Duggan, 1970). Some aspects of the evolution and the ecology of tsetse and trypanosomiases in the prehistoric African environment are covered by Lambrecht (1964).

Control of trypanosomiasis was initiated by the colonialists who by 1908 saw that the sheer numbers of people involved and the obvious economic implications of the disease were a serious barrier to material progress. Various scientific committees were therefore dispatched to the field and some control measures, based on apparently ad hoc reports and recommendations, were embarked upon with the aim of eradicating the disease. Thus, tsetse and trypanosomiasis control started with very little scientific knowledge of the system that was involved in the prevalence of the disease. This lack of sufficient basic knowledge is reflected in the

wide variety of control strategies that were tried. The main ones included the mass diagnosis and treatment of the disease, preventing people at risk from coming into contact with tsetse and the destruction of vegetation (tsetse habitats) and game animals (hosts). These methods were applied to varying degrees and in various combinations in different parts of Africa. The results obtained were equally varied, ranging from total failure in most places to eradication in a few. A comprehensive review of the various control strategies that were employed and their successes and failures, is given by Duggan (1970). He also pointed out that during all this time very little attention was being given to basic scientific research into a better understanding of the system involved. By 1940 when it was realized that a more complex situation of several tsetse species and parasites was involved, it was concluded that eradication was not possible and that a better scientific understanding was necessary for more effective control.

Thus, by the 1950s, more attention was being directed towards basic research but the pace was slowed with the advent of DDT and other insecticides that rekindled the hopes of vector eradication. Allsopp (1984) gives a comprehensive review of the use of insecticides in tsetse control. Although eradication or successful control was achieved in some places with insecticides, reinfestation of control areas remained a major problem.

The limitations of insecticide application were apparent by the 1970's. Apart from the fact that no permanent control was being achieved in most cases, the high cost of insecticides and environmental pollution had to be taken into account. Following this realization, the search for alternative control measures was intensified. This started with the search for methods of refining the insecticidal control technique. Considerable research was carried out on the vector behaviour and ecology to provide information for discriminative and selective application of insecticides. Efforts were also put into the search for cheaper and less toxic insecticides and more economical and effective methods of insecticide application.

The use of insecticides still remains the most widespread method of tsetse control today despite its attendant problems. Owing to a shortage of foreign exchange, many African countries cannot afford the cost of insecticides to maintan the recurrent application which is necessary in most cases. Furthermore, the most effective methods of insecticide application require the use of aircrafts which again is high technology and out of the reach of most African countries. Hence control by these techniques is largely dependent on foreign aid.

Several lines of research on control strategies alternative to the sole use of insecticide were embarked upon by various workers. These include the search for a vaccine against trypanosomes, the breeding of trypanotolerant animals,

the search for biological control agents for the vector, genetic control by the Sterile Insect Technique (SIT), physiological control and the development of effective baited traps and insecticide impregnated targets. There have been various degrees of progress in these fields of research. Jordan (1986) gives an up to date appraisal of the various approaches and their future prospects. He identifies SIT and the use of baited traps and targets as the most promising approaches to vector control.

The SIT involves the release of large numbers of laboratory-bred sterile males into a wild population to compete with the wild males and produce sterile progeny. In theory this approach is most effecient for low density populations since the number of sterile males released should be about 10 times that of the wild males. Field trials of the SIT have therefore involved the initial reduction of the target tsetse population by insecticides followed by the release of the sterile males. By this approach, successful control was claimed in Tanzania against *G. m. morsitans* (Dame *et al.*, 1980) and in Burkina Faso against *G. p. gambiensis* (Cuisance *et al.*, 1980) and *G. p. palpalis* (Politzar and Cuisance, 1982). However, the technique does not appear practicable on a large scale basis because of the high cost involved in rearing and sterilizing large numbers of male tsetse flies.

The research into developing effective odour baited traps and targets appears to be the most promising approach to

achieving long term tsetse control. Researchers in this field believe that effective control can only be achieved on a sound knowledge of the tsetse/trypanosomiasis system involved; the failure of past control attempts is attributed largely to the lack of adequate knowledge of the target systems. One vital requirement for understanding any tsetse/trypanosomiasis system is adequate knowledge of the population dynamics and behaviour of the tsetse species. This in turn requires effective sampling techniques.

For many years, most of the information gained on the distribution and ecology of tsetse was through the fly-round sampling technique. This placed limitations on the knowledge about those species that did not lend themselves to this sampling method. Therefore, research into trap development was initially aimed at producing effective sampling tools for population studies. The development of the biconical trap (Challier and Laveissière,1973) was a success in this respect. The trap has been used for studying the distribution and ecology of important vector species in many parts of Africa. Better parasitological and epidemiological data have also been obtained from the samples taken by the improved sampling technique. More recent research has concentrated on the improvement of trap efficiency for control purposes. This involves the development of more effective trap designs and the search for effective odour baits.

It is along this line that a project was undertaken at Nguruman, by a team of ICIPE scientists, with the objective of

developing new approaches to tsetse and disease control through a greater understanding of the population dynamics and disease epidemiology and more appropriate tsetse control strategies (Dransfield *et al.*, 1986a). To better achieve this, a multi-disciplinary approach was adopted to gather comprehensive information on all possible aspects of the tsetse/trypanosomiasis system in the area. Such information could then be used to build an epidemiological model on which any control strategy could be based.

The Nguruman area is in a semi-arid zone of Kenya in the Rift Valley. In a general survey on the distribution of tsetse in the Maasai reserves, Lewis (1934) reported the presence of both *Glossina pallidipes* Austen and *Glossina longipennis* Corti in the area. It is also known that animal trypanosomiasis is prevalent. The pastoral Maasai tribe depend mainly on cattle, goat and sheep for their livelihood and cattle especially are of great local economic and social importance. Therefore, the control of tsetse would be a great contribution to the needs of such a community. Research by the ICIPE team was concentrated in an area of about 100 square kilometres, occupied by one of the local Group Ranches.

The biconical trap (Challier *et al.*, 1977) was initially adopted as a sampling tool for the tsetse population. This soon yielded much information on the G. *pallidipes* population (Dransfield *et al.*, 1986a) but very little on G. *longipennis*. Through odour bait technology at Nguruman by Dransfield *et al.* (1986b), the efficiency of the biconical was greatly increased

for G. *pallidipes* but less so for G. *longipennis*. However, there were adequate numbers of flies dissected to show that G. *longipennis* was also infected with both *Trypanosoma congolense* and *T. vivax*, the parasites responsible for trypanosomiasis in the cattle. Since the ultimate aim of the Nguruman project was to control the disease it would be desirable for a more complete operation to gather information on G. *longipennis* as well.

It was against this background that the study reported here on *Glossina longipennis* Corti was undertaken at Nguruman. *Glossina longipennis* belongs to the *fusca* group of *Glossina* which include *G. fusca* Walker, *G. nigrofusca* Newstead, *G. brevipalpis* Newstead and eight others (see Chapter 2). This group of relatively large tsetse flies have been broadly described as forest dwelling species but G. *longipennis* and G. *brevipalpis* have become associated with drier climatic zones although the latter species still tends to be restricted to the most humid parts of such habitats. Like many *fusca* flies these two species have a crepuscular behaviour pattern. They are, however, known to be peculiar for feeding on large game and are limited in distribution to eastern Africa, thus forming the East African sub-group of the *fusca* flies. Here they may be found existing sympatrically or allopatrically with other species of *Glossina* including well-known vectors such as G. *pallidipes* Austen. G. *longipennis* has been recorded from all countries in East Africa especially Kenya, where it has a particularly wide distribution.

The first objective was to develop an adequate sampling technique for *G. longipennis* which would then be used for further studies on the species. The main sampling methods that have been independently developed for tsetse include the fly round technique, the use of stationary or mobile bait, trapping and the capture of resting tsetse. Trapping has however emerged as the most favoured technique owing to such advantages as the possibility of sampling populations at several places at the same time, the suppression of human factors and the use of standard materials (Challier, 1982). Several trap types have been designed and developed for different species of tsetse but owing to the general lack of attention on G. *longipennis* very few of these traps have been tested for this species (Owaga, 1981).

Trapping and odour bait technology was therefore chosen as the line along which studies should be directed in the search for a sampling tool. A successful trap if developed would then be used to study the dynamics of the resident G. *longipennis* population. Moreover, one of the objectives of the Nguruman project was to develop a technology to allow local Maasai to control rather than eradicate tsetse, probably utilizing odour baited traps or screens (Dransfield et al., 1986a). Thus if the efficiency of the developed trap could be increased to cost-effective levels through odour bait technology, it could be incorporated in such a control programme.

If tsetse control programmes are initiated in areas with both *G. pallidipes* and *G.longipennis* with a system that is more effective for *G. pallidipes* the results could be disappointing for two main reasons. First, although it is generally regarded as a minor vector possibly because of our inability to sample it, it could actually be important in disease transmission. Secondly, it is possible that *G. longipennis* could replace *G. pallidipes* as a vector if the latter species were successfully controlled. Evidence of such a possible 'take-over' from one species by another has been reported from a number of control experiments carried out in Cote d'Ivoire (Laveissiere *et al.*, 1988).

In one case Laveissière and Couret (1983) observed that after 5 months of control operation carried out against a mixed population of *G. palpalis* and *G. tachinoides*, the total apparent density of the two species remained unchanged because the population of *G. palpalis* increased at the same rate as the population of *G. tachinoides* was being reduced. A similar observation was made on *G. pallicera* replacing *G. palpalis* as the latter was being controlled (Laveissière and Hervouet, 1988). In both situations the traps or targets used for the control operation were more effective for one species than for the other. According to Laveissière *et al.*, (1988), the more affected species leaves an ecological opening for the less affected one to colonize up to the carrying capacity of the habitat. The disease situation may become more serious if the new dominant species is a better vector. He concludes that to

avoid this risk, it is safer to carry out research into control strategies that are effective for all the tsetse species in a given system. The work reported here on *G. longipennis* seeks to achieve this objective for the *G.pallidipes / G.longipennis* system.

CHAPTER TWO

LITERATURE REVIEW

1. INTRODUCTION

Literature on tsetse and trypanosomiasis dates back to the turn of the century when various colonial governments began to take control measures against disease outbreaks in their colonies. Most of the early information, which concentrated mainly on the identification of disease foci and the vector tsetse species, was documented in government reports. A few workers carried out some basic research on the biology and ecology of the important vector species which were published in various scientific journals e.g. Nash (1930, 1937) and Swynnerton (1921, 1936). Most of the early work was synthesized by Buxton (1955) featuring the general biology of tsetse flies. Subsequent work on various aspects including tsetse distribution, ecology and control strategies have been well reviewed by Glasgow (1963), Mulligan (1970) and Ford (1971).

Despite the vast amount of literature existing today on tsetse and trypanosomiasis, there is very little information on the fusca flies in general and *G. longipennis* in particular probably because they were never implicated in any disease outbreak. There is some information on the distribution of those fusca species

that could be detected in the course of surveys but very little research work has been carried out on their bionomics. Since recent findings indicate that some of the *fusca* species could be important in disease transmission it is vital to gather more background information on the group. The present chapter therefore aims at bringing together all available information on the *fusca* group in general and *G. longipennis* in particular. In the various sections, the information on the *fusca* flies or *G. longipennis* is presented in a background relative to other *Glossina* species.

2. DISTRIBUTION OF *GLOSSINA LONGIPENNIS* AND OTHER *FUSCA* SPECIES

2.1. Geographical distribution

Various schemes have been put forward by a number of glossinologists in an attempt to explain the present distribution of the various *Glossina* species (Evens, 1953; Machado, 1959; Glasgow, 1963). Synthesizing the different views, Ford (1970) described the distribution in the light of various factors including paleontology, feeding habits, climate and vegetation. He concluded that the dispersal of the genus leading to its separation into the phylogenetic groups *fusca*, *morsitans* and *palpalis* took place in the remote past. Climatic factors are considered most important in influencing the distribution of the various species. The humidity and temperature

experienced by the puparia and adult are critical for a number of species. In a new analytical approach to tsetse population dynamics and distribution, Rogers (1979) showed how the distribution limits of some *Glossina* species can be defined by temperature and humidity ranges.

There are a number of publications on the distribution of various *Glossina* species in Africa including maps prepared by individual countries. The first edition of tsetse distribution maps was prepared by Potts (1953-54) and a second edition by Ford and Katondo (1977a). A revision by Ford and Katondo (1977b, 1979) provided separate maps for the three subgeneric groups using international colours and symbols for the various species as provided by OAU/STRC(1971). In the latest revision by Katondo (1984) it is pointed out that there is a lack in knowledge on the general distribution of the *fusca* group compared to the other two groups. This is partly because members of the *fusca* group are considered of less economic importance and partly because they are more difficult to detect.

Fig. 2.1 shows the general distribution of the *fusca* group according to Ford and Katondo (1977b). It is alleged to have dispersed from a central point around the Congo Basin with *G. brevipalpis* and *G. longipennis* evolving separately as they moved eastwards and were subsequently isolated by the East African Pleistocene

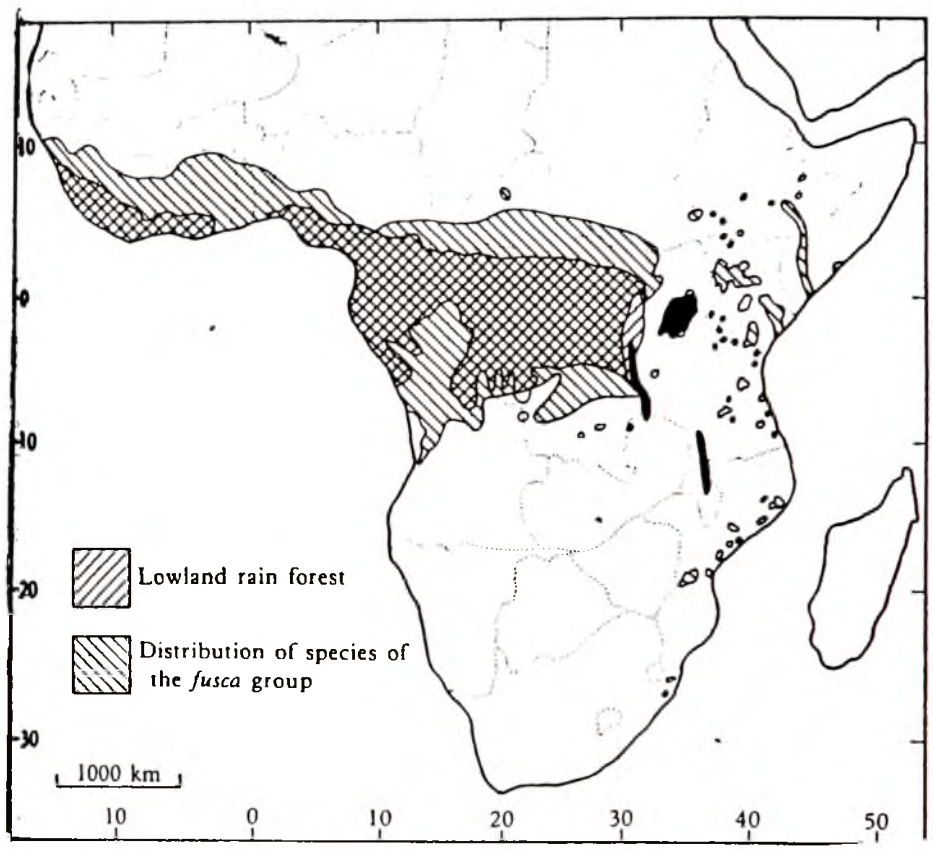

Figure 2.1: The distribution of the fusca group of Glossina in relation to the two zones of lowland rainforest (Map taken from Jordan, 1986)

forest (Ford, 1970) and/or the eastern Rift Valley (Evens, 1953). Thus, Machado (1959) recognizes two major subgroups each composed of relatively closely related species. One comprising *G. fusca*, *G. fuscipleuris*, *G. haningtoni*, *G. nashi*, *G. schwetzi*, *G. tabaniformis* and *G. vanhoofi*, generally has a west and central African distribution. The second subgroup comprising of *G. brevipalpis* and *G. longipennis* has an east African distribution. The remaining three species, *G. medicorum*, *G. nigrofusca* and *G. severini*, appear to be intermediary between the two groups both in phylogeny and in distribution.

When *G. longipennis* was first described by Austen in 1895 from records of the species in Kenya and Somalia, it was then speculated that it also occurred in Tanzania and Uganda. The distribution maps today show that the species generally occurs between latitudes 8° N and 5° S in Ethiopia, Kenya, Somalia, Sudan, Tanzania and Uganda (Ford, 1971; Ford and Katondo, 1977b). However, Kenya remains the country in which it is most widely distributed. *G.longipennis* occurs in the north, south-west, east and the coastal hinterland of the country. *G. brevipalpis* on the other hand occurs in all the above mentioned countries but extends along the coast as far south as Mozambique. Fig. 2.2 shows the distributions of *G.longipennis* and *G. brevipalpis* mainly in Kenya and near its borders in neighbouring countries.

THE DISTRIBUTION OF G. LONGIPENNIS AND G. BREVIPALPIS IN KENYA AND NEAR ITS BORDERS

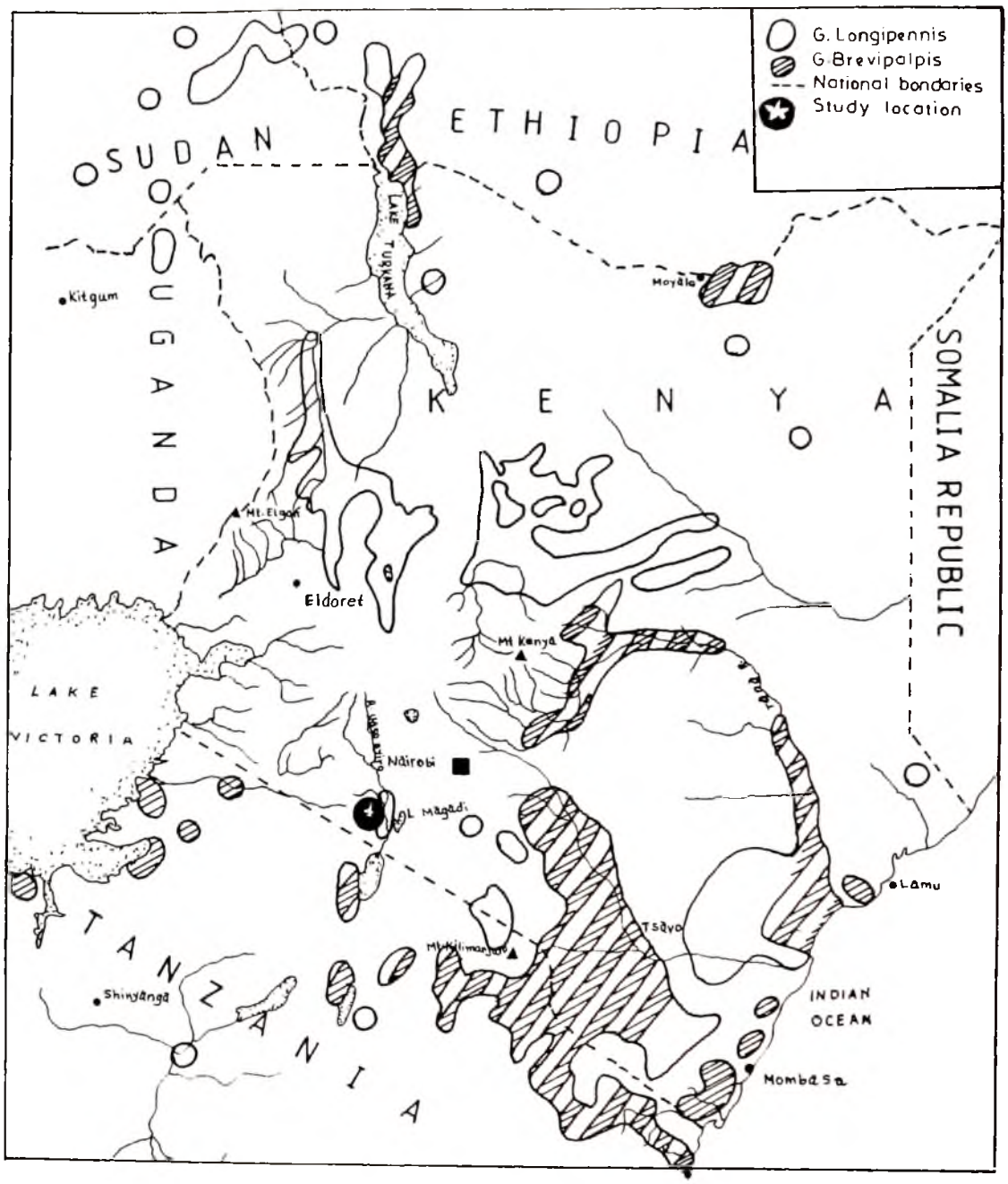

Figure 2.2: The distribution of *G. longipennis* and *G. brevipalpis* in Kenya and near its borders.

2.2. Ecological distribution (Habitats)

Generally, all tsetse flies in Africa are found in various parts of the two basic vegetation types on the continent; the large zones of lowland rain forests in west and central Africa, separated by areas of savannah and the lowland savannahs and isolated forests in east Africa. Within these main climatic zones, tsetse tend to inhabit certain vegetation types but not others. Tsetse infested areas of vegetation were termed 'fly belts' by pioneer workers (Buxton, 1955). Furthermore, different species appear to show preference for different types of vegetation cover, such that some species are referred to as woodland or game tsetse and others as forest or riverine species. Descriptions of some typical tsetse habitats by different workers have been reviewed by Buxton (1955) and Mulligan (1970). Ford (1970) gives an outline of the general habitats of the three subgeneric groups. Generally, the *morsitans* group is described as woodland inhabiting, the *palpalis* group as riverine and the *fusca* group as forest dwelling. Swynnerton (1936) and Jackson (1955) provide detailed descriptions of the habitats of many East African species of tsetse. Various other workers have described the habitats of different species in different parts of Africa as reviewed by Challier (1982). The different habitats presumably offer the optimal ecological conditions to which the various species are adapted.

However, as observed by various workers in Challier (1982) and Katondo (1984), some tsetse species can be encountered in habitats with which they would not normally be associated. On the other hand, certain vegetation cover may appear suitable for some species of tsetse but found to be without tsetse. Such anomalies may be due to changes in climatic factors or due to certain human activities which could force out resident tsetse populations or invite other species to an area.

Of the *fusca* group eleven of the twelve species inhabit various types of forest:

a) The lowland rainforest species, which are confined to the Congo Basin and the forests of Gabon, Cameroons and the Guinea Coast. These include *G. haningtoni* Newstead and Evans, *G. nashi* Potts, *G. tabaniformis* Westwood, *G. vanhoofi* Henrard, *G. severini* Newstead and in some areas *G. nigrofusca* Newstead.

b) *G. fusca* Walker, *G. medicorum* Austen, *G. fuscipleuris* Austen, *G. schwetzi* Newstead and Evans and *in some localities G. nigrofusca* Newstead occupy areas outside the lowland rainforest. They can be found along the edge of the forests, in the tongues of forest along water courses, and in the savannah in the forest islands far from the main forest block.

c)*G. brevipalpis* Newstead is found in the islands of forest often associated with water courses in East Africa.

d) *G. longipennis* Corti. occurs in arid habitats of East Africa.

Jordan (1962a) gave detailed descriptions of the local distribution of most of the west African fusca flies in relation to vegetation climate and seasons.

G. brevipalpis and *G. longipennis* are usually encountered together in the dry climatic zones of East Africa,. However, *G. brevipalpis* still seeks out the most humid and shady parts of such zones to inhabit. Swynnerton (1921) remarked that *G. brevipalpis* is rarely found away from heavy shade. Moggridge (1949) described *G. brevipalpis* in the Kenyan coast as being confined to vegetation along water courses.

From various reports by different workers *G. longipennis* on the other hand seems to be well adapted to dry climate. Neave (1912) observed large numbers of *G. longipennis* in dry semi-desert thorn bush country between rivers while on the river banks it was replaced by *G. brevipalpis*. He described *G. longipennis* as a 'desert haunting species..... seen to be entirely independent of water and indeed rather avoids it.' He thinks it is absent from the sea coast because the climate is too humid for it. Other descriptions of *G. longipennis* habitats as given by various workers include; relic secondary forest patches or thickets, dry grasslands with patches of bushes and trees, savannah woodlands and wooded steppes. The habitat of *G. longipennis* at the

Kenyan coast has been described in Challier (1982) as semi-arid *Acacia/Commiphora* thorn bushland. Power (1964) also described the habitat of *G. longipennis* in his study area near lake Jipe, Kenya, as 'typical of the extensive dry *Commiphora/Acacia* bush which occupies almost half of Kenya and forms the principal habitat of *G. longipennis*. Owaga (1981) and Dransfield *et al.*, (1986a) described the Nguruman study area as belonging to a semi-arid zone with the vegetation consisting of open plains and *Acacia* dominated woodland.

Lewis (1934) gave a description of the Nguruman area and reported an unusual encounter with *G. longipennis* in moist swampy flats and on river banks. Potts (1937) also reported such an atypical situation where *G. longipennis* was inhabiting moist country with *G. brevipalpis* in Tanzania. He remarked that *G. longipennis* is sometimes forced to shelter in the riverine forest and thickets as it cannot always stand the dryness and heat of the semi-desert.

3. THE ECOLOGY AND BEHAVIOUR OF *FUSCA* FLIES

Most of the early works on tsetse ecology in general, were reviewed by Buxton (1955). Since then there have been updated reviews by Nash (1960), Mulligan (1970), Jordan (1974) and Challier (1982). Progress in ecological studies has undoubtedly been tied to the development of sampling techniques. Because of this, far

less is known of the behaviour and ecology of the *fusca* than of the *palpalis* and the *morsitans* groups since the former are less amenable to the known sampling techniques.

3.1. Breeding Sites.

Because the puparia of tsetse require certain environmental conditions for development, pregnant females usually select the most conducive parts of the habitat to deposit larvae. Saunders and Phelps (1970) describe the characteristic breeding sites of the three subgeneric groups of *Glossina* based on puparia collected by various researchers. More recent work on breeding sites has been reviewed by Challier (1982). The selection of breeding sites by tsetse depends on the type and nature of the habitat and the prevailing climatic conditions.

Of the *fusca* flies, the forest dwelling species which live in a relatively uniform climate tend to scatter their puparia, such that no specific breeding sites have been recorded. The other species, being in less uniform and more open habitats, restrict larval deposition to sites characterized by maximum vegetation cover. Lewis (1939) recorded the puparia of *G. fuscipleuris* under logs in dense riverine thickets. The puparia of *G. fusca* and *G. medicorum* were also found under logs but more in the dry season than in the wet season (Page, 1959). Lamborn (1921) and Swynnerton (1936)

found large numbers of *G. brevipalpis* puparia under the shade of big trees in loose sandy soil with much humus. Although he did not find large numbers of puparia, Moggridge (1949) observed that *G. brevipalpis* appears to have preference for logs and the bases of thickets.

Lewis (1942) identified the most favoured breeding sites of *G. longipennis* as beneath logs, leaning tree trunks or stumps of felled trees near shrubby and woody thickets. Fewer puparia were found in the open country in the shade of isolated trees. He observed that puparia were usually deeply buried in friable soil of a mound but under logs were only one to two inches deep. Numerous sites were located throughout the *Commiphora/Acacia* savannah but puparia were most abundant in sites near dense bushes. In the Nguruman study area a few puparia of *G. longipennis* were recorded by Adabie (1987) in the riverine thickets which was found to be the best dry season breeding site for *G. pallidipes* in the same habitat.

The influences of relative humidity and temperature on the duration, mortality and emergence of tsetse puparia have been discussed by several researchers including Nash (1931), Glasgow (1963), Challier (1973) and others reviewed by Challier (1982). The larger size of the *G. longipennis* puparium is thought to contribute to its survival in drier conditions because it loses less water due to the smaller volume/area ratio than the

smaller puparia of other species.

3.2. Resting Sites

In a general review on tsetse sampling techniques, Muirhead-Thompson (1968) dealt with the early studies on resting sites. More recent studies have been reviewed by Hadaway (1977) and Challier (1982). The earliest detailed studies on resting sites were conducted by Nash and Davey (1950) on *G. medicorum* and *G. fusca* which like most *fusca* flies were not readily caught by the fly-round technique. Later on Nash (1952) showed through resting site studies that *G. medicorum* was a carrier of trypanosomes. Since then, very little work has been done on the resting sites of the *fusca* flies.

The search for resting flies by Nash and Davey(1950) in Nigeria yielded more *G. medicorum* and *G. fusca* flies than were obtained by any other sampling method. *G. medicorum* were found resting on the trunks of saplings, 1-3 inches thick, in the high forest. Flies were usually resting head downwards on the shaded side of the trunk. They observed a daily variation in resting height ranging from one and half to 8 feet above ground. *G. fusca* on the other hand was not found resting in the high forest but in an adjacent teak plantation without undergrowth. Flies also rested head downwards 5-9ft above ground on the bark of the teak trees. Swynnerton (1921) showed in a cage experiment that *G. brevipalpis* rested on rough tree

trunks, placing themselves in holes and grooves in the bark of the trunks that had colours close to that of the fly. He also observed that it was easier to locate males than females and pregnant females could not be located by searchers unless disturbed. He observed that flies could rest as high as 9ft in the cages. Jack (1941) observed large numbers of *G. brevipalpis* settling on roads and paths late in the evening. Moloo et al., (1980) recorded *G. brevipalpis* resting on branches and trunks of trees and to some extent on rocks. There are no published reports on the resting habits of *G. longipennis* but Dransfield (pers. comm.) observed the species at Nguruman resting in the morning sun on rocks.

3.3. Activity

Before the idea of searching for resting tsetse was recognized, all tsetse sampling methods depended on flies coming to man, animal baits or traps. Thus, most of our knowledge on tsetse populations have been gathered on the active sections of the population. It was observed quite far back that the numbers of flies caught by these bait methods are dependent in part on their numbers in the area and in part on their activity at the time of sampling. Buxton (1955) gives a comprehensive review of some of the early researches into the factors influencing tsetse activity and pointed out the difficulties in separating the various factors involved.

Activity in nature, which implies movement, is initiated for various life processes; the search for food, mates, and larviposition sites. In the past, several researchers have addressed the question of what controls the timing of tsetse activity. While recognizing the possibility of a complex interaction of climatic factors, different parameters have been emphasized to varying degrees by different investigators; Vanderplank (1948) on saturation deficit, Pilson and Pilson (1967) on temperature and Harley (1965) and Power (1964) on light intensity. According to Pilson and Pilson drastic depression in activity occurred above 32°C degrees but Barrass (1970) observed that high light intensities inhibit activity even below 32°C.

In more recent years it has been possible, through intensive laboratory studies by Brady (1970, 1972, 1973) and field studies by various workers reviewed by Challier (1982), to isolate the activity element i.e the readiness of the flies to move and come to baits. From the laboratory experiments, it was observed that tsetse flies exhibit spontaneous activity in relation to available energy reserves and that this spontaneous activity is controlled by an endogenous circadian clock (Brady, 1972, 1973; Crump and Brady, 1979).

Very little work has been done on the fusca flies in general and *G. longipennis* in particular. Whereas most species of the morsitans and palpalis groups are active

during the day, the few reports show that most *fusca* species are crepuscular. Nash (1952) reported on *G. medicorum* as being active in twilight hours. He concluded that the species was more active in the early morning than in the late evening. On the same species in Ghana, Chapman (1950) found that the largest number collected in a slow moving vehicle was taken at dawn (0600h). In one hourly catches made from bait bullock and buffalo, Kangwagye (1974) recorded more *G. fuscipleuris* in the evenings than in the mornings. Relatively low numbers were recorded throughout the daytime and the nighttime.

In a brief note on the activity pattern of *G. brevipalpis* Lamborn (1921) observed that flies were most active at dusk between 1800h and 1815h and no flies after then. Swynnerton (1921) also reported that *G. brevipalpis* remained quiet throughout the day but moved freely and buzzed at sunset, coming out to settle on unprotected vegetation. A detailed study on the activity pattern of *G. brevipalpis* was carried out by Harley (1965). Using a bait oxen he carried out hourly catches over 24 hours in different parts of the habitat in Lugala, Uganda. Peak activities were regularly recorded soon after sunset and before sunrise. He further observed that in shaded sites the morning peak was one hour later than in open sites, for both sexes. The evening peak occurred one hour earlier but only for males. By using hurricane lanterns, a few flies were also caught throughout the night. He

was, however, not sure whether such flies were attracted to the light or to the bait animal. Among the various environmental factors that he measured during the study, he concluded that light intensity was the most important factor influencing activity.

On *G. longipennis* Neave (1912) observed that the species was inclined to feed early in the morning and late in the evening. Lewis (1942), using a screen-aided fly-round sampling method, recorded two flies during the day, more flies in the early morning and the largest catch in the evening. Peak catches were made at about 1820h, when the sun was disappearing beneath the horizon. Attempts were made using powerful torches and lanterns in the dark but no flies were caught after dusk. Stationary lights were also set near the tents but no flies were attracted to them.

Power (1964) carried out a more detailed study on *G. longipennis* at the Kenyan coast near lake Jipe using the fly-round technique. Four catching teams each carrying a 3 x 6ft brown screen were put on different straight paths (100yds long). The catchers walked back and forth along the paths stopping at 6 minutes intervals to catch flies with hand nets. Catching took place from dawn till about 0900h and from 1745h till dark each day, for a fortnight. Measurements were made of temperature, relative humidity and light intensity. The results showed that the species was very active just after sunset, considerably less

active at dawn and virtually inactive during the day. The percentage catch on females was very low so the data were only analyzed for males. He also suggested that light intensity appeared the most important factor influencing activity with temperature playing a minor role.

3.4. Host Preference

The host preference of *Glossina* can be determined through the identification of blood meals from recently fed flies. The various methods available for blood meal identification has been reviewed by Weitz (1970). It has been shown through such studies that the feeding habits are very characteristic for different species of *Glossina*, although some variations may be observed at different times of the year under different climatic conditions. However the feeding habits of some species are similar to a large extent and can therefore be grouped according to the host most frequently fed on. Five groups of tsetse have been created based on their feeding habits, details of which can be found in Weitz (1970) and Challier (1982).

According to this grouping scheme, *G. longipennis* and *G. brevipalpis* belong to the group of flies that feed mainly on mammals other than suids and bovids. The earliest record on the host of *G. longipennis* came from 9 blood meals identified as belonging to rhinoceros (Weitz and Glasgow, 1956). Subsequently, Weitz et al. (1958)

collected 336 blood meals from resting *G. longipennis* at Kiboko, Kenya which were identified as follows: 74% were from rhinoceros (*Diceros bicornis*), 16% from buffalo (*Syncerus caffer*), 10% from birds, elephant, pigs, cats and unidentified bovids. They suggested that ostrich (*Struthio camelus*) probably contributed the blood meal due to birds. Single feeds were found for man, dog, porcupine and aardvark. They concluded that since rhinoceros and buffalo were comparatively less available in the area than other animals like impala, hartebeest, Grant's gazelle the results showed a very strong dependence of *G. longipennis* on rhinoceros and buffalo.

4. SAMPLING TECHNIQUES FOR *FUSCA* GROUP FLIES

Sampling of tsetse started with reconnaissance studies, by workers involved in tsetse control in the early years of the century. Some of the early investigators made records of the numbers of flies caught on humans at certain spots over certain routes and kept notes on the type of species, pregnancy and hunger stages and age of flies caught (Buxton, 1955). These methods later developed into what is described as the 'fly-round' and the procedure for carrying it out was defined by Potts (1930). The technique was subsequently adopted as a sampling technique, first for assessing the efficiency of control operations and later on for general ecological studies (Smith and Renninson, 1961).

As more emphasis was being laid on the need for a better understanding of tsetse ecology and behaviour to enhance better control strategies, other sampling methods were developed. Some of these later methods were aimed at sampling those tsetse species that did not respond to the fly-round sampling technique whilst others were meant to provide more information on tsetse populations than could be obtained by the fly- round technique. The main sampling methods that were developed included the use of stationary bait, capture of the resting population and trapping. All these methods including the fly-round technique have been developed modified and applied to varying extents in different geographical regions for different species of *Glossina*. Ford *et al.* (1959), Glasgow and Phelps (1970), Muirhead-Thompson (1968) and Potts (1970) have given general reviews on tsetse sampling techniques. More recent developments in sampling methods are reviewed in a section of Challier (1982).

4.1. The fly-round technique

Basically, the method involves using a group of fly-boys who act as combined bait and catchers to move along a path that is laid across a range of vegetation types in the habitat. They then stop at intervals to collect, using hand nets, the flies that land on them and on objects near them. Overall, the method has not been very effective for the fusca group of flies.

Of the forest species in West Africa, Chapman (1950), Nash (1952, 1959) attempted sampling *G. fusca* and *G. medicorum* by this method. They made the common observation that these species were not attracted to man, even when dark screens were carried to increase the attractiveness of target. Very few *G. fusca* were recorded and *G. medicorum* was virtually undetected. Chapman (1950) was successful in sampling the species in Ghana only by using a slow moving vehicle. More extensive studies carried out by Jordan (1962a) on these species and the other west African *fusca* flies confirmed that the technique was not effective.

In East Africa, the method was also used in general surveys on the distribution of *G. brevipalpis* and *G. longipennis*. Lamborn (1921), Swynnerton (1921) and Jack (1941) made the common observation that *G. brevipalpis* did not land readily on man but flies could be caught with hand nets in the most active periods as they came out and landed freely on nearby vegetation and paths. Jack (1941) observed that even when screens were carried, the attraction was poor. By using straight paths across different sections of the habitat, Moggridge (1949) was able to record adequate numbers of *G. brevipalpis*. He found that individual flies were taken in during the day, more flies at dawn and the most at dusk. All these workers observed that males formed the bulk of the catches and Jack (1941) found from fat content analysis

that these were not hungry flies.

In general surveys on the distribution of *G. longipennis*, Neave (1912), Lewis (1934) and Potts (1937) all used the fly-round method. The numbers of flies caught were very low, single flies on some occasions, that only served to indicate the presence of the species in the area. Lewis (1942) however, incorporated a dark screen and was able to identify the most active period of the species from the catches made. A more intensive study was carried out by Power (1964) using four catching teams along straight paths. Each team carried a 3 x 6ft brown screen and walked back and forth stopping at 6 minutes intervals to make catches. The success of the technique was such that he was able to carry out a mark release recapture study to estimate the male fly population in the habitat.

The main drawback of the fly-round technique is the very low yield in female catch as has also been observed for non-fusca species. With the forest species, the main difficulty lies in penetrating the thick habitat. Generally, the numbers of flies caught depends on the catching efficiency of fly-boys. To get round the latter problem, Rogers and Smith (1977) developed a portable electric back-pack which can be worn by fly-boys so that flies coming to them get electrocuted.

4.2. The Stationary Bait Technique

In this method large animals especially cattle are tethered and continuous catches carried out of the flies coming to them. This technique was developed with the aim of catching species that were not readily attracted to or are repelled by the presence of man. The method also has the added advantage that it is more feasible to extend the sampling periods longer than those used in the fly round method (Page, 1959).

The stationary bait technique has been found to be quite effective for detecting some *fusca* species which are not frequently attracted to man. Jordan (1962a) used it to sample *G. fusca*, *G. haningtoni*, *G. nashi*, *G. tabaniformis* and *G. medicorum* after failing to catch these species by the fly-round method. It was by this method of sampling that the vectorial status of *G. fusca* in West Africa was assessed by Nash (1965a). Among several animals that were tried, bait oxen were the most effective and sheep and domestic pig were least attractive. Kangwagye (1971, 1973, 1974) studied the activity pattern and ecology of *G. fuscipleuris* through catches made from bait bullock and buffalo. An intensive study was carried out by Harley (1965) to determine the activity pattern and vectorial capacity of *G. brevipalpis* using bait oxen (see section on activity for details). There are no published reports on the use of the animal

bait method to sample *G. longipennis* but Dransfield et al. (unpublished) recorded fed flies in electric screens around a bait cow at Nguruman.

A number of factors have been observed to influence the catches made by the stationary bait technique. These include the variation in bait size, colour and scent (Saunders, 1964), the presence of alternative host in the neighbourhood and the visibility of the host depending on vegetation cover (Muirhead-Thompson, 1968). Vale (1974a) has showed that the presence of man can actually have a repellent effect on the catches of *G. m. morsitans*. He therefore used electrified grids of fine wire around the tethered oxen to electrocute flies attracted to the animals. This modification has the added advantage that the catch size no longer depends on the skill of the catcher.

4.3. Sampling the resting population

For many years, sampling methods were directed towards the active population. Nash and Davey (1950) initiated studies on sampling the resting populations. The technique simply involves getting into the fly habitat and searching for resting tsetse.

Following the failure after several attempts to sample *G. fusca* and *G. medicorum* by the fly-round technique in the Olokemeji forest, Nigeria, Nash and Davey decided to search for resting flies. Observations

were made over four days in an area of about 25 km^2. Search on the tree trunks in the high forest produced unprecedented catches of *G. medicorum*; 20 males and 17 females (one blood-fed and one carrying a third instar larva). *G. fusca* was not found in the high forest but rather in a neighbouring teak plantation. They described the technique as being tedious, requiring a lot of patience and caution. One needs to move through the habitat pausing methodically to study every trunk; by first looking down the whole profile of the trunk on all sides then scrutinizing the bark. One should always advance into the sun as flies mostly rested on the shaded side of the trunk. Flies were caught with hand nets swooped downwards at a moderate speed. Fast swoops were observed to be ineffective. There are no reports of such intensive searches made on any other *fusca* species elsewhere. Chapman (1950) found it difficult to apply the method on *G. fusca* in Ghana because the vegetation was too thick to penetrate. For blood meal analysis to determine the preferred host of a number of *Glossina* species in Kiboko, Kenya, Weitz et al. (1958) obtained fed *G. longipennis* mainly by collecting resting flies from tree trunks.

The main problem with this method, in general, is the difficulty in locating motionless tsetse which often blend in colouration with that of their background (McDonald, 1960). The technique is also difficult to

standardize because it depends very much on the skill of the searcher.

4.4. Trapping

The few attempts that have been made at using traps to sample some *fusca* species have shown traps to be least effective compared to other methods. Dransfield (1984) used the unbaited biconical trap to sample mixed populations of *G. pallidipes*, *G. brevipalpis* and *G. austeni* but recorded only low numbers of the latter two species. The biconical trap was also used by Gouteux (1983) to study the population dynamics of *G. fusca* and *G. nigrofusca* in the Ivory Coast. They remarked that the numbers recorded were very low. Kaminsky (1987) also reported relatively low catches of these two species in Liberia using biconical traps. A number of traps including Moloo's trap (Moloo, 1973), Langridge's trap (1968) and the biconical trap (Challier *et al.*, 1977) were tried for *G. longipennis* at Nguruman with very little success (Owaga, 1981). Since one of the objectives of this study is to develop an effective trap for this species a more general literature review on trapping technology, is given below.

5. TRAP/ODOUR BAIT TECHNOLOGY

This technique involves the use of devices to catch the flies after they have been attracted with a stimulus

of some kind. For various reasons, more attention has been directed at improving trapping as a sampling technique, than the other methods. Glasgow and Phelps (1970) think that trap catches are less biased than human catches and that a population can be conveniently sampled at different places at the same time using several traps and over long periods. An efficient trap can also be incorporated in a control campaign.

Challier (1977) reviewed trapping technology including the description and performance of various traps and screens, the use of odour attractants with traps and the behaviour of tsetse in relation to traps. He classified traps into three categories based on the principle on which they function. These include; attracting screens, falling cages and artificial refuges and traps proper ('tridimensional').

Attracting screens are simple visual attracting surfaces of dark coloured materials. Flies attracted to them are either collected by hand nets, electrocuted, glued to the surface, trapped in water and detergent or killed by insecticides sprayed on the surface. Falling cages depend on the flies being attracted to a bait under a net or a cage and the flies being trapped when the cage is dropped. Artificial refuges can be built from various materials including boxes, huts and concrete pipes. Flies are caught with hand nets or other trapping mechanisms after they have entered these in search of resting sites.

Tridimensional traps are designed in such a way that the flies are trapped mechanically when they enter the trap. Several types of such traps have been developed either independently or based on previous designs for different *Glossina* species at different places. Challier (1977) gives a list of the different trap types, most of them taking their names from their designers. The main ones include: the Harris trap (Harris, 1930), Chorley's trap (Chorley, 1933), Swynnerton's trap (Swynnerton, 1933; 1936), the Animal trap of Morris and Morris (1949), Langridge's trap (Langridge, 1968) and Moloo's trap (Moloo, 1973). The more recently developed traps include, the biconical trap (Challier and Laveissiere, 1973; Challier et al., 1977), the 'A' and 'C' series traps of Hargrove (1977), the beta trap (Vale, 1982b), the F2 and F3 traps (Flint, 1985) the monoconical trap (Lancien, 1981) the pyramidal trap (Gouteux and Lancien, 1986) and the Vavoua trap (Laveissière et al., (unpublished report).

Generally, tsetse traps, mechanical or otherwise, rely on one or a combination of the following stimuli for attraction; colour, shape and movement. The earliest traps, were designed to resemble common mammalian hosts in some aspects of size, shape and colour. Recent researches in trapping technology have adopted a more analytical approach, paying more attention to the various component parts of the trap.

5.1. Colour stimulus

It was generally accepted by early workers that tsetse are more attracted to dark surfaces than light ones. Based on this knowledge, Maldonado (1910) made his plantation workers wear black cloth on their backs, smeared with glue, to trap *G. p. palpalis* on the Island of Principe. This was the earliest idea in trapping technology. Dark screens have been used by a number of workers including Jack (1941) and Swynnerton (1936) to trap various *Glossina* species. More recently, work by Barrass (1970) and Vale (1969; 1974a) has confirmed the greater attractiveness of dark surfaces compared to lighter ones. Lambrecht (1973) assessed the performances of solid panels of different colours and colour combinations to study the landing behaviour of *G. m. centralis*. He, however, found that white screens gave the best results probably due to better contrast with the background. Dransfield *et al*, (1982) tested different coloured water traps for *G. m. submorsitans* and *G. tachinoides* and found that white was most effective for the former species but black for the latter. Whereas the previous workers thought that colour preference by tsetse was a response to the brightness contrast with the background, Dransfield *et al*. (1982) suggested the importance of the intensity of reflected light especially in the UV range.

In more recent years coloured screens (targets) have been tried in a number of tsetse control experiments. Blue and black screens impregnated with deltamethrin were effective in reducing the populations of *G. palpalis* and *G. tachinoides*.in West Africa (Laveissiere and Couret, 1981). Vale et al., (1986, 1988) also showed that insecticide impregnated targets were also effective for controlling *G. pallidipes* and *G. morsitans* in Zimbabwe. (see section 4.6 for more details).

Colour has also been exploited in the design of mechanical traps for tsetse. The first mechanical trap of Harris (1930) was based on the attracting screen principle; it was basically an attractive screen which was partially enclosed by a trapping device and almost all traps that follow are variations of this model. The colour component of various trap types have been investigated to varying extents by number of researchers. The improvement on the efficiency of the biconical trap by Challier *et al.* (1977), when the white lower cone was replaced by a blue one is a classical demonstration of the importance of colour in trap design. Owaga and Challier (1981) found that a sky-blue biconical trap was less efficient for *G. pallidipes* than a dark blue one. Gouteux *et al.* (1981) compared the performances of several biconical traps of different colours on *G. palpalis* and showed that royal blue was the most effective. Vale (1982a) used electric screens to study

the trap oriented behaviour of tsetse around traps of different colours and colour combinations. He concluded that white on the outside and black on the inside were the most effective colour combinations for inducing entry response. These findings led to the empirical study by Vale (1982b) and later Flint (1985) in developing the beta trap and the F2 and 3 traps respectively. The relative performances of black, blue and white biconical traps were also tested by Flint (1985) for *G. pallidipes* and *G. morsitans* but no significant differences were found between trap catches.

Challier (1977) made an earlier remark that the attraction of *Glossina* to colours is a complex phenomenon that has not yet been satisfactorily explained and this has hitherto been confused by the variation in results obtained by different investigators. Dransfield *et al.* (1982) observed that the significance of colour to tsetse depended on which aspect of the behaviour is involved. They found that among several colours of water traps used for *G. m. submorsitans* and *G. tachinoides* in northern Nigeria, black and white coloured ones were most attractive. Inferring from the high proportion of blood-fed female flies, they suggested that most of the flies attracted were seeking resting sites.

More intensive laboratory and field studies have since been directed at understanding the response of tsetse to colour using more objective techniques. Green and Jordan (1983) investigated the spectral response of *G. m. morsitans* using the behavioral response to variously coloured lamps in Insect-O-Cutor traps. They observed that flies were more attracted to ultraviolet (UV) lamps than white ones. In a more detailed study, using behavioral techniques, with various wavelengths of monochromatic light ranging from UV to red, Green and Cosens (1983) observed that tsetse showed colour preference in the decreasing order of UV blue, red, white, yellow and green. From further investigation with the electro-retinogram technique, they identified three main areas of maximum sensitivity; UV, blue/green and red. The relative position of black can not be assessed in this manner although it is known to be quite attractive to tsetse. Vale (1982a) observed that in addition to being attractive, black encourages a greater landing response in tsetse than other colours. From the above findings Green and Cozens, 1983 and Jordan and Green, 1984 remarked that the discrepancies in the findings from different studies in the past may be due to the failure to take UV wavelengths into consideration as earlier on suggested by Dransfield *et al.* (1982).

To assess the relative attractiveness of various colours in the field, some preliminary field trials were

carried out with different coloured traps on *G. morsitans* and *G. pallidipes* by Jordan and Green (1984). They, found no apparent simple relationship between trap score and trap colour. The most important determinant of the catches seemed to be the proportion of attractive blue to unattractive green and yellow. More recently, Green and Flint (1986) carried out field experiments using 53 different colours of F2 traps selected on the bases of spectral reflectivity in the colour ranges visible to *Glossina*. They observed that trap catches depended on relative amounts of spectral reflectivity in four distinct wavebands corresponding to UV, blue-green, green-yellow, and orange and red. Blue-green and red reflectivity were positively correlated with trap catches, whilst UV and green-yellow-orange were negatively correlated. Thus the best trap material turned out to be royal blue cotton cloth reflecting blue green strongly and very little of UV or green-yellow-orange.

The above field results are not in total agreement with the laboratory observations especially on the relative position of UV reflectivity. Thus, although the importance of colour as an essential component part of tsetse traps has been established more research is still needed to explain the phenomenon of tsetse responses to colours.

5.2. Trap design

Almost all mechanical traps for tsetse combine colour with shape in their design. Generally, dark surfaces and shaded cavities and a variety of shapes that contrast well with the background are the characteristic features of tsetse traps. The essential components of a typical trap are described by Challier (1977). The trapping mechanism is based on the fly being attracted to and entering the body of the trap, in search of either shade for larviposition and resting sites or food. Once in the dark body cavity of the trap the flies are next attracted towards a lighted summit of the trap into which they climb, passing a 'no-return' device and into a retaining cage.

The earliest trap designs, reviewed by Swynnerton (1933) and Buxton (1955), were roughly of the size and shape of small animals but today the most effective traps take no regard of animal shapes. However, the size of the device is apparently still an important factor. Vale (1974a) and Hargrove (1980b) used electric screens to study the response of tsetse to a model (a horizontal cylindrical drum). It was observed that if the linear dimension of the model was increased three-fold the number of flies visiting it was higher. Gouteux et al. (1981) observed that smaller biconical traps did not significantly reduce catches until the trap was reduced

5.2. Trap design

Almost all mechanical traps for tsetse combine colour with shape in their design. Generally, dark surfaces and shaded cavities and a variety of shapes that contrast well with the background are the characteristic features of tsetse traps. The essential components of a typical trap are described by Challier (1977). The trapping mechanism is based on the fly being attracted to and entering the body of the trap, in search of either shade for larviposition and resting sites or food. Once in the dark body cavity of the trap the flies are next attracted towards a lighted summit of the trap into which they climb, passing a 'no-return' device and into a retaining cage.

The earliest trap designs, reviewed by Swynnerton (1933) and Buxton (1955), were roughly of the size and shape of small animals but today the most effective traps take no regard of animal shapes. However, the size of the device is apparently still an important factor. Vale (1974a) and Hargrove (1980b) used electric screens to study the response of tsetse to a model (a horizontal cylindrical drum). It was observed that if the linear dimension of the model was increased three-fold the number of flies visiting it was higher. Gouteux et al. (1981) observed that smaller biconical traps did not significantly reduce catches until the trap was reduced

to a third.

From a more detailed study of the behaviour of tsetse around and inside traps, Vale (1982a) demonstrated that trap design is of critical importance in determining whether a fly will enter it or not. After having tested different sizes, colours and colour combinations of traps he concluded that in bringing flies to a trap any fairly large trap of any shape would be satisfactory. He, however, recommended a horizontal entrance located at the base with tunnel-like openings into the inside of the trap. The importance of an appropriate colour combination in designing an effective trap has recently been investigated by Green and Flint (1986). By varying the colours on the inside and outside of the F2 trap they observed that the external colour affected both the attractiveness and efficiency of the trap for *G. pallidipes* and *G. m. morsitans*. Yellow and green traps were unattractive but efficient, black and red were attractive but inefficient, blue attractive and efficient and white moderately attractive and very efficient. The landing response was strongest on black and weakest on white material.

The performances of different trap designs have been observed to vary between species and locality. The Harris' trap was very successful for *G. pallidipes* in Zululand (Harris, 1930) and was later also used in Zaire, Tanzania and Botswana by other workers. However the

Morris' trap which was originally designed for West African species had to be modified for East African species. The blue biconical trap (Challier *et al.*, 1977) has proved quite successful for a good range of *Glossina spp.* and has become widely adopted for sampling both the *palpalis* and *morsitans* species in many parts of Africa. Takken (1984) evaluated the biconical trap as a sampling device for tsetse in Mozambique. The square-shaped F3 trap of Flint (1985) has been shown to be more efficient than the biconical trap for *G. pallidipes* (Flint, 1985; Vale *et al.*, 1986). Thus, if trapping is to be adopted as a sampling technique for tsetse, more work is required to produce appropriate designs for the various species in different localities.

5.3. Movement

The attraction of tsetse to moving objects has long been known and was exploited in developing the fly-round sampling technique. There have been attempts by various researchers to incorporate movement in tsetse trapping with varying degrees of success. Vale (1969) showed that mobile screens and black rotating drums caught more *G. pallidipes* than stationary ones. Slow moving vehicles have been used by many workers to sample some species (Ford *et al.*, 1972). Mobile components have been added to some mechanical tsetse traps in an attempt to increase trap efficiency but with very little success. Two white

and blue screens revolving around the base of a biconical trap, proved to be less efficient for *G. pallidipes* than the stationary trap but when the speed was reduced with intermittent stops the performance was near that of the stationary trap (Owaga and Challier, 1981). Gouteux et al. (1981) also incorporated revolving screens at the base of a cylindrical version (lower cone only) of the biconical trap and found no significant increases in catches of *G. palpalis*. Generally, tsetse thus seem to be attracted by certain movement patterns but not others and more knowledge is required on this before movement can be effectively incorporated in trap designs.

5.4. Odour baits

The conventional fly-round and the baited cages sampling techniques combined odour and visual attraction of the host to capture tsetse. Generally, smell plays a role from longer distances than vision but the relative importance of these two senses seem to vary from species to species (Challier, 1977).

Olfactory attractants have been used by various workers to increase trap catches. These include host residues, organic wash-offs from host animals and various chemicals. Chorley (1948) observed that odours from cattle dung and urine were responsible for the concentration of *G. m. morsitans* and *G. pallidipes* in host resting places and further showed that these

residues could be used to increase the catches of these species. Langridge (1961) and Persoons (1967) applied petroleum extracts of pig washing to hessian screens of traps to increase the catches of *G. fuscipes* and *G. pallidipes*. Vanderplank (1944) and recently, Vale et al.(1986) showed that animal bedding is significantly attractive to tsetse. Frezil and Carnevale (1976) used dry ice (CO_2) to increase trap catches of *G. fuscipes quanzensis*.

Ox odour was shown by Hargrove (1980a), Hargrove and Vale (1978) and Vale (1980) to increase catches of *G. pallidipes* and *G. morsitans* and the combination of ox odour and carbon dioxide was found to be even more attractive (Vale 1982a). The attractancy of various chemicals was tested by Vale (1980) for *G. pallidipes* and *G. morsitans*. He observed that short chain ketones especially acetone, as well as formaldehyde and propionaldehyde were attractive but long chain ketones, heptaldehyde and caproic acid were repellent. He also showed that acetone dispensed together with carbon dioxide was more effective than either compound on its own. Through electro-antennographic techniques, Hall et al. (1984) identified 1-octen-3-ol (octenol) as the most potent attractive component of the volatiles from cattle. It was shown to significantly increase the upwind flight of *G. m. morsitans* at concentrations as low as 0.9 ngl^{-1}. In field trials using beta traps, octenol increased the

catch of both *G. m. morsitans* and *G. pallidipes* by up to three times relative to catches in unbaited traps when dispensed at dose rates between 0.5 and 50 mg hr^{-1}. When dispensed together with odour from a pit containing an ox the catches at an electrocuting net were significantly increased by up to 2.5 times for *G. morsitans* and up to 1.5 times for *G. pallidipes* at dose rates between 0.5 and 5 mg hr^{-1}. The efficacy of 1-octen-3-ol has since been demonstrated in the field by various workers(Vale and Hall, 1985; Vale et al.,1986; Dransfield et al ,1986a; Bursell et al., 1988; Vale et al., 1988) for *G. pallidipes* and *G. morsitans* in Zimbabwe and Kenya and for *G. m. submorsitans* in Burkina Faso (Politzar and Mérot, 1984). The effects of various doses of ketones and octenol on the catch size and composition of *G. pallidipes* were assessed by Dransfield *et al* (1986b).

The attractancy of bovid urine to tsetse has been demonstrated by various workers. Working at Nguruman, Kenya, Owaga (1984) observed that buffalo urine increased the catches of *G. pallidipes* in biconical trap by a factor of ten. She further compared the efficacies of buffalo urine and cow urine (Owaga, 1985) and reported that the buffalo urine was about 7.1 times more effective than cow urine. The potency of buffalo urine as a tsetse attractant was also reported by Saini (1986) using electro-antenogram techniques. More intensive investigations were carried out on cow urine and buffalo

urine in combination with other chemical attractants by Dransfield *et al.* (1986b) at Nguruman. They showed that cow urine on its own increased the catches of *G. pallidipes* in biconical traps up to 4 times and 9-15 times when dispensed together with acetone. They, however found no significant difference between the effects of cow urine and buffalo urine. In Zimbabwe, Vale *et al.* 1986b also showed that both cow urine and buffalo urine increased the catches of *G. pallidipes* by several-fold but there was no significant difference between the two. The latter authors and Owaga (1985) observed that the potency of the urine increased with the age of the sample. This aging process which presumably results in the higher concentration of the attractive components of the urine, was thought to be the possible source of discrepancy between Owaga's finding and the others' in comparing buffalo urine and cow urine (Vale et al., 1986b). The potent attractants in buffalo urine and cow urine have since been identified by Hassanali *et al.*, (1986) and Bursell *et al.*, (1988) as derivatives of phenol. Among eight of the derivatives occurring naturally in cattle urine, four of them, 3-methylphenol, 4-methylphenol, 3-ethyl phenol and 3-n-propylphenol were electro-antennographically active and induced upwind flight in wind tunnel bioassays in *G. pallidipes* and *G. m. morsitans*. When tested with traps baited with acetone and octenol all except 4-methylphenol were attractive to

both species in Zimbabwe, but a marked sex difference was observed in the response of both species to the latter compound (Bursell *et al.*, 1988).

There are no published reports on the response of *fusca* group flies to odour baits. Dransfield (pers. comm.) observed that the catches of *G. longipennis* by biconical trap at Nguruman appeared to increase when the trap was baited with acetone and cow urine. On the *palpalis* group, most of odours tested for *G. p. palpalis* in West Africa do not seem to be effective (Laveissiere *et al.*,1986). However, Cheke and Garms (1988) recently observed that biconical traps baited with octenol or acetone caught twice as many *G. p. palpalis* in Liberia as an unbaited trap.

4.5. Trap efficiency

Trap efficiency, as considered by most workers, means the comparative catches of insects by different trap types and the relationships between the characteristics of the traps and numbers of insects caught. Various workers have observed that the performances of traps do vary with the location of the traps. Harris (1930) recommended that traps should be located in optimal light and shade conditions. Morris and Morris (1949) placed traps in sites where host were suspected to frequent ("hunting grounds") in order to obtain maximum trap yields. Glasgow and Duffy (1961)

observed that siting traps in relation to the sun and biotypes are also important. They recorded the highest catches of *G. pallidipes* on one side of a thicket before noon and on the opposite side after noon. Challier and Laveissière (1973) recorded maximum catches by siting traps in more open and even sites. Langridge (1977) noted that traps should not be set in shade but in direct sunlight to give maximum contrast of light and shade on the body of the trap. Muirhead-Thompson (1968) however, thought that the exact location of the best trap site depends on trial and error.

Hargrove (1977) developed a method for estimating trap efficiency by comparing the performance of the traps with that of an electric net of Vale (1974b) under the same conditions in a randomized block design. By this method Hargrove (1977) assessed the efficiencies of the Morris and Moloo's traps as 10% and 15-25% respectively. He observed that the day-to-day variation in trap performance (the numbers of tsetse caught by traps) was very great thus yielding very large coefficients of variation.

Vale and Hargrove (1979) considered that the above method in fact estimated the relative efficiency of the trap instead of the absolute efficiency which they then defined as the percentage of the flies approaching the trap that are actually caught by it. To estimate this, they developed the technique of placing an incomplete

ring of electric nets around the trap to be tested and were able to estimate the number of flies which escaped the trap as well as the number caught by it. Odour attractants were used to help concentrate flies around the trap, so that the absolute efficiency of the trap then depended solely on its ability to capture the flies around it. They observed that estimates obtained by this technique, from several replicates, had smaller coefficients of variation compared to the previous method. Using the above technique they found that the A7C trap of Hargrove (1977) was a very efficient trap for *G. pallidipes* and *G. morsitans*, as its efficiency was comparable to that of an electric net also placed in the incomplete ring. Using the incomplete ring technique, Hargrove (1980b) was able to rapidly assess the efficiencies of various new trap models as modifications were being made. The efficiencies of three biconical traps were also estimated as 40-70% for *G. morsitans* and 50-80% for *G. pallidipes* as against 70-90% for the small electric net whose efficiency was also estimated by placing it in the incomplete ring of electric nets. Details of the calculations involved are given by Vale and Hargrove (1979) and Hargrove (1980b).

5.6. The role of traps in tsetse control

Although traps have been used extensively for sampling tsetse flies, they have until recently been

least considered in tsetse control campaigns. There are a few records from the early years of tsetse control where traps were incorporated in control operations. The most primitive trapping technology by Maldonado (1910) (plantation workers wearing sticky black cloth) was the first to be incorporated in a control campaign on the Island of Principe against *G. p. palpalis*. Harris (1936) used large numbers of his trap in an attempt to eradicate *G. pallidipes* in Zululand but without success. The Morris and Morris trap was used in Nigeria against *G. p. gambiensis* to reduce the population below transmission level and was later also incorporated in a control programme when *G. p. palpalis* re-invaded Principe. With the advent of insecticides, investigations on the potential of traps for control were abandoned. However, the development of the more effective biconical trap by Challier and Laveissière (1973), the increasing cost of insecticides and the lack of foreign exchange for insecticidal control led to the renewed interest in the possibility of using traps for control. As such, a number of workers have recently carried out control experiments with the biconical trap. Laveissiere and Couret (1981) deployed 600 biconical traps impregnated with deltamethrin along a 62 km river bordering Burkina Faso and Ivory Coast against *G. p. gambiensis* and *G. tachinoides*. The catch of *G. tachinoides* was reduced by 85% after 3 days and by 98% after twelve days and

remained so for four months. The experiment was repeated by Laveissière and Couret (1981) using blue screens (targets) also impregnated with deltamethrin. The effect was slightly less but the cost was also reduced. They observed that the effectiveness would be less in the rainy season but the potential had been demonstrated and the economics worked out. Lancien (1981) used a cheaper and more simplified trap, the monoconical trap, in a control campaign against *G. f. quanzensis* in the republic of Congo. In the forest region of Ivory Coast, biconical traps (Laveissiere *et al.*, 1980) and screens (Gouteux *et al.*, 1981) were also shown to reduce populations of *G. p. palpalis*.

Following the promising results of these preliminary control experiments, considerable research work has been directed at improving the efficiency and reducing the costs of traps and methods of target installation and insecticide application (Laveissière and Hervouet, 1988). Further control experiments have been carried out alongside to assess some of the research findings. Gouteux *et al* (1987) have demonstrated that with community participation, a non-insecticide impregnated pyramidal trap could effect 97-98% reduction in tsetse populations in three villages in the Ivory Coast.

With the progressive discovery of tsetse odour attractants the potential of traps and targets for control is becoming greater. The prospects for using

stationary baits for sampling and control of tsetse was discussed by Vale (1981). In Zimbabwe, Vale et al. (1986) showed that isolated populations of *G. m. morsitans* and *G. pallidipes* could be eliminated rapidly with a sparse placement of odour baited targets impregnated with insecticide (Vale et *al.* 1986). More recently, Vale *et al.* (1988) used black cloth targets flanked by netting baited with 1-octen-3-ol and acetone or butanone coated with deltamethrin against a *G. pallidipes* population in a 600 km² on the Rifa triangle in the Zambesi Valley Zimbabwe. A 99.99% reduction in the population of *G. pallidipes* was achieved in about six months. They discussed the effectiveness, practicability and ecological impact of targets in a large area that had abundant tsetse and was subject to strong invasion. According to Laveissiere *et al* (1986), no effective odour baits have been found to significantly increase the catches of *G. palpalis* in West Africa.

Jordan (1986) gives a review of the role of traps in past and present control campaigns and also provides an insight into the potential of trapping technology for future control efforts. The potential of odour baited traps and targets in tsetse control has been discussed by Vale (1987). Generally, there is every indication from ongoing research that any long lasting control strategy for tsetse will in future incorporate some degree of trapping technology.

CHAPTER THREE

DESCRIPTION OF THE STUDY AREA

3.1. INTRODUCTION

All the field studies were carried out at Nguruman in the Kajiado district of the Rift Valley Province in south- western Kenya. The area is situated in a generally semi-arid zone and was formerly classified as a Maasai Reserve area. A wide variety of game animals are found there with herds of zebra and wildebeest moving in during the rains from the Serengeti ecosystem. Today the area is still inhabited mainly by the Maasai who keep herds of cattle, goats, sheep and donkeys. However, people belonging to other Kenyan tribes have recently migrated into the area and taken to small scale, irrigated farming, producing mainly maize and a variety of fruits and vegetables.

The area has considerable potential for development. Firstly, the rangeland could be used for improved animal production for the benefit of the local Maasai community and for the nation as a whole. Secondly, the irrigation scheme could be extended to increase agricultural crop and vegetable production. Finally, the abundant game could be a tourist attraction if tourist facilities were to be developed in the area.

One of the reasons why the area has not been fully exploited for these resources has been the presence of large

numbers of tsetse flies, specifically *Glossina pallidipes* and *Glossina longipennis*. Apart from the fact that tsetse flies can be a nuisance to man when numbers are very high, the species found in the area are vectors of animal sleeping sickness (nagana). Considerable numbers of Maasai cattle have been reported to regularly die from the disease especially during drought periods when the resistance level of the animals is very low and animals expose themselves to higher tsetse challenge by moving into the denser woodland in search of food. The control of tsetse flies and the disease would contribute enormously to the development of the area.

Since the presence of tsetse flies was reported in the area by Lewis (1934), no tsetse control has been carried out there. A project was undertaken by ICIPE in the area to carry out research into the understanding of the dynamics of the tsetse/trypanosomiasis system in order to develop suitable control strategies. At the start of the project, most of the work was concentrated on *Glossina pallidipes* which was thought to be a more important vector than *G. longipennis*. It was, however, realized that for a complete understanding of the system it was vital to have adequate knowledge of both species. Therefore the work to be reported was undertaken to provide information on *G. longipennis* that could be useful in the study of the tsetse/trypanosomiasis situation in the area.

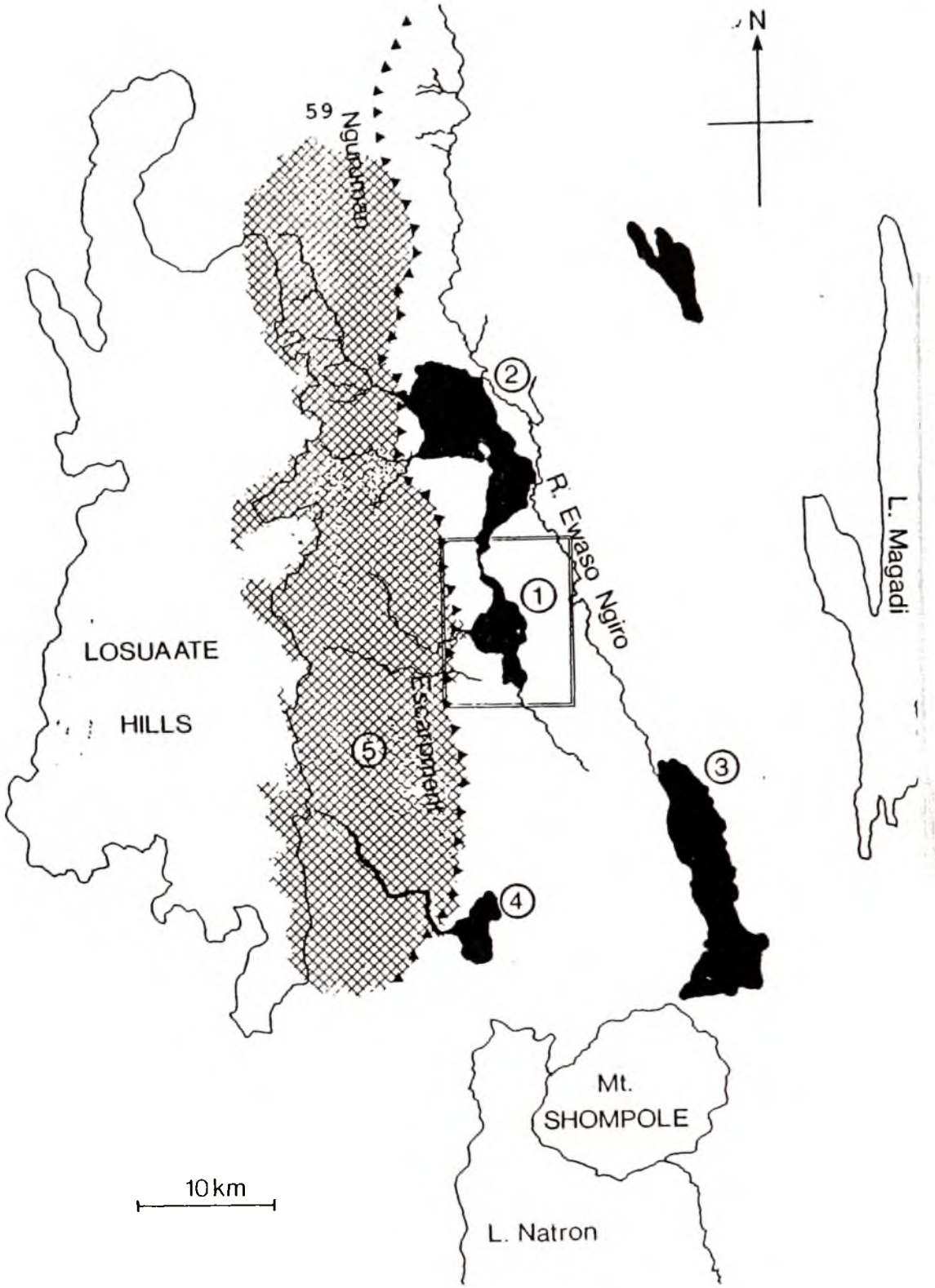

Figure 3.1: Location of the main study area (boxed) in relation to major geographical landmarks and other tsetse infested areas of the Nguruman tsetse fly belt.

3.2. LOCATION OF THE NGURUMAN AREA

Figure 3.1 shows the location of the study area (boxed and labelled 1) in relation to other tsetse infested areas (numbered on the map) within the Nguruman tsetse belt. The area which forms part of the alluvial plains of the Rift Valley of East Africa is located between latitude 1° 48'N and longitude 35° 56'E and lies at 600-700m above sea level. According to Sayad and Sayad (1980), the dense wooded area covers 330km² measuring 35km from north to south and 10km from east to west.

The major landmarks are the Ewaso Ngiro river to the east, the Nguruman escarpment rising to about 3000ft in the west and Mount Shompole about 20km to the south. To the north, the study area extends mainly as a strip of narrow vegetation along the Oloibototo to join a bigger tsetse infested area in the Olkeramatian plains. Within the latter area and about 10 km from the centre of the study area are located the irrigated farms.

3.3. CLIMATE AND WEATHER

Climatic data for the duration of the study are shown in Fig. 3.2. The Nguruman area generally experiences a mean annual rainfall of about 500-700mm. Mean monthly maximum temperatures range from 32-41°C and minimum temperatures from 18-22°C. Over the study period minimum relative humidities (taken at 1500h local time) ranged from 24% in February 1986 to 48% in May 1987. However, previous records show that

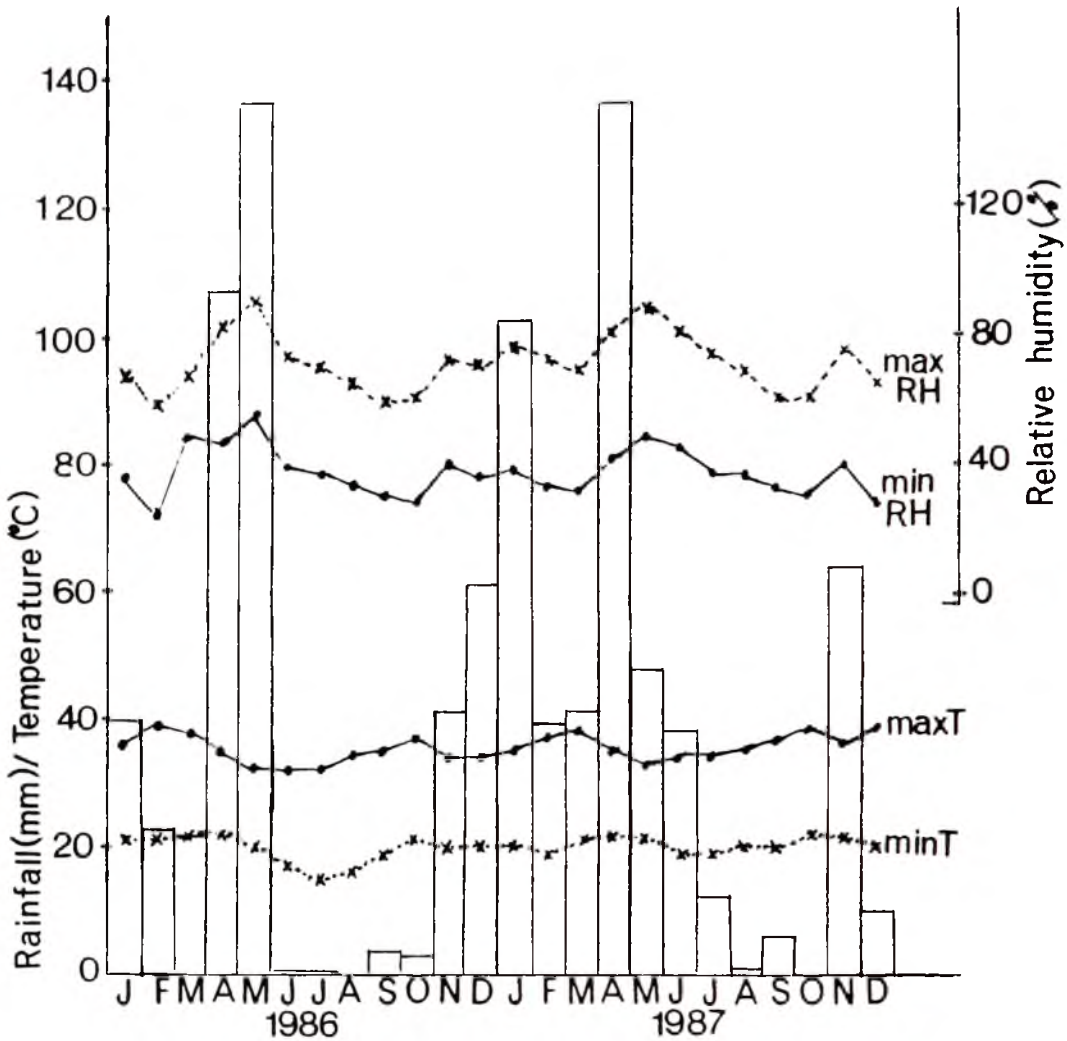

Figure 3.2: Profiles of monthly rainfall (histogram), mean monthly minimum and maximum temperature and mean monthly minimum and maximum relative humidity recorded at Nguruman over the study period.

minimum relative humidities can go as low as 21% in the hot dry months of January and February.

Rainfall generally occurs in two seasons in a year; short rains occurring more or less in November and December and the long rains from late March till May. These are separated by hot dry months from January to early March and cold dry months from June to September. During the rains, grasses and shrubs grow rapidly and food is generally abundant for both domestic and wild animals. In the dry seasons, most grasses die leaving the ground bare, deciduous trees and bushes loose their leaves and there is a general scarcity of food for animals. Some species of game migrate to other places whilst domestic animals are grazed more in the thicker woodland and eventually moved up the escarpment if the dry conditions persist any longer than usual.

The main drainage systems of the area include the Ewaso Ngiro river, which flows permanently and the Oloibototo, Sampu and Lentore rivers which are seasonal. During very heavy rains, the study area may get flooded as the seasonal rivers overflow their banks.

3.4 VEGETATION

The vegetation in the Nguruman area has been described by Lewis (1934), Sayad and Sayad (1980) and Dransfield et al. (1986a). Figure 3.3 (taken from Dransfield et al., 1986a) shows the main vegetation types in the study area. In moving from the Ewaso Ngiro river to the base of the escarpment one

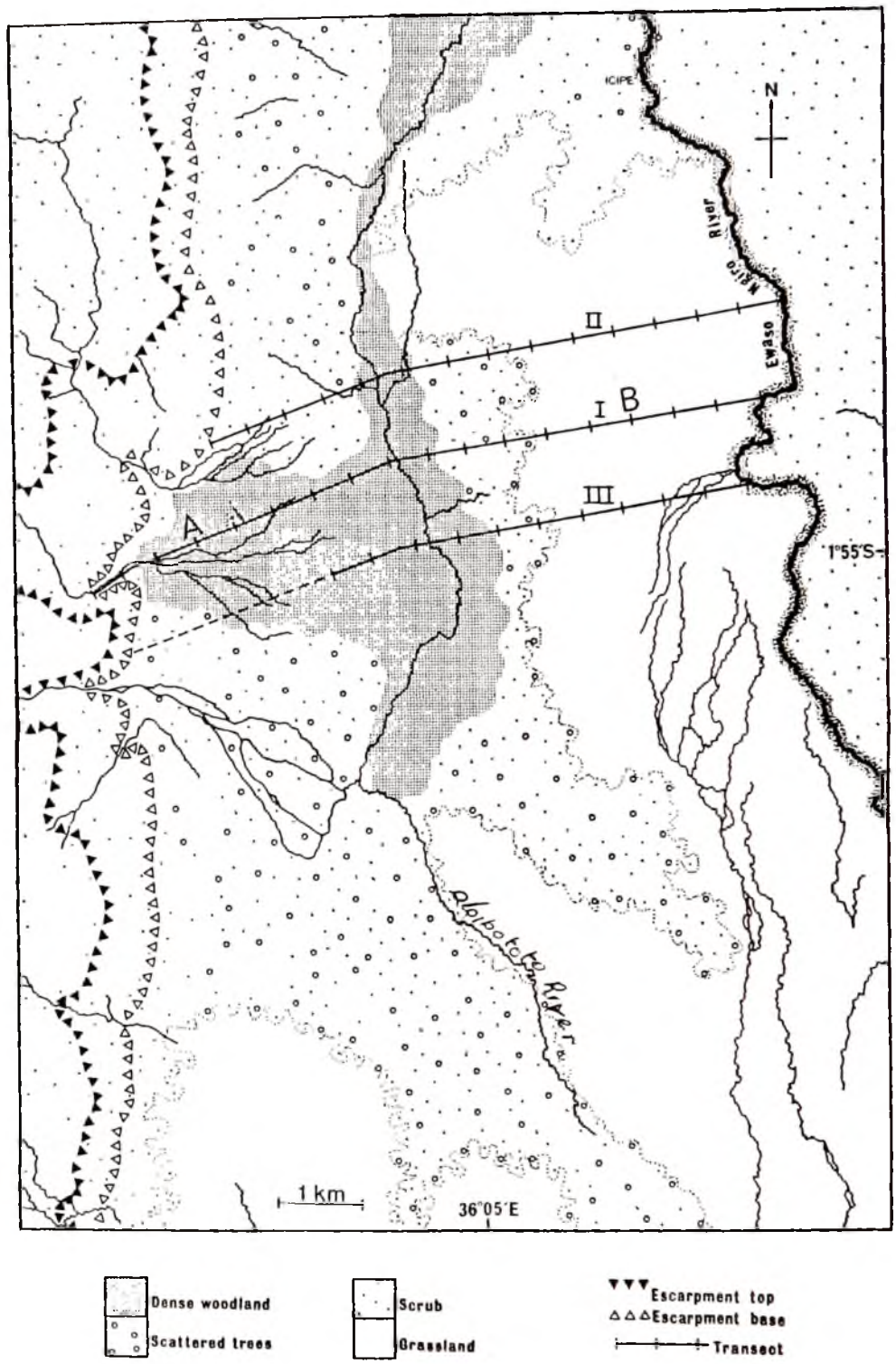

Figure 3.3: Map showing the different vegetation types in the main study area.

traverses five main vegetation types as follows:

a. The Open Plains

This starts immediately after the wooded fringes of the river. The section is mainly grassland with isolated trees mainly of *Acacia seyel fistula* and *A. siberiana*. In the dry season the ground here is parched and bare except for some dry tussocks. During the rains however the area is covered with tall grasses and shrubs and most animals graze in this area. When the general area is hit by drought people tend to move their animals into the thicker woodland.

b. The Acacia Woodland

This is characterized by a closer distribution of various *Acacia spp*, including *A. albida, A. seyel fistula* and *A. tortilis*. The rest of the ground is taken up by grasses and thicker shrubs than found in the plains.

c. The Riverine Thicket

This forms a strip of lowland woodland around the Oloibototo river which runs from north to south through the central part of the study area. The riverine vegetation is characterized by a close canopy of tall trees, shrubs liannas and bushes. The section is generally characterized by densely shaded thickets which form the main breeding sites for *G. pallidipes*. The dominant trees include *Euphorbia candelabrum, Acacia pennata* and *Cassine aethiopica* and shrubs include *Sautia myrtina* and *Aloe spp*.

d. The Lower and upper woodland

This is a wooded bush-land consisting mainly of close stands of thick shrubs and scattered *Acacia* and other trees. The dominant shrubs in this section include *Boscia coriacea* and *Aloe spp*. The ground becomes covered with tall grass during the rains. This area provides most animals with the bushes for browsing during the dry season.

The vegetation becomes thinner as the area rises to rocky ground towards the base of the escarpment. The tall trees give way to shorter scattered xerophytic acacia trees such as *Acacia mellifera* and thorny bushes. The grasses here are shorter and the ground is generally more open than the previous section.

e. The Valley Woodland

This is a dense wooded valley lying at the base of the escarpment consisting of tall trees mainly of *Ficus spp* and various types of shrubs and grasses. The vegetation becomes thicker along the course of the Sampu river coming down from the escarpment.

Both species of tsetse are found in all these vegetation types in varying densities but become more evenly distributed during the rainy season.

3.5. MACRO-VERTEBRATES

A wide range of both domestic and wild animals form the macro-vertebrates population in the area. Domestic animals kept by the Maasai include cattle, goats, sheep and donkeys. A

few dogs and cats are kept as pets. The Maasai households which form the Olkeramatian group ranch in the area together own about 7000 cattle, 18000 sheep and 19000 goats.

A variety of wild animals are encountered as one moves from the plains into the woodland although the distribution is not sharply distinct neither is it constant throughout the year. Generally, the open plains are characterized by herds of zebra (*Equus zebra* L.), Grants gazelle (*Gazella granti* Brooke), wildebeest (*Connochaetes taurinus*) and less commonly hartebeest (*Alcelaphus buselaphus* Thomas). The zebra and wildebeest migrate into the area during the long rains. Also found in the plains are smaller numbers of eland (*Taurotragus oryx* (Pallas)), waterbuck (*Kobus ellipsiprymmus* (Ogilby)) and warthog (*Phacochoerus aethiopicus* L.). The big cats, lion (*Panthera leo* (L.)), and cheetah (*Acinonyx jubatus* (Schreber)) may also be encountered in the plains as well as the scavengers, black-backed jackal (*Canis mesomelas* Schreber), side-striped jackal (*Canis adustus* Sundevall) and the spotted hyena (*Crocuta crocuta* Erxleben). Packs of African hunting dog (*Lycaon pictus* (Temmick)) also move into the area at some times of year. The cape hare (*Lepus capensis* L.) is a very common sight on the plains and aardvark (*Orycteronyx afer* (Pallas)) are also found there. A number of large bird species found mainly in this area include ostrich (*Struthio camelus* L.), Kori bustard (*Ardeostis kori*),and the secretary-bird (*Sagittarius serpentarius*). Guinea fowls (*Numida spp.*) and francolins (*Francolinus spp.*) may be encountered both in the

plains and in the acacia woodland.

Impala (*Aepyceros melampus* Lichtenstein) and giraffe (*Giraffa camelopardalis* (L.)) are encountered more frequently at the edge of the woodland with giraffe being more frequent in the acacia woodland. Large troops of baboon (*Papio anubis* (Fischer)) roam between the plains and the edge of the woodland whilst vervet (*Cercopithecus sp.*) and colobus (*Colobus spp.*) monkeys are found in the thick woodland. In the thickest parts of the woodland are found buffalo (*Syncerus caffer* Sparrman) which tend to graze near the river bed in the morning and late evening and withdraw into the heavy shade along the river bed in the hot afternoon. The ungulates here include bushbuck (*Trangelaphus scriptus* Pallas), and dikdik (*Madoqua guentheri* Thomas). Occasional sighting of leopard (Panthera pardus (L.)) and porcupine (*Hysterix sp.*) have been made. Some of the animals appear to move out of the study area during the dry season but baboons, warthog, buffalo, impala and giraffe remain the whole year round.

CHAPTER FOUR

DEVELOPMENT OF AN EFFECTIVE TRAP/ODOUR BAIT SYSTEM

4.1. INTRODUCTION

Trapping has several advantages over other methods of sampling tsetse. First, it is a more objective technique of sampling because it eliminates the human element which sometimes introduces unacceptable variability into sampling data. Secondly, different parts of the habitat can be sampled at the same time and over long periods without interruption. Owing to the above reasons and others outlined by Glasgow and Phelps (1970), trapping is the most reliable and convenient technique for sampling tsetse populations. However, due to the lack of an efficient and convenient trap for *G. longipennis*, the method remained inapplicable until recently.

The development of the biconical trap (Challier and Laveissière, 1973; Challier *et. al.*, 1977) marked the beginning of the widespread use of traps for sampling tsetse populations. It was developed primarily for species of the *palpalis* group in West Africa but was later also shown to be effective for *G. pallidipes*. Owaga (1981) used the biconical trap for *G. longipennis* but recorded very low numbers.

More recently, some other trap designs have been produced and shown to be more effective than the biconical trap for *G. pallidipes* and *G. morsitans*. These include the Beta trap (Vale, 1982b) and the F2 and F3 traps (Flint, 1985). These

traps are, however, less widely used than the biconical trap as sampling traps because they are bulkier and more expensive. However, their designs were based on the principles recommended by Vale (1982a) for producing an efficient trap, after intensive studies on the trap-orientated behaviour of tsetse. Thus, they can be regarded as model traps from which effective but cheaper and more convenient traps can be developed.

Besides the work on various trap designs, attention has also been directed to identifying odour attractants that could be used to improve trap efficiency. Intensive recent research has confirmed that various substances can be used to greatly increase trap catches for a number of *Glossina* species (see literature review on odours). So far, most of these attractants have only been found to be effective to varying degrees for tsetse species of the *morsitans* group. A few have been tested on the *palpalis* group and found to be less effective. There are no published reports on the response of the *fusca* species to these attractants. Dransfield *et al.* (unpublished data), however, recorded higher numbers of *G. longipennis* when the biconical trap was baited with both cow urine and acetone, although acetone alone was ineffective.

In the search for an effective trap/odour bait system for *G. longipennis*, the first step was to test a number of odour baits known to be effective for other *Glossina* species. The biconical trap, which is still the most widely used sampling trap for many tsetse species, was taken as the standard trap

for these experiments. Having identified effective odour attractants, the biconical trap was compared with the F2 and F3 traps and with a series of new traps developed at Nguruman. It was hoped that this approach could produce a cheaper and more convenient trap. Further experiments on odour attractants were then carried out using the best of the new traps. Following the establishment of the most effective odour baits on the best trap design, the absolute efficiency of the system was estimated using the technique developed by Hargrove and Vale (1979). This involves the use of electric screens around the baited trap.

4.2. MATERIALS AND METHODS

4.2.1. Traps tested.

a) The biconical trap.

Plate 1 shows a biconical trap of the type used in this study. Basically, the trap consists of two cones joined together at their bases over a metal ring of about 60 cm in diameter. The inverted blue lower cone, which forms the attractive part of the trap, has three vertical oval entrances . The upper cone is of white netting. A black piece of cloth is sewn on to the inner walls of the trap in a cruciform manner such that areas of it are visible from outside through the entrances. These areas function as targets to attract flies into the body of the trap after they have been attracted to the vicinity by the blue. Constructional details of the original version of the trap are given by Challier and

Plate 1: The blue biconical trap

Laveissière (1973) and of the improved version by Challier et al. (1977).

For this study, traps were constructed from locally manufactured light weight polyester/cotton for the lower cone (blue or white) and cotton for the black cruciform inner screen(target). The upper cone was of white nylon netting. The blue version was taken as the standard with which all test traps were compared.

b) The F2 and F3 traps

These are basically the same trap type, differing only in the colour of the trap body; white for the F2 (Plate 2) and blue for the F3 (Plate 3). Essentially, the trap is a 1m x 1m x 1m cube of cloth pulled tightly over a metallic frame with a horizontal entrance (1m x 0.3m) at ground level on one side. A target of black cloth (1m x 0.3m) is located on the inner wall of the back directly opposite the entrance of the trap. The cone is recessed in the trap and is made of grey netting. Details of construction are provided by Flint (1985). The traps used in this study were supplied by Low and Bonar, Harare, Zimbabwe. Trap materials were of a heavier weight cotton than that used for the biconical traps. Unlike in the original design, the F2 traps used were set by tying strings from the trap to external poles (see Plate 2). The F3 traps were stretched over aluminium poles as originally designed.

Plate 2: The Zimbabwe F2 trap.

Plate 3: The Zimbabwe F3 trap.

c) The NGU traps

All other traps that were tested were new trap designs, developed at Nguruman jointly with Mr. Brightwell and referred to as the NGU series of traps. These were the NG1A, NG1B, NG2A, NG2B, NG2C, NG2D, NG2E, NG2F, NG3A, NG4A and NG4B traps. The code numbers were given according to the type of netting cone design on the trap. Thus, traps bearing the same number have the same netting cone type and belong to the same model. Different letters within the same model indicate variations in some other parts of the trap body. Constructional details accompanied by diagrams in Figures 4.1, 4.2, 4.3, and 4.4 are given below. In all the figures, cloth measurements are given in width(w) units, where 1w = 1 yard (0.9m), the width of locally purchased cloth in Kenya.

The NG1 Model

This is essentially a triangular version of the F3 but with netting on only two sides of the cone. Two versions were tested, the NG1A and NG1B. The numbered component parts of the NG1A shown in Figure 4.1 are as follows;

1- Body (blue): This was folded along the dotted line in the middle.

2- Target (black): This was the first part of the trap to be affixed to the body as shown in the diagram.

3- Shelf/Front (blue): This was fixed after the target.

The upper half of the rectangular section was fixed along the marked edges of the trap body as shown in Fig. 4.1(1). It was backed on the inside with an equal area of black cloth. The lower half was then tucked inwards and affixed along the horizontal sides of the body to form a shelf above the entrance of the trap as shown in the side view of the trap front (Fig. 4.1(8)).

4 & 5 - Netting cone (white): A 1w x 1w piece of netting was folded diagonally as shown in Fig. 4.1(4) to give Fig. 4.1(5). This was fixed to the body and front of the trap as per points TXYZ indicated on the three component parts (body, netting and front). A 1 cm diameter hole was then cut in the apex and reinforced with cotton stitches.

6- Base (blue): this was affixed last. The entrance of the trap was thus at ground level measuring 1w x 0.5w.

7- shows an assembled NG1A.

To produce the NG1B the following modifications were made;

i) the base was removed.

ii) the target was rotated 90° and affixed as in NG2 model (see below).

iii) the shelf above the entrance was removed (see Fig 4.1(8)).

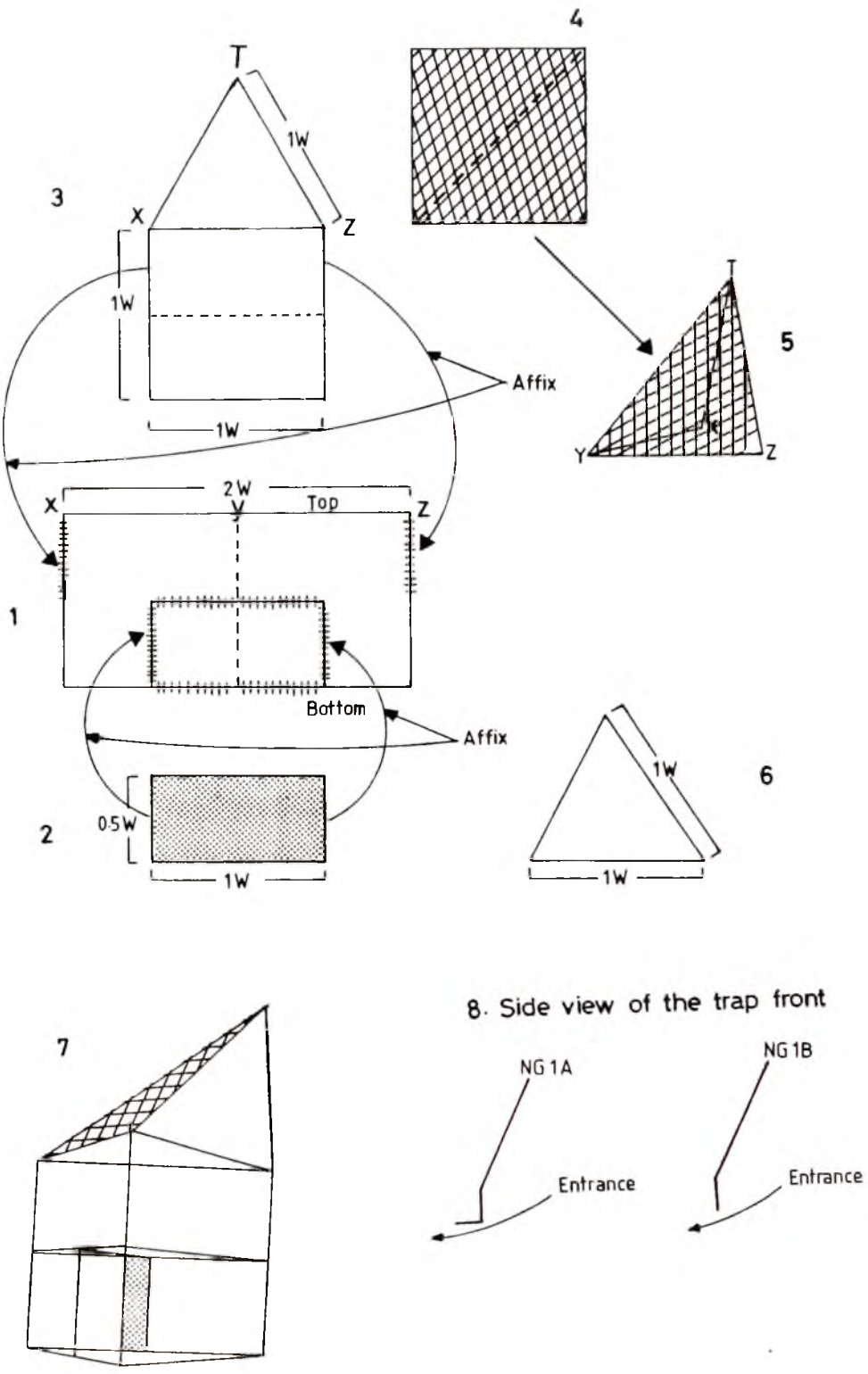

Figure 4.1: Construction of the NG1 trap model.

The NG2 model

The versions produced and tested were the NG2(A - F). The following descriptions based on the diagrams in Figure 4.2 refer to the NG2A.

1- Body (blue): folded along middle dotted line.

2- Target (black): affixed as shown in the diagram.

3- Front: blue on the outside backed by black on the inside and affixed as shown in the diagram.

4- Netting cone (white nylon): A 1w x1w netting was folded along the dotted lines shown in Fig. 4.2(5). A triangular 1/4 piece was cut off as in Fig.4.2(6). Joining the cut edges produced a cone shown in Fig. 4.2(7). The base XYZ of the cone was fixed to the top of the trap by two sides to the blue body and one side to the front. A hole was cut at the apex as before. A diagram of an assembled NG2A trap is shown in Fig.4.2(8).

The variations for the other NG2 models were as follows;

NG2B: The front consisted only of black cloth.

NG2C: i) The front in the NG2B was extended 20cm downwards so that the entrance was reduced.

ii) The lower half of the target was of double thickness.

NG2D: The black front was affixed vertically instead of slanting inwards as indicated in the diagram.

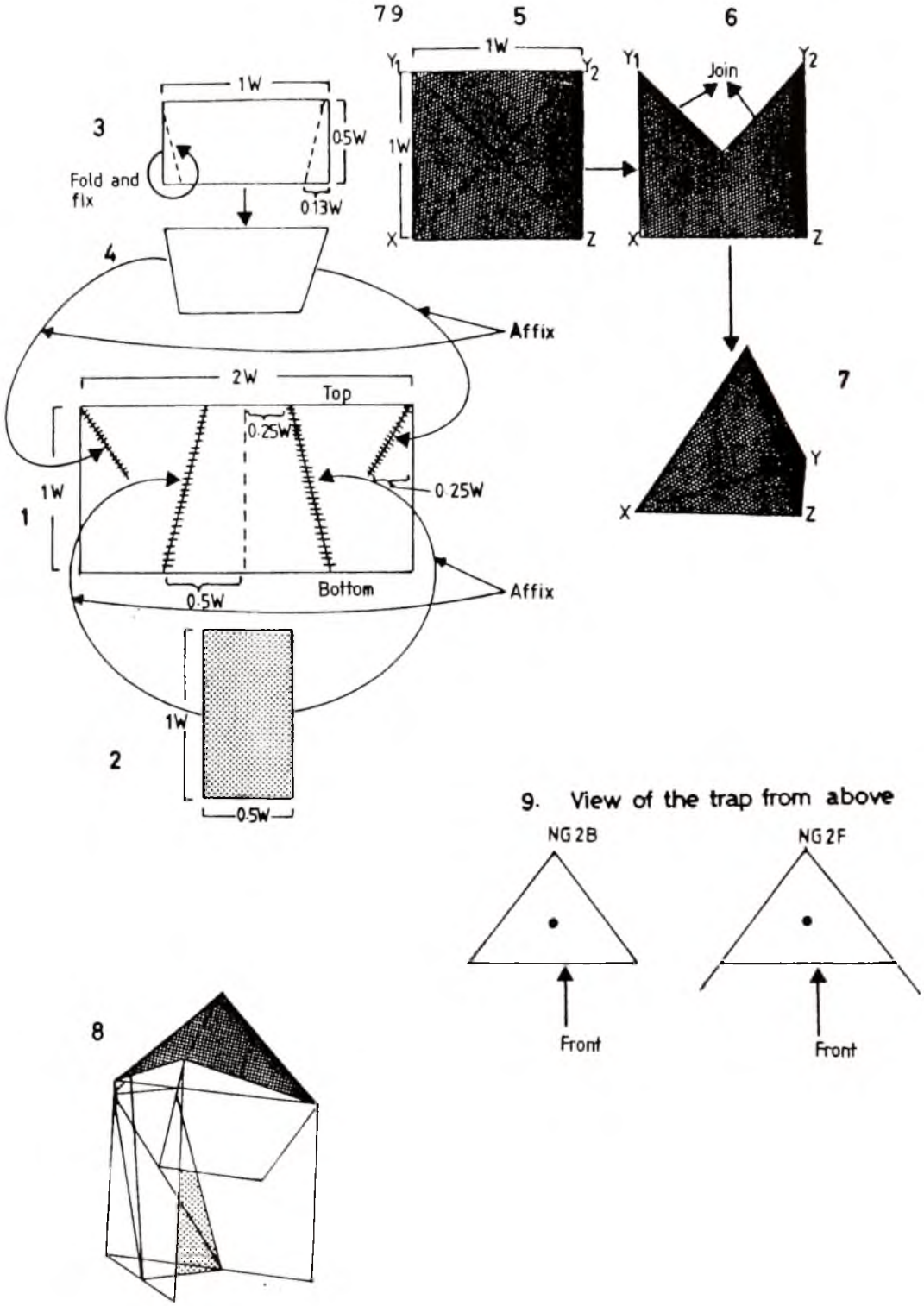

Figure 4.2: Construction of the NG2 trap model.

Plate 4: The ICIPE NG2B trap.

NG2E: White cloth was used for the body instead of blue. Other parts were as for NG2B.

NG2F: Two 1w x 0.5w 'wings' of blue cloth were added to the front sides of the NG2B. Fig. 2(9) shows the difference between the NG2B and NG2F when viewed from above.

Plate 4 shows the NG2B trap, for which Brightwell *et al* (1987) provide a more detailed description of its construction. This includes a description of the 'control' version of the trap. i.e. as would be appropriate for a local control campaign which involves reducing the cost of the trap by replacing the metallic supports with wooden ones. The net cage which was used for experiments was also replaced by a large polythene bag.

The NG3 model

Only one version, the NG3A, was tested. The following descriptions are based on Figure 4.3.

1- Body (blue): The folds in the body of this trap are determined more by the attachment to the netting cone (see below).

2- Target (black): affixed as shown in the figure.

3- Front/shelf (black): affixed as shown in the figure.

4- Netting cone (white): A 1w x 1w square was cut diagonally Fig.4.3(4). One half was folded along the dotted line as shown in Fig.4.3(5) and the marked edges Fig.4.3(6)

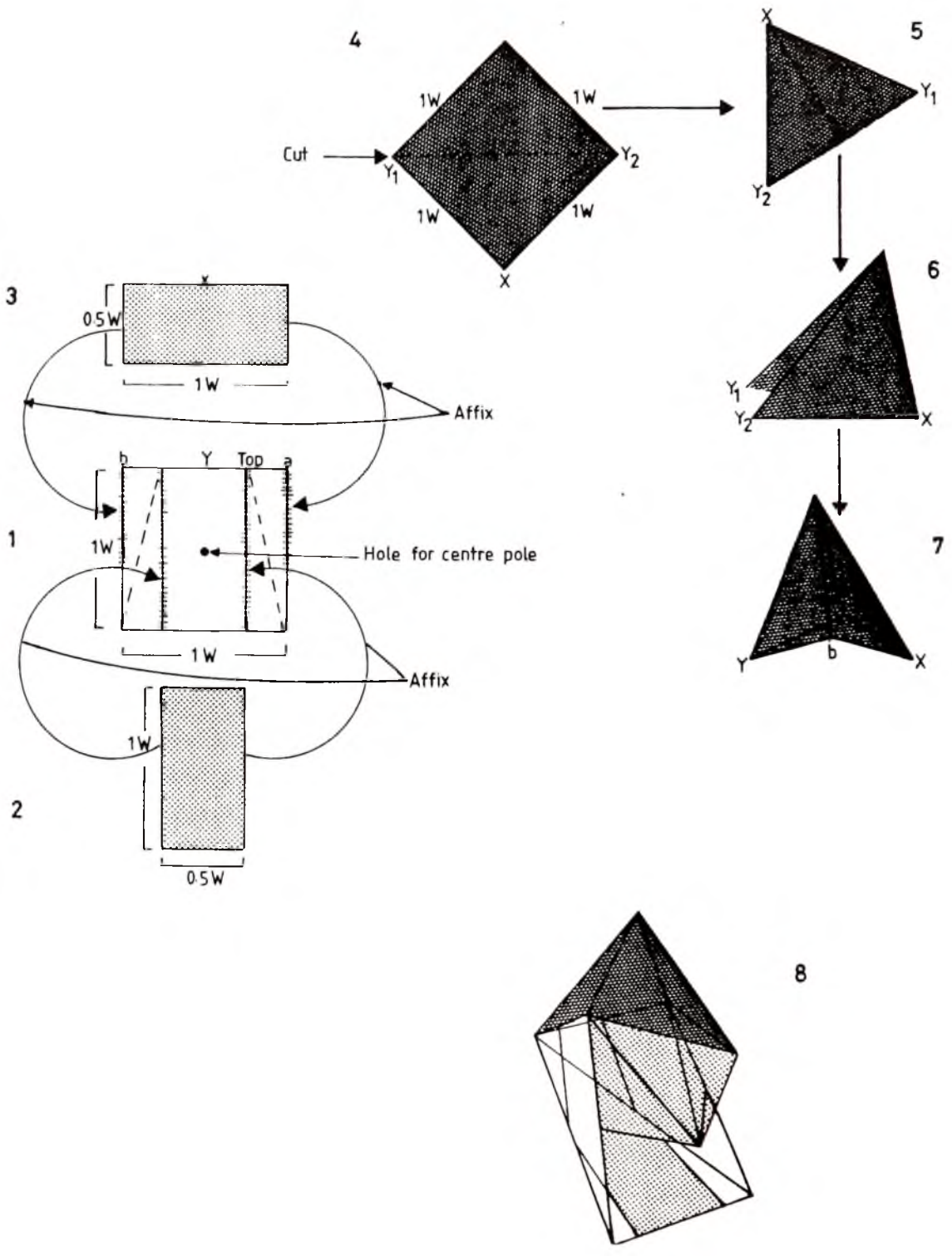

Figure 4.3: Construction of the NG3 trap model.

were joined up. When folded again as was done in Fig.4.3(5), a "hat" was produced with the edges of the base inclined upwards as shown in Fig. 4.3(7). This was affixed to the top of the trap; 'a' and 'b' to the two corners, X and Y to the centres of front and back. A hole was cut in the apex as before. This trap required an additional internal support between X and Y to hold the trap open. The centre pole, carrying the supporting cone underneath the netting (when the trap is set), passed through the position indicated on the body of the trap. A diagram of the assembled trap is shown in Fig.4.3(8)

The NG4 model

The versions tested were the NG4A and NG4B. The descriptions given below are based on Figure 4.4 and refer to the NG4A.

1- Body (blue): no distinct folds.

2- Target (black): affixed to body as indicated.

3- Shelf (black): affixed as shown in the diagram.

4- Netting cone (white): A 0.5w x 0.5w piece was affixed to the top of trap as per points "abcd" shown in the netting and body. The flat piece was pushed up into a convoluted cone shape when the supporting cone was positioned centrally underneath it. An assembled NG4A trap is shown in fig. 4(5)

The NG4B was similarly produced by affixing an equilateral triangle (lw xlw xlw) of netting to an NG2B trap body as shown in Fig.4 (6).

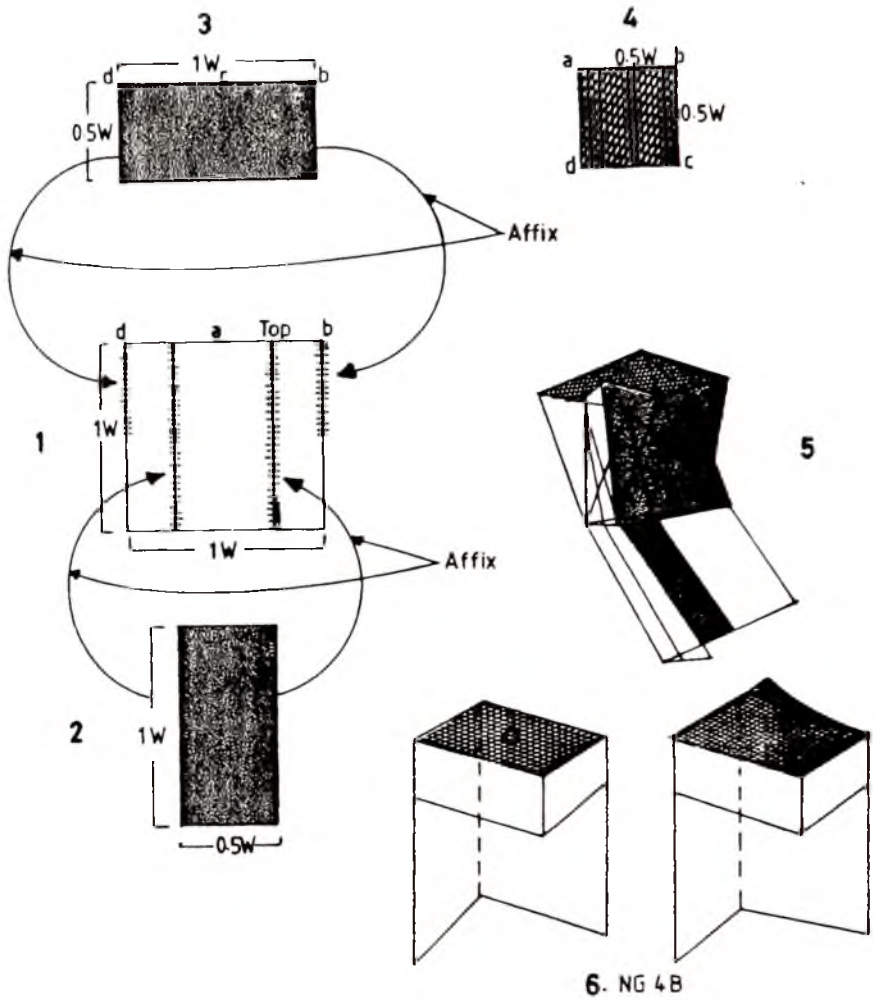

Figure 4.4: Construction of the NG4 trap model.

When set, the netting cones of all traps were supported by a small cone of galvanized wire. A ring opening in the apex of the conical frame coincided with that in the apex of the netting cone of the trap to form the no-return exit hole for flies passing into the collecting cage on top.

The same type of collecting cage was used for all experiments unless otherwise stated. Cages consisted of rectangular bags of nylon netting pulled over rectangular galvanized wire frames measuring 20 x 10 x 7cm. When set, cages were secured over the exit hole at the apex of the trap by a couple of rubber bands put around the sleeve end of the cage.

4.2.2. Odours Baits

Cow urine was collected from local East African Zebu cattle at Nguruman. Buffalo (*Syncerus cafer* Sparrman) urine was obtained from animals in captivity at the Veterinary Laboratories, Kabete, Kenya. Prior to use, the cow urine was usually stored at ambient temperatures for about three weeks in stoppered bottles. The sample of buffalo urine was kept at 4°C for about one week before use. Acetone, methyl ethyl ketone (MEK), 1-octen-3-ol (henceforth termed octenol) and 3-buten-2-ol (butenol) were obtained from the commercial market.

Odour baits were dispensed from glass jars at different dose rates effected by varying the aperture of the container. The following containers were used for the various dose rates;

Cow urine and buffalo urine: These were dispensed from glass jars (600 ml) with an aperture 4.5 cm in diameter which according to Dransfield *et al.*, (1986b) gave a dose rate of *c.* 1000mg/h at afternoon temperatures of 30-35°C. This was considered medium dose rate for cow urine in this study. High and low doses of the urine were obtained from glass jar dispensers with aperture diameters of 8.5 cm and 0.6 cm respectively.

Acetone, MEK and 3-buten-2-ol: High dose (*c.* 2500mg/h) and medium dose (*c.* 500mg/h) were obtained from GIBCO bottles with apertures of 2.2 cm and 0.6 cm respectively whilst low dose (*c.* 150mg/h) was dispensed from a 15-ml bottle with an 0.2 cm aperture. Low dose MEK and 3-buten-2-ol were dispensed from the same dispenser type as used for low dose acetone.

1-Octen-3-ol: This was dispensed from a 10-ml bottle with the top replaced by a rubber septum kept in contact with the chemical by a folded pipe cleaner. This was estimated to give a dose rate of about 0.5mg/h (Dransfield *et. al.*,1986b).

Except where the effect of different odour positions were being tested, odour dispensers were positioned on the ground, 30 cm from the entrance of the trap (from the pole of a biconical trap). Odours were sheltered from the sun and rain by metal tin cans, suitably cut out and clipped over the dispenser openings, leaving enough space underneath for the escape of odour.

4.2.3. Experimental design

Each experiment was conducted using a Latin square design, where the different treatments under comparison were incorporated in replicated Latin squares of treatments x sites x days. This involved the daily rotation of treatments (traps, odours etc.) between sites such that by the end of the experiment each treatment operated in every site. By this design, data collected can be analyzed to separate the effects due to treatments from those due to sites and days.

Traps were normally set about 200 m apart and 30 m away from the vehicle track. For logistical reasons, most experiments were run jointly with the ICIPE research team collecting data on *G. pallidipes*. Therefore, most experiments were run from 1530 h and trap catches collected at 1.5 h intervals until 1830 h when collecting cages were left on overnight for a last collection at 0730 h the following morning. These times include the active periods of both species.

Precautionary measures that were routinely taken to minimize experimental errors included;

i) Setting up the experiment well before starting time and double-checking to ensure that each treatment was at the right site.

ii) Shifting round treatments several hours before running time (especially when comparing odour baits) to be sure that there was no residual effects from previous treatments. For the same reason odour containers were usually

kept tightly closed until the start of each experimental run and the rain/sun covers were continuously shifted round with their respective odour dispensers throughout the experiment.

iii) Collecting cages were usually checked very carefully for holes, before setting them on traps and when catches were being collected. Traps were also regularly inspected for holes, especially in the netting cone.

iv) All odour containers were thoroughly washed after every experiment to ensure that they were clean for subsequent use.

Unless specified otherwise, in the experiments in which different trap types were being compared, traps were usually baited with medium doses of cow urine (CU(m)) and acetone (A(m)), the experiments were run from 1530 h and trap catches collected at the time intervals previously specified.

4.2.4. Details of experiments

Expt. 1

This was to test the efficacy of cow urine and buffalo urine when dispensed on their own and in combination with acetone, using the standard blue biconical trap. (Acetone on its own was already known to have little effect on the catch; Dransfield, *pers. comm.*) Medium dose rates of the urines and

acetone were used in all treatments. The treatments were as follows;

a) unbaited biconical (-)

b) baited with cow urine only (Cu)

c) baited with cow urine and acetone (Cu+Ac)

d) baited with buffalo urine only (Bu)

e) baited with buffalo urine and acetone (Cu+Ac).

Cf. Table 4.1 A and B for the results.

Expt. 2

From the above experiment no significant difference was observed between cow urine and buffalo urine (cf. Table 4.1A) and considering the ready availability of the former, it was selected for further testing. This experiment was to test the effect of octenol on catches, when dispensed together with cow urine and acetone. The effect of reduced dose rate of cow urine was also tested. Again, blue biconical traps were used with the following bait treatments;

a) medium doses of cow urine and acetone

b) medium doses of cow urine and acetone + octenol (0.5mg/h)

c) low dose cow urine and medium dose acetone

The method of dispensing to obtain these dose rates are given in section 4.2.2.

Expt. 3

The experiment on the effect of dose rate of cow urine was repeated with three dose levels; high, medium and low. Another known chemical attractant, methyl ethyl ketone (MEK) was also tested in place of acetone. The blue biconical traps were thus baited as follows;

a) medium doses of cow urine and acetone

b) high dose cow urine and medium dose acetone

c) low dose cow urine and medium dose acetone

d) medium dose of cow urine and low dose MEK

The experiment was run from 1730 h each day, one catch collected at 1830 h and a last collection at 0730 h the following morning. The results of this experiment are given in Table 4.1A and B.

Expt. 4

The effect on trap performance, of adding a light source to a trap was investigated. The light source was provided from a special chemical light-stick 'Cyalume', obtained from Cyanamid Chemical Light Department, New Jersey, U. S. A. This is a cylindrical plastic stick (152 mm long, 90 mm in diameter) containing two different chemicals, one in an inner glass ampule. When the flexible plastic is bent slightly, the inner tube breaks releasing an energy-producing solution that mixes with a greenish fluorescense in the outer tube. A strong chemical reaction, based on peroxyalate chemiluminescence, produces a greenish yellow light. Spectrometer analysis has

Expt. 3

The experiment on the effect of dose rate of cow urine was repeated with three dose levels; high, medium and low. Another known chemical attractant, methyl ethyl ketone (MEK) was also tested in place of acetone. The blue biconical traps were thus baited as follows;

a) medium doses of cow urine and acetone

b) high dose cow urine and medium dose acetone

c) low dose cow urine and medium dose acetone

d) medium dose of cow urine and low dose MEK

The experiment was run from 1730 h each day, one catch collected at 1830 h and a last collection at 0730 h the following morning. The results of this experiment are given in Table 4.1A and B.

Expt. 4

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shown that this light gives a single emission peak at 510 nm. More details of this can be obtained from Service and Highton (1980).

The light stick was tied to one of the inner corners of the collecting cage frame just before setting the cage on the trap. Other treatments included for comparison were the white biconical trap, baited with two dose levels of cow urine (medium and low) each with medium dose acetone. All baited blue biconicals were with medium doses of cow urine and acetone. Thus, the treatments effected in this experiment were as follows;

a) unbaited blue biconical

b) baited blue biconical

c) baited blue biconical + light

d) baited white biconical

e) white biconical (low dose cow urine)

The experiment was run from 1730 h each day, and the trap catches were collected in the same time periods as in the previous experiment. Results are given in Table 4.1A and B.

Expt. 5

Having observed from the preceding experiments that cow urine and acetone produced a substantial increase in catch (cf. Table 4.1B) but neither additional odours nor light significantly increased catches, attention was then directed at testing the performances of different trap types. In this experiment the blue and white biconical traps and the Zimbabw

F2 and F3 traps were tested. All traps were baited with medium doses of cow urine and acetone.

a) baited blue biconical

b) baited white biconical

c) baited F2

d) baited F3

The experiment was run from 1730 h each day and catches collected at the same time periods as specified above. The results are included in Table 4.2A and B.

Expt. 6

This was, essentially, a repeat comparison of the performances of white and blue biconical traps owing to the low catches that were recorded in the previous experiment. Unbaited and baited white biconical traps were compared with a baited blue biconical trap in a 3 x 3 Latin square. All traps were baited with medium doses of cow urine and acetone. See Table 4.2B for results.

Expt. 7

This was designed, mainly, to assess the performance of the Zimbabwe F3 trap in its complete form and in a slightly modified version. In one treatment the trap was set, complete with the blue detachable plastic floor and in another the floor was omitted. The first trap of the NGU series, the NG1A was included as a third treatment. Thus, the three traps all

baited with medium doses of cow urine and acetone were;

a) F3 (with base)

b) F3 (without base)

c) NG1A

he results are included in Tables 4.2 A and B.

Expt. 8

Owing to the poor performance of the NG1A some modifications were made on it to produce the NG1B (see Fig. 4.1). This was tested together with two other traps of a new model (NG2A and NG2B). Unbaited and baited biconical traps were included for comparison. Thus, in a 5 x 5 Latin square design, the following treatments were effected;

a) unbaited biconical

b) baited biconical

c) NG1B

d) NG2A

e) NG2B

See Tables 4.3 A and B for results.

Expt. 9

Based on the results of the previous experiment the NG2B was selected for further testing. Two more new NGU trap models, NG2C and NG3A, were then tested together with the NG2B. These were again compared with the baited and unbaited

biconical traps in a 5x 5 Latin square with the following treatments;

a) unbaited biconical

b) baited biconical

c) NG2B

d) NG2C

e) NG3A

Expt. 10

Based on its superior performance in the previous experiment, the NG2B was again selected from the previous experiment and tested together with another couple of new traps (NG2D and NG4A). Baited and unbaited biconical traps were as usual included as controls giving rise to five treatments;

a) unbaited biconical

b) baited biconical

c) baited NG2B

d) baited NG2D

e) baited NG4A

Expt. 11

The NG2B which again showed up best in the previous experiment, was tested together with another set of two NGU

trap models (NG2E and NG4B) and compared with biconical traps as above. Treatments were as follows;

a) Unbaited biconical

b) baited biconical

c) baited NG2B

d) baited NG2E

e) baited NG4B

Expt. 12

The results of the above experiments indicated that the NG2B was more effective than the biconical trap especially for female *G. longipennis*. Therefore the former trap was used in this experiment for a repeat test of the separate and combined effects of cow urine and acetone. A baited blue biconical trap was included for comparison. Medium doses of cow urine and acetone were used in the following treatments;

a) baited biconical

b) unbaited NG2B

c) NG2B baited with acetone alone

d) NG2B baited with cow urine alone

e) NG2B baited with acetone and cow urine.

The experiment was run from 1730 h each day, with one collection at 1830 h and another at 0730 h the following morning.

Expt. 13

This was to investigate the effect of different odour positions on catches by the NG2B trap. Using the usual medium doses of cow urine and acetone, four bait positions were selected and tested;

a) baits placed 30 cm in front of the trap

b) baits placed 90 cm in front

c) baits placed 30 cm behind

d) baits placed 30 cm in front plus another jar of cow urine (also medium dose) positioned 10 m in front.

A similarly baited blue biconical trap (baits in the usual position) was included for comparison.

Expt. 14

The effect of urine temperature on trap catches was investigated by baiting NG2B traps with urines at different temperatures. The urine temperatures were maintained at 20, 3(and 40°C ± 1°C, by immersing the urine jars in water at these temperatures in 15-litre polystyrene boxes. These three temperature regimes were compared with urine at ambient temperatures in a 4 x 4 Latin square design. In all the treatments the urine (medium dose) operated in combination with acetone (medium dose) at ambient temperatures. The experiment was run from 1730 h each day and catches collected as in the previous experiments.

Expt.15

It was often observed that some trapped flies remained perched on the inner walls of the netting cones of the traps. This led to some modification on the cone of the NG2B trap aimed at getting flies to move up faster into the collecting cage. First, a different type of cone material was introduced. This was polyester/cotton netting with a coarser mesh compared to the original cone material which was of fine nylon mesh. Next, a 3-inch-wide strip of black cloth was sewn along the full length of each of the three corners of the cones (both old and new types). In a third treatment, the black shelf (above entrance) was replaced by a white one. A fifth treatment was to test the effect of a lower dose rate of acetone on catch by the NG2B trap. The five treatments were as follows;

a) NG2B (original)

b) NG2B (old cone) + black strips

c) NG2B (new cone) + black strips

d) NG2B white front

e) NG2B (original), (low dose acetone)

All traps were baited with medium doses of cow urine and acetone except in treatment 'e' where the medium dose acetone was replaced by low dose.

Expt. 16

A direct comparison of the F3 and NG2B traps was made. The 'bait-behind' position with the NG2B trap was also repeated in this experiment as one treatment. The fourth treatment was the control version of the NG2B trap. In this version most of the metallic supports of the trap were replaced by wooden ones and a large polythene bag drawn out into a tetrahedron was used for the collecting cage. Constructional details can be obtained from Brightwell *et. al.* (1987). All traps were baited with medium dose cow urine and low dose acetone; (from the previous experiment it was observed that low dose acetone did not reduce catches and could thus be conveniently used in place of medium dose). The experimental treatments were as follows.

a) NG2B (original)

b) F3

c) NG2B (bait behind)

d) NG2B (control version).

Expt. 17

The new cone material (polyester/cotton, open mesh) was tested again without the black strips along the corners. Another modification was made on the NG2B to increase the area of attractive blue; a 1 x 0.5 metre piece of blue cloth 'wing' was sewn on lengthwise to each of the front sides of the trap. The resultant version was termed the NG2F or "winged NGU". A fourth treatment was to test the efficacy of 3-buten-2-ol

(0.5mg/h), dispensed in combination with medium dose cow urine and low dose acetone . The other traps were baited only with similar doses of cow urine and acetone. The treatments effected were:

a) NG2B (old cone); cow urine (med. dose) + acetone (low dose)

b) NG2B (new cone); cow urine (med. dose) + acetone (low dose)

c) NG2F; cow urine (med. dose) + acetone (low dose)

d) NG2B; cow urine and acetone as above + 3-buten-2-ol (0.5mg/h).

4.2.5. Analysis of data

Separate analyses were carried out on numbers of males and females so as to be able to detect any differences between the two sexes in their responses to the various treatments. For each experiment, data from the two replicates of the Latin square design, were subjected to an analysis of variance. Before analysis the data were subjected to a log transformation (N + 1 ,to take care of zeros) to normalize the data. By this method, treatment effects can be separated from those due to days and sites. Where the treatment effect was significant, the differences between treatment means were further compared by the Duncan's multiple range test.

The relative efficacies of the different odour baits tested were estimated by computing an index of catch increase over an unbaited biconical trap; i.e. the ratio of the

detransformed mean catch with the odour bait to that of an unbaited biconical trap. To assess the performances of the different trap types (including new trap designs), an index of increase over a similarly baited biconical trap was computed. The effects of further modifications on the NG2B were also assessed by comparing mean catches by the modified versions to those of a similarly baited original NG2B. The ovarian aging method (Saunders, 1960; Challier, 1965) was used to age female *G. longipennis* from all experiments. In brief, this technique categorizes female flies into eight age groups (Oa&b-7) according to the stage of the follicular development. Categories Oa & Ob flies are very young flies which have never larviposited and are termed nulliparous whilst flies in groups 1-7 have larviposited once or more times and referred to as parous (See Chapter 7 for more details). Differences between the age compositions from different trap types and odour baits were tested using the chi-square analysis.

4.2.6. Test of trap efficiency

The efficiency of the best trap model (the NG2B) was estimated using the technique developed by Vale and Hargrove (1979) and later improved by Hargrove (1980b). This involved making an incomplete ring of electric screens round the baited trap. The number of flies caught by the trap and those caught on the outside and inside surfaces of the screen were then used to estimate the efficiency of the trap.

The electric screens used for this study were of the type designed by Vale (1974b). The same screens, measuring 90cm x 90cm were used for the activity pattern studies described in detail in chapter 5. Two NG2B traps, similarly baited with cow urine (c. 1000mg/h) and acetone (c. 500 mg/h), were set about 200 m. apart in open glades in the woodland. One of the traps was surrounded by three screens each placed at about 3 m from the base of the trap, with one screen facing the entrance of the trap whilst the other two faced the two lateral sides of the trap, thus forming an incomplete ring. A shallow tray filled with water was placed at the base of each side of the screens to retrieve electrocuted flies. The other trap was similarly set up but without screens. At about 1700 h the screens were turned on, the odour baits opened and a collecting cage put on each of the trap. Collections were made at hourly intervals from the screens and the trap until 2000 h when evening activity ceased. Catches were also made during the morning activity period. The test was repeated four times alternating the screens between traps on alternate days. Thus, for each test, the unscreened trap acted as a control. Flies caught from the inside and outside surfaces of the screens and in the retaining cage of the trap were kept separate. The data were, however, pooled over the four days before carrying out the analysis because of the small numbers caught on individual days but the data on males and females were kept separate.

4.3. RESULTS

4.3.1. Efficacy of odours

Results of the initial tests of odour attractants are given in Table 4.1A, showing detransformed mean catches of male and female *G. longipennis* with the indices of increase of odour baits in relation to an unbaited trap in Table 4.1B. Neither cow urine nor buffalo urine on their own increased catches over an unbaited trap. However, they both showed significant increases when dispensed together with acetone. The trends were the same for both sexes. Taking the average for both sexes, there was a 4.9X increase with buffalo urine and acetone and 3.6X increase for cow urine and acetone. There was, however, no significant difference between the cow and buffalo urine.

There were differences between the different dose rates of cow urine with the highest dose rate giving the highest index of increase, similar in fact to medium dose buffalo urine. There was a significant reduction in the catches of both sexes with low dose cow urine.

Catches were also reduced but not significantly when MEK instead of acetone was dispensed with medium dose cow urine. When 1-octen-3-ol was tested the treatment effect was not significant, but the raw data showed that the octenol treatment yielded the highest mean catches on both sexes (expt. 2). It does appear that octenol has the potential to increase catches but the catches in this experiment were

Table 4.1A: Total trap catches, detransformed means, and ANOVA F-ratios for *G longipennis* using various odour baits.

		G. longipennis					
		Males			Females		
Expt.	Odour	Tot	Detr. mean	F-ratio &df	Tot	Detr. mean	F-ratio &df
1.	-	60	3.9b		28	2.0b	
	Cu(m)	56	2.9b		37	2.9b	
	Cu(m),A(m)	212	14.0a	11.90***	88	7.2a	12.90***
	Bu(m)	51	3.3b	(4,24)	27	1.7b	(4,24)
	Bu(m),A(m)	240	17.8b		137	10.6a	
2.	Cu(m),A(m)	23	2.8		3	0.4	
	As above+octen	28	4.4	2.15ns	5	0.7	0.27ns
	Cu(l),A(m)	12	1.3	(2,4)	3	0.4	(2,4)
3.	Cu(m),A(m)	122	12.6ab		52	4.7ab	
	Cu(h),A(m)	218	16.6a	4.10*	62	6.2a	4.90*
	Cu(l),A(m)	56	5.2b	(3,12)	28	3.0b	(3,12)
	Cu(m),MEK(l)	123	9.3ab		41	2.9b	

Means followed by the same letter are not significantly different from each other ($P<0.05$); F-ratios: *=$P<0.05$; **=$P<0.01$; ***=$P<0.001$

4.1B.:Indices of increase for *G. longipennis* for various odour baits relative to an unbaited trap.

	Males	Females
Unbaited	1.0	1.0
Cu(m)	0.7	1.5
Bu(m)	0.8	0.9
Cu(l),A(m)	1.6	2.9
Cu(m),A(m)	3.6	3.6
Cu(h),A(m)	4.7	4.7
Bu(m),A(m)	4.6	5.3
Cu(m),MEK(l)	2.5	2.2
Cu(m),A(m)+Octen	5.8	6.5
Expt.8-11: Cu(m),A(m)		
i)	15.0	6.3
ii)	4.1	4.5
iii)	3.0	6.3
iv)	6.3	4.7
Weighted mean	7.5	5.6

generally very low. The experiment needs repeating, using the more efficient NG2B trap, for a confirmation of these results.

Considering various other experiments in which medium doses of cow urine and acetone were compared with the unbaited biconical trap (expts. 8-11), the index of increase of the cow urine/acetone ranged from 3.0-15.0 for males and 4.5-6.3 for females. The weighted mean indices taken from these experiments were 7.5X for males and 5.6X for females. The higher value for males results from the weighting factor for experiment 8 when the largest numbers of *G. longipennis* were caught; examination of all the data reveals little evidence for any difference between males and females in the response to cow urine and acetone.

4.3.2. Trap performance

Having identified medium doses of cow urine and acetone as effective attractants for *G. longipennis*, various established trap types were tested using these odour baits. The results for these experiments are given in Table 4.2A with the indices of increase in Table 4.2B. The addition of the chemical light did not improve catches by the blue biconical trap. In fact the trap without light yielded higher mean catches on both sexes than the lighted trap.

There was much variability in the performance of the white biconical trap. In experiment 4, the white biconical trap caught significantly more males than the blue one. The treatment effect on the female catch was not significant but

Table 4.2A.: Total trap catches, detransformed means, and ANOVA F -ratios for *G. longipennis* using various trap designs.

		G. longipennis					
		Males			Females		
Expt.	Odour	Tot	Detr. mean	F-ratio &df	Tot	Detr. mean	F-ratio &df
4.	Blue bicon	36	2.1b		8	0.6	
	Blue bicon (+light)	30	1.8b		8	0.4	
	White bicon	55	4.0a	3.20*	22	1.2	2.45ns
	White bicon Cu(l),A(m)	31	1.9b	(4,24)	6	0.4	(4,24)
	Blue bicon (unbaited)	12	0.9c		3	0.1	
5.	Blue bicon	18	1.6		5	0.4	
	White bicon	25	1.9	0.25ns	17	0.7	2.55ns
	F3	18	1.7	(3,12)	17	1.4	(3,12)
	F2	18	1.2		26	1.6	
6.	Blue bicon	89	11.3a		23	3.8	
	White bicon	39	4.5b	18.23*	11	1.3	2.13ns
	White bicon (unbaited)	12	1.5c	(2,4)	9	1.3	(2,4)
7.	F3 (+Base)	48	3.5ab		47	3.6ab	
	F3 (-Base)	101	6.8a	6.81***	95	8.5a	12.21***
	NGlA	20	1.2b	(2,4)	18	1.3b	(2,4)

Table 4.2B. Indices of increase for *G. longipennis* for various trap types relative to a biconical trap.

		Males	Females
Blue bicon		1.0	1.0
Blue bicon (+light)		0.9	0.7
White bicon	i)	1.9	2.0
	ii)	1.2	1.8
	iii)	0.4	0.3
Weighted mean		1.3	1.4
F3 (+Base)		1.1	3.5
F3 (-Base)		2.1	8.3
F2		0.8	4.0

the white biconical trap still recorded the highest catches. In experiment 5, the white biconical trap again recorded slightly higher catches than the blue but the treatment effects were generally not significant. The white and blue biconical were again compared in experiment 6, where the treatment effect was just significant at the 5% level only on the male catches but not on the females. Here, the blue biconical came out significantly better on the males and also recorded the highest female mean catch. A re-analysis after combining both sexes showed no significant treatment effects for both sexes. The weighted mean indices of increase of the white biconical trap over the blue (taken for experiments 4, 5, and 6) were 1.3 for males and 1.4 for females. Thus, the two colours were basically similar in performance for *G.longipennis*.

In the experiment that the F2 and F3 traps were tested (expt.5) together with the blue and white biconicals traps, the treatment effect was not significant. Catches were generally very low in the area where the experiment was carried out. Both the F2 and F3 traps caught similar numbers of males as the blue biconical trap but 3.5-4X more females. The F3 caught slightly more males than the F2 whilst it was the reverse for females. The F3 trap performed better for both male and female *G.longipennis* when set without the blue plastic base than with the base although there were no significant differences between their mean catches. On

average, the trap was twice as effective without the base (expt. 7).

The results on the tests of new trap designs are given in Table 4.3A. with the indices of increase in Table 4.3B. The first new trap to be tested was the NG1A in experiment 7. Compared to the biconical trap, this trap was less effective for males but slightly more effective for females. There was a considerable improvement in performance when the base of the NG1A trap was removed giving rise to the NG1B (expt. 8). Whereas the NG1A was about as effective as a biconical for females, the NG1B was nearly 5x as effective. However in the same experiment the two versions of the NG2 model were even better than the NG1B so efforts were concentrated on these.(expts 8-11).

There was no significant difference in catch between the NG2A and the NG2B so since the NG2B used rather less material than the NG2A, it was adopted for further experiments. Subsequent modifications (NG2C - E) did not increase catch significantly. Averaging over the six experiments when the NG2B was compared with the biconical, the NG2B trap was consistently more effective (4.0X) for females. On males, however, the NG2B yielded a significantly higher mean catch than the biconical on only one occasion (expt. 8), giving an average of 1.2X the catch in a biconical trap. The average percentage female catch by the NG2B trap was 46.5 $\pm$ 8.8% as compared to 24.8 $\pm$ 8.9% for the biconical trap. The NG3A and

Table 4.3A: Total trap catches, detransformed means,and ANOVA F-ratios for *G longipennis* using the new NGU traps.

		G. l o n g i p e n n i s					
		M a l e s			F e m a l e s		
Expt.	Trap type	Tot	Detr. mean	F-ratio &df	Tot	Detr. mean	F-ratio &df
8.	Bicon Unbaited	4	0.3c		6	0.4c	
	Bicon	80	4.5b	18.90***	39	2.5b	29.85***
	NG1B	98	5.9ab	(4,24)	188	12.1a	(4,24)
	NG2A	108	7.4ab		206	13.6a	
	NG2B	171	13.1a		288	19.2a	
9.	Bicon (Unbaited)	35	2.2b		16	1.1	
	Bicon	147	9.0a	5.52**	94	4.9a	13.51***
	NG2B	98	8.7a	(4,24)	137	10.7a	(4,24)
	NG2C	110	8.9a		121	9.6a	
	NG3A	43	3.2b		37	2.0b	
10.	Bicon (Unbaited)	45	3.6b		5	0.3b	
	Bicon	147	10.8a	8.27***	33	1.9a	14.28***
	NG2B	67	6.2a	(4,24)	43	3.4a	(4,24)
	NG2D	69	6.0a		48	4.2a	
	NG4A	28	2.1b		6	0.4b	

Table 4.3A (contd)

G. l o n g i p e n n i s

Expt.	Trap type	Males Tot	Males Detr. mean	Males F-ratio &df	Females Tot	Females Detr. mean	Females F-ratio &df
11.	Bicon (Unbaited)	11	0.9c		4	0.3c	
	Bicon	76	5.7ab	19.33***	21	1.4b	12.17***
	NG2B	102	7.7a	(4,24)	53	4.1a	(4,24)
	NG2E	60	3.2b		63	4.7a	
	NG4B	50	4.5ab		21	1.7b	

Means followed by the same letter are not significantly different from each other (P<0.05); F-ratios: *=P<0.05; **=P<0.01; ***=P<0.001

Table 4.3B.:Indices of increase for *G. longipennis* for traps of the NGU series.relative to the blue biconical trap.

		Males	Females
Baited Bicon		1.0	1.0
NG1A(expt.7)		0.4	1.4
NG1B		1.3	4.8
NG2A		1.6	5.4
NG2B	i)	2.9	7.7
	ii)	1.0	2.2
	iii)	0.6	1.8
	iv)	1.4	2.9
expt. 12	v)	1.5	5.1
expt. 13	vi)	0.5	1.6
Weighted mean		1.2	4.0
NG2C		1.0	2.0
NG2D		0.6	2.2
NG2E		0.6	3.4
NG3A		0.4	0.4
NG4A		0.2	0.2
NG4B		0.8	1.2

NG4A models were significantly less effective than the biconical trap whilst the NG4B gave similar catches.

4.3.3.Efficacy of odours with the NG2B trap

Table 4.4A shows the results of further tests, using the NG2B trap, on the influence of certain factors on odour bait efficacy, with the indices of increase in Table 4.4B. The apparent synergistic effect of cow urine and acetone for *G. longipennis* was confirmed in experiment. 12. Neither cow urine nor acetone on their own increased catch significantly, but together increases were 5.2X for males and 4.2X for females.

In the test on odour positions the treatment effect was not significant meaning, there were no significant differences between the mean catches from the different odour positions tested (expt. 13). However, positioning the bait 30 cm behind the trap did appear to increase catches markedly. When the test was repeated in experiment 16, this position again yielded higher (but again not significant) mean catches of both sexes.

The effect of temperature on the efficacy of cow urine was also not significant. However, catches at 20_oC were consistently lower than those at 30_oC whilst catches at ambient temperature (32oC) and 40oC were consistently higher. This indicates a reduction in catch with decreasing temperature on both sexes and suggesting that if the urine temperature goes below 30°C, catches could be reduced.

Table 4.4A.: Total trap catches, detransformed means, ANOVA F-ratios for *G. longipennis* using different odour baits.

		G. longipennis					
		Males			Females		
Expt.	Odour/ Treament	Tot	Detr. mean	F-ratio &df	Tot	Detr. mean	F-ratio &df
12.	Unbaited	54	4.5b		56	5.4b	
	Cu(m)	80	6.7b	10.08***	112	8.4b	6.88***
	A(m)	77	6.8b	(4,24)	96	7.7b	(4,24)
	Cu(m), A(m)	263	23.4a		289	22.9a	
	Bicon (Cu(m),A(m))	244	15.3a		66	4.5b	
13.	30cm in front	172	12.7		139	10.3ab	
	90cm in front	208	16.4	2.22ns	226	16.9a	4.17*
	30cm behind	179	13.4	(4,24)	272	17.7a	(4,24)
	30cm in front (+10m in front)	222	15.1		200	15.3a	
	Bicon	483	23.6		97	6.5b	
14.	Ambient	72	6.5		49	4.7	
	Urine 20°C	33	3.0	2.00ns	27	1.8	1.86ns
	Urine 30°C	47	5.6	(3,12)	33	2.6	(3,12)
	Urine 40°C	62	6.4		46	4.3	

Means followed by the same letter are not significantly different from each other ($P<0.05$); F-ratios: *=$P<0.05$, **=$P<0.01$, ***=$P<0.001$

Table 4.4B Indices of increase for *G. longipennis* for various experimental treatments relative to an unbaited NG2B trap.

	Males	Females
Unbaited	1.0	1.0
Cu(m)	1.5	1.6
A(m)	1.5	1.4
NG2B Cu(m),A(m)	5.2	4.2
90cm in front	6.8	6.7
30cm behind	5.7	7.1
30cm + 10m in front	6.2	6.3
Urine 20°C	2.6	1.7
Urine 30°C	4.7	2.5
Urine 40°C	5.2	3.8

Table 4.5A summarizes the results on the effects on trap performance of lowering the dose rate of acetone, of using 3-buten-2-ol (an octenol analogue) in conjunction with the cow urine/acetone and of further modifications on the NG2B. Indices of increase are given in Table 4.5B. There was little evidence of any difference between the two dose levels of acetone, so subsequent experiments were carried out using the low dose rate of acetone. Putting the baits behind the trap again increased the catch but not significantly. The use of butenol in addition to the cow urine and acetone resulted in a significant reduction in female catch. On the males the treatment effect was not significant but the mean catch with cow urine/acetone alone was still higher than that with butenol.

Further modifications on the cone of the NG2B trap (expts. 15 & 17) did not improve the performance of the trap. Replacing the black front with a white one gave a slight increase in catch on the females but not on males. The 'control version' of the NG2B yielded a substantial increase in the male catch as well as a slight increase in the female catch. The NG2F model also recorded a higher female catch (1.4X more) than the original NG2B trap but there was no significant difference between their mean catches. On the males, the treatment effect was not significant but again the NG2F recorded the highest catch.

Compared to the F3 trap, the NG2B trap caught significantly less males. The treatment effect on females was

Table 4.5A: Total trap catches, detransformed means and ANOVA F-ratios for *G. longipennis* using various odour baits and modifications of the NG2B.

		G. longipennis					
		Males			Females		
Expt.	Odour/ Treament	Tot	Detr. mean	F-ratio &df	Tot	Detr. mean	F-ratio &df
15.	NG2B (Cu(m),A(l))	34	2.9		23	2.0	
	NG2B (Cu(m),A(m))	29	2.6		36	2.6	
	NG2B+strips (Cu(m),A(m))	39	2.7	0.20ns	26	2.3	1.54ns
	New cone NG2B +strips(Cu(m),A(m)	28	2.3	(4,24)	26	2.2	(4,24)
	NG2B(white front) (Cu(m),A(m))	34	2.5		37	3.4	
16.	NG2B(Cu(m),A(l)	24	1.8b		23	2.3	
	NG2B(Cu(m),A(l) (Baits behind)	37	3.3ab		29	2.7	
	NG2B(Cu(m),A(l) (control version)	71	6.5a	4.5*	37	3.2	0.87ns
	F3 (Cu(m),A(l))	60	5.2a	(3,12)	67	5.2	(3,12)
17.	NG2B(Cu(m),A(l)	38	4.3		37	3.7a	
	As above +butenol	26	2.7	2.22ns	31	2.0b	7.42*
	Newcone NG2B (Cu(m),A(l)	25	2.7	(3,12)	37	3.1a	(3,12)
	NG2F(Cu(m),A(l)	45	5.1		5.6	5.3a	

Means followed by the same letter are not significantly different from each other (P<0.05); F-ratios: *=P<0.05, **=P<0.01, ***=P<0.001.

Table 4.5B.: Indices of increase for *G. longipennis* for various odour baits and trap modifications relative to a NG2B trap baited with low dose acetone and cow urine.

	males	females
Odours:		
CUAc(l)	1.0	1.0
CUAc(m)	0.9	1.3
CUAc behind trap	1.8	1.1
butenol	0.6	0.5
Trap modifications:		
NG2B standard	1.0	1.0
+ black strips	1.1	0.9
+ poly/cotton cone#	0.7	0.9
+ white front	1.0	1.3
control version	3.6	1.4
NG2F	1.2	1.4
F3	2.9	2.3

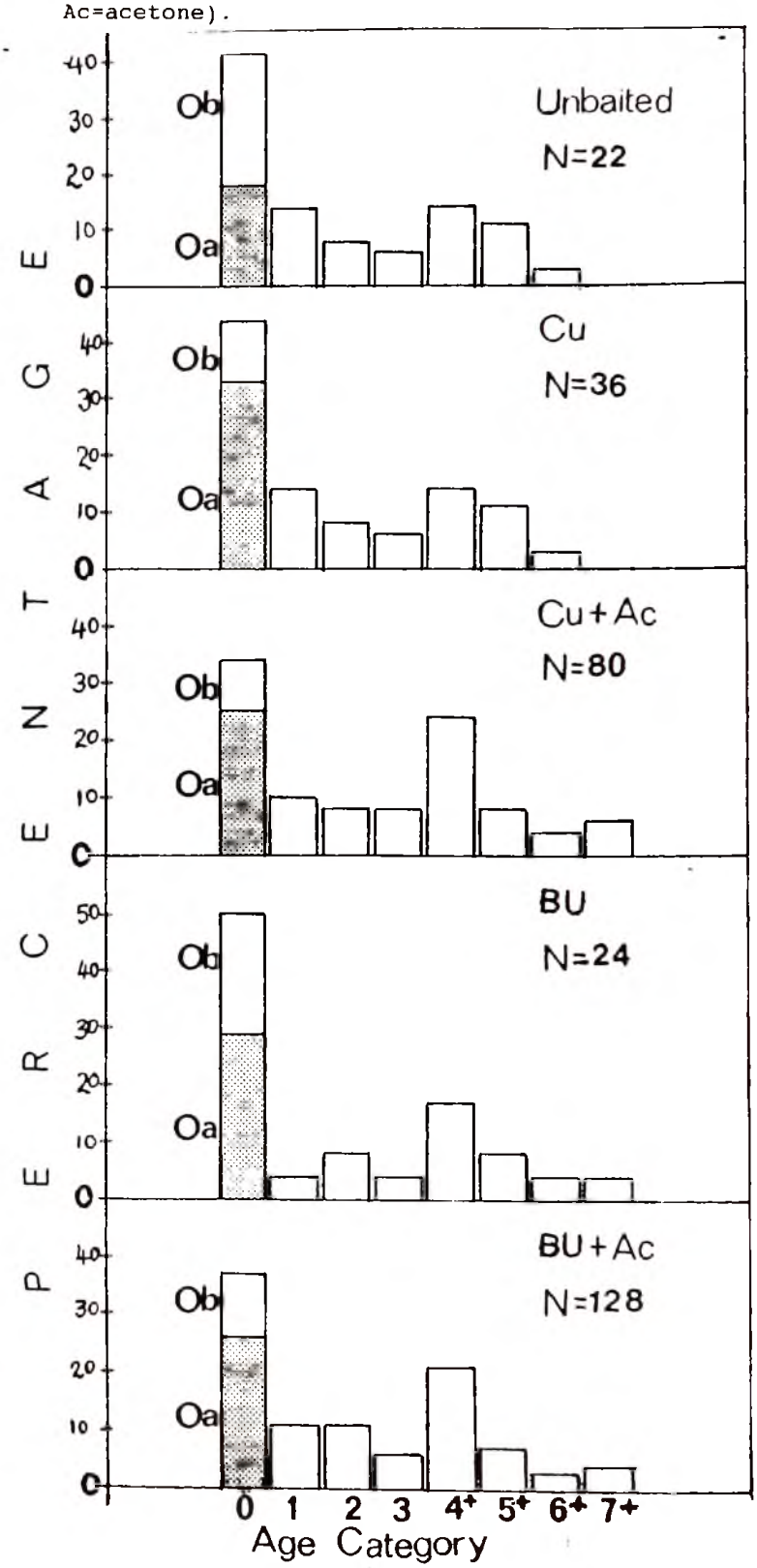
N.B. Index for poly/cotton cone alone was obtained by taking mean of values from expts. 15 and 17.

not significant although the F3 trap again caught about twice as many as the NG2B trap. The data suggest however that a 'control' version of the NG2F would do as well as if not better than the F3 trap for *G. longipennis*.

Figure 4.5 gives the age distribution of females from biconical traps baited with different chemicals. The chi-square test showed no significant association between age composition and bait treatment (X^2 = 4.5^{ns}, df=3, P>0.05). Generally, there is a relatively high preponderance of Oas and Obs which is characteristic of the biconical trap as shown below.

The age distributions of females from three different NGU trap models and a similarly baited (cow urine and acetone) biconical trap are given in Figure 4.6. A chi-square analysis on the age compositions grouped into nulliparious (categories Oa and Ob) and parous (categories 1 -7) flies (Challier, 1965) showed a significant association between trap type and age composition (X^2 = 31***, df=3, P<0.001). Generally, the NGU traps caught a higher proportion of older flies than the biconical trap.

Figure 4.5: Age distribution of female G. longipennis caught in the blue biconical trap baited with different chemicals (CU=cow urine, BU=buffalo urine and Ac=acetone).



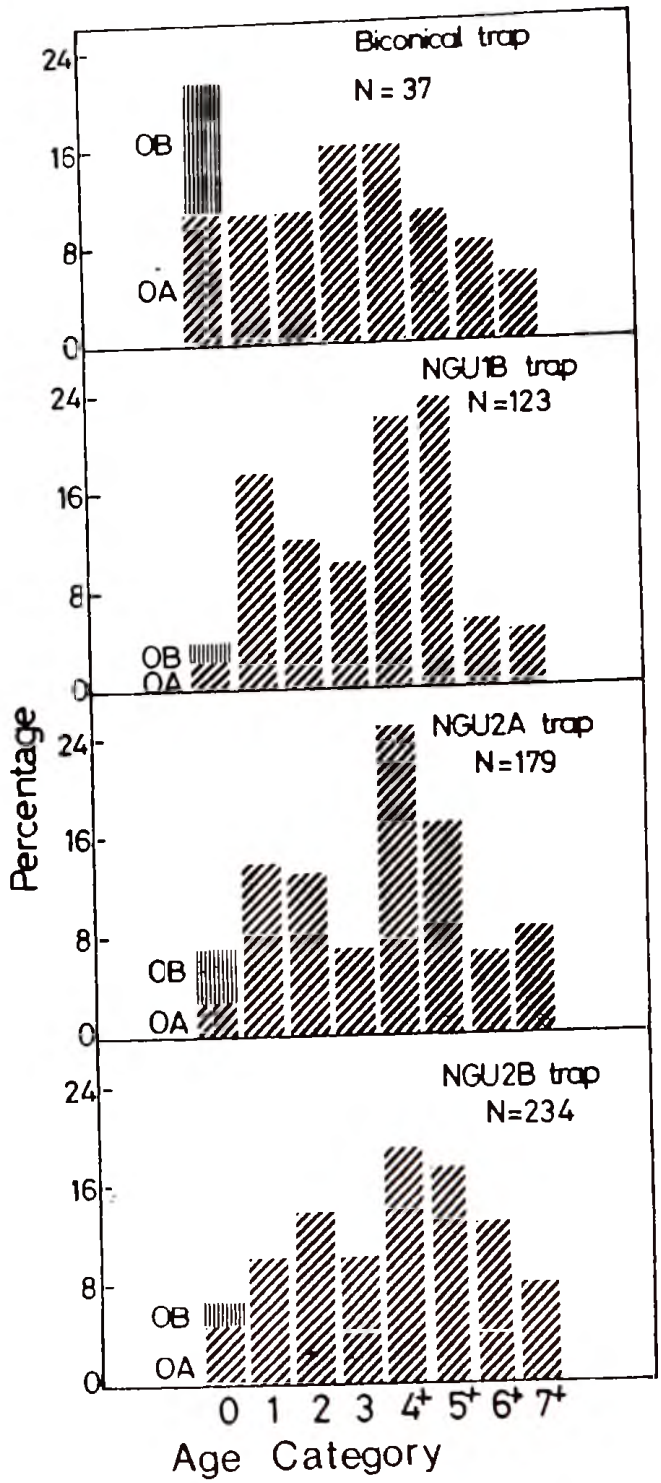


Figure 4.6: Age distribution of female *G. longipennis* caught in the different trap types all baited with similar doses of cow urine and acetone.

4.3.4. Efficiency of the NG2B trap.

Hargrove (1980b) provided the following formula for estimating the efficiency of the test trap, using the numbers of flies caught on the insides of the screens and those caught in the collecting cage of the trap:

$$\text{Efficiency} = y \times 100 \,/\, y + (x/p) \qquad (1)$$

where

y = the number of flies caught in the cage of the test trap,

x = the total number caught by the insides of the screens and

p = the proportion of the perimeter of the ring covered by the electric screens.

The validity of these analyses are based on the general assumption that flies approach and depart from the trap only once and in random directions.

Given that each screen measured 90 cm x 90 cm and screens were placed at a radius of about 3 metres (300 cm), the proportion of perimeter covered by the screens (p) was estimated as 0.14.

The same figure was used in a second approach to estimate the efficiency by using the total numbers caught in the outside of the screens as follows:

$$\text{Efficiency} - y \times 100 \,/\, ((z/p) \quad z) \qquad (2)$$

where

z = the number of flies caught on the outside of the screens.

In both formulae the denominator gives the estimate of the total number of flies getting pass the screens and actually arriving at the trap. The efficiency is therefore the

Table 4.6.: Numbers of *G. longipennis* caught on the screens and in the cage of the NG2B trap and the estimated trap efficiency (E) for males and females.

	SCREENS						NO SCREENS	
	Males			Females			Males	Females
Day	In	Out	Cage	In	Out	Cage		
1	11	8	4	13	9	4	11	8
2	4	10	8	6	9	4	2	1
3	11	28	7	4	6	2	3	4
4	6	9	3	9	4	2	11	9
Tot.	42	55	22	32	28	12	27	22
(%fem)	56.8	66.2	46.7	43.2	33.8	35.3	55.1	44.9
E(%)	8.8	6.5		5.00	7.0		6.9	11.0

percentage of these flies that are caught by the trap.

Assuming that the same number of flies visiting the trap with screens are also visiting the one without screen, the trap efficiency can be estimated a third way as follows:

$$\text{Efficiency} = y \times 100 / (z/p) \qquad (3)$$

where

y = the number of flies caught in the cage of the trap without the screens and z and p have the same notations as equation (2) above.

The numbers of *G. longipennis* caught in the system of electric screens and traps over the four days and the trap efficiency estimated by the above analyses are given in Table 4.6. The estimates by the three approaches all lay within the same range. A chi-squared analysis showed that there were no significant differences between the estimates by the different approaches nor between the estimates for males and females. Taking the averages of the efficiency estimates by the three approaches, the trap efficiency for the males was 7.3 percent and that for the females was 7.9 percent.

4. DISCUSSION

The finding that there was no significant difference between buffalo urine and cow urine as odour baits agrees with the results obtained for *G. pallidipes* by Dransfield *et al.*, (1986b) at Nguruman and by Vale *et al.*, (1986b) in Zimbabwe. Owaga (1985), however, reported that buffalo urine was several times more effective than cow urine. Recent biochemical

analysis (Hassanali *et al.*, 1986; Bursell *et. al*, 1988) has shown that the two urines contain identical attractive phenolic compounds. Therefore, differences between urine samples are probably due to differences in the concentrations of these compounds. Cattle drink more water than buffalos, so it is likely that their urine is more dilute. It was observed by Owaga (1985) and Vale *et al.*, (1986b) that the efficacy of urine increases when allowed to age over a period of time. In this study the cow urine had been 'aged' three weeks at ambient temperatures whilst the buffalo urine was kept at about 4°C prior to use. Thus in this experiment it is likely that the phenolic concentrations were similar in the two types of urine.

Vale (1986b) remarked that undesirable variables are introduced when host residues are tested in their raw states as odour baits, due to variations in the batches of residues. He recommended that, ideally, known doses of chemically identified attractants should be used. However, phenolic components in bovid urine are expensive and at the start of this work had not been identified. Moreover, Dransfield *et al.*, (1986b) have shown that despite such variability, catches with urine baited traps are still closely correlated with those from unbaited traps. Hence, cow urine was selected for further experimentation on trap types and for regular sampling.

The apparently synergistic effects of cow urine and acetone on catch size of *G. longipennis* were quite different

from their effects on *G. pallidipes* in the same habitat. When baited with either cow urine or acetone alone, there were no significant increases in catches of *G. longipennis* by the NG2B trap; the indices of increases were 1.5x on males and 1.4X on females for acetone whilst those for cow urine were 1.5X and 1.6X respectively. When dispensed together, there were significant increases of 5.2X and 4.2X on males and females respectively. From data collected on *G. pallidipes* at the same time, Dransfield (unpublished data) observed that both acetone and cow urine had significant independent effects on catches viz. 3.1X and 4.1X with acetone and 2.8X and 3.4X with cow urine for males and females respectively. When dispensed together the increases were 6.5X for males and 9.0X for females. Thus for *G. pallidipes*, increases when the two were used together were equal to or less than would be expected, in contrast to *G. longipennis* where they are more than would be expected. Increases with acetone and cow urine are still, however, lower for *G. longipennis* than they are for *G. pallidipes*.

Like the *fusca* group, the *palpalis* group has also proved to be less responsive to odour baits than the morsitans group. Carbon dioxide was formerly the only attractant known to be effective for *G. p. palpalis* (W.H.O, 1986). More recently, however, Cheke and Garms (1988) have showed in Liberia that acetone, dispensed at 100mg/h, doubled the catch of *G. p. palpalis* by the biconical trap. In the same experiment, they observed that a mixture of phenolic compounds found in cow

urine ('TF 86/05') was not effective, either on its own or in combination with acetone and octenol. Relative to the concentration of 4-methylphenol, 'TF 86/05' contains 4-methylphenol (100), phenol (1.4), 3-methylphenol (9.9), 3-ethylphenol (1.1), 4-ethylphenol (2.1), 3-propylphenol (2.5), 4-propylphenol (0.8) and 2-methoxyphenol(0.4). The mixture has been shown to increase the catches of *G. pallidipes* in traps baited with acetone and 1-octen-3-ol in Zimbabwe (Vale et al., 1988)

Thus, the response of various species to cow urine and acetone appears to be quite varied. These differences could mean that the odours either elicit different behavioural responses in the different species or they are simply less effective for some species than for others. The differences between sympatric species in their response to odour baits has also been observed by Vale et al., (1986) in Zimbabwe. They found that cow urine was only effective for *G.pallidipes* and not for *G. m. morsitans*.

In the present study, considering the flight periods of *G. longipennis* and judging from the trend of catches in the experiment with urines at different temperatures (expt.14), temperature could be having an effect on the efficacy of the cow urine for this species since there was a general trend of increasing catches with increasing temperature. Since *G. longipennis* flies at dawn and dusk, the relatively lower temperatures at these periods could render the urine less effective.

Octenol (dispensed alone or in combination with other odours) has been shown to significantly increase the catches of *G. pallidipes* in Kenya (Dransfield *et al.*, 1986b) and in Zimbabwe (Vale and Hall, 1985; Vale *et al.*, 1986b). In this study, the octenol did cause an increase in the catches of *G. longipennis* although the increases were not significant. More trials should be carried out using this attractant.

On the variability of the index of increase of baited traps over unbaited ones, Dransfield *et al.* (1986b) observed that the index of increase of a baited (cow urine/acetone) biconical trap over an unbaited one increased with increasing temperature during the day for *G. pallidipes*. They suggested a temperature-mediated entry response, such that below 30°C fewer flies actually enter the biconical trap although very many may be attracted to it by the odour bait. More recently, Rogers *et al.* (in press) showed from fat-haematin analysis of *G. pallidipes* from the study area that baited traps tend to catch a higher proportion of less hungry flies than unbaited traps. Since the proportion of less hungry flies is likely to be higher at higher temperatures (probably because hungry flies would not risk their low fat reserves at high temperatures), the index of increase of the baited trap will tend to increase with increasing temperature.

This is the first time that odour attractants have been shown to be effective for a species of the *fusca* group, but compared to *G. pallidipes* the odours so far tested appear to be less effective for *G. longipennis*. Given the crepuscular

activity of the latter, one would expect olfaction to play a major role in host seeking. If the right host has to be identified within the very short activity period then the olfactory cues must be very specific. Therefore it is likely that more odours have yet to be identified. The results from this study indicate that the effectiveness of odours may rest on synergism and more trials will be required to identify effective combinations of attractants.

The F3 trap has been shown to be more effective than the biconical for *G. pallidipes* (Flint 1985, Brightwell et al., 1987). This is the first time the performance of the F3 trap for *G. longipennis* has been reported. It is clearly more effective than the biconical trap for this species, even more so when the blue floor is removed. This is probably because flies that entered a trap with the floor were settling on it and later on escaping instead of going up. It was quite common to observe *G.longipennis* settling on rocks or other objects on the surface of the ground. A similar explanation can be offered for the considerable improvement on the NG1A trap when its floor was removed as a modification to produce the NG1B.

Although the treatment effect was not significant when the F2 and F3 traps were compared (probably due to low numbers), the F2 (white) seemed to do slightly better on females than the F3 trap. During the main evening activity females tend to fly later than males(cf. Chapter5). as such the light intensities during the peak female activity would be lower than that during the male's. Thus the better perfomance

of the F2(white) over the F3 (blue) for females could be due to the fact that the former was more visible at the time of peak female flight. The experiment however needs repeating for confirmation.

The F3 trap and the control version of the NG2B trap were comparable in performance. The polythene bag cage is probably the main reason why the latter did so well since there should be better light transmission above the exit hole leading into the cage leading to a better entry response. The F3 trap uses twice as much blue material as the NG2B trap and is more difficult to construct and less convenient to use. The NG2B trap is therefore a more cost-effective trap than the F3 trap. Brightwell *et al.* (1987) discussed the economics of the NG2B trap in terms of catch per unit area of trap material.

Although some models of the NGU series of traps were found to be similar in performance to the NG2B, the latter model was selected for various reasons. The NG1B, NG2A and NG2C, were eliminated because they required more material for construction. The NG2E trap (white cloth in place of the blue) was not selected because white cloth easily looses its brightness, becoming yellowish and soiled with the exposure to the sun and handling. This problem was experienced by Flint (1985) who had to re-paint white traps monthly with polyvinyl alcohol emulsion paint in order to revive trap efficiency. Such an expensive maintenance would only be worthwhile if the white trap was found to be considerably more effective than the blue one.

The index of increase of the baited NG2B trap over a similarly baited biconical trap was quite variable between experiments, especially on females (range 1.6X -7.7X). Brightwell *et al.*, (1987) compared the performance of the baited NG2B trap to that of a similarly baited biconical trap for *G. pallidipes*. They showed that below 30°C the NG2B trap was up to eleven times more effective than the biconical trap but only twice as effective above this temperature. In the case of *G. longipennis*, no records were kept of the temperatures when the experiments were being run, but differences in mean temperature between different experiments could also be influencing the relative efficiencies of the two trap types. On the other hand since light intensity has been shown to be a critical factor influencing the level of activity of this species (see chapter 3), the entry response to the different trap designs may be influenced by the light intensity, which can vary considerably between seasons. Both these speculations need confirmation through further experimentation with accurate records of these physical factors.

Compared to the biconical traps, the NG2B and F3 traps were several times more effective on females. The average percentages of female catches in the biconical and NG2B traps were 24.8% and 46.5% respectively. Flint (1985) also recorded more female than male *G. pallidipes* and *G. morsitans* in F3 traps in Zimbabwe. Considering that the similar odour baits attracted similar sections of the population to the different

trap types, the higher preponderance of females in the NG2B and F3 traps should be due to a better entry response by the females to these traps.

Until traps became widely used for sampling, female tsetse were always poorly represented by other sampling methods. Rogers (1984) pointed out that the improvement of traps should aim at increasing the proportion of sections of the populations that are underrepresented. In this respect, the NG2B trap is an improvement over the biconical trap. Female samples are particularly useful for various studies, including ovarian aging and for the establishment of laboratory colonies.

It was observed that difference in trap design was more important than different odour baits in influencing the age composition of catches. Dransfield *et al.*, (1986b) also found that the age composition of *G. pallidipes* caught in odour baited and unbaited biconical traps were not different. The difference in the age composition of the samples from the two trap types was most likely due to a difference in entry response but there seem to be no obvious reason why older flies enter the NG2B trap more readily than the biconical trap. The possibility that gravid females could be seeking larviposition sites in the more enclosed ground shade provided by the NG2B trap was investigated by comparing the percentages of third instar bearing females in both trap types but no apparent difference was observed. It could be that parous females generally fly lower than nulliparous ones so that the

anomaly was not observed in the overall male catch, although on two days the inside of the screens caught more males than the outside. It is, therefore, suggestive that more females than males were being killed that could have been caught by the trap. This implies that the females were moving round the trap in wider circles than the males. It is quite logical that male flies which may be seeking mating partners will tend to remain closer to the host (trap in this case) for easier location of landing females whilst females that are in the refractory phase will tend to stay further away from the trap. The idea is supported by the higher female percentage caught in the trap without screens although the difference just failed to be statistically significant by the chi-squared test. This difference also resulted in the higher efficiency estimated by using the catch from the trap without screens.

The general impression is that the screens were too close to the trap and the test needs repeating probably using more screens placed at a greater distance. However, the difference this could make on the estimate is not likely to be very much and the fact remains that there is considerable room for improvement on either the trap design or odour baits or both.

From the results of this study it was concluded that the NG2B trap baited with medium dose (c. 1000mg/h) cow urine and medium (c. 500mg/h) or low dose (c. 150mg/h) acetone was the cheapest most effective trap for sampling *G. longipennis* at Nguruman. More work on the use of octenol and the 'winged' NGU

lower entrance of the NG2B trap would be more accessible to them than those of the biconical trap.

The efficiency of the NG2B trap recorded for *G. longipennis* was very low for both males and females (7.3% and 7.9% respectively). In the same experiment, data were collected on *G. pallidipes* and the trap efficiency estimate was about 56% for both sexes (Dransfield pers. comm.). According to Hargrove (1980b) the efficiency estimated by this technique is considered the minimum efficiency of the trap because some flies that get intercepted by the outside of the screen could have been caught if they got to the trap and others that could have been caught by the trap were probably caught by the inside of the screens as they circumnavigated the trap. Vale and Hargrove (1979) actually observed flies being electrocuted by the screens as they were moving within the ring. The technique thus tends to underestimate trap efficiency.

Looking back at Table 4.6, a higher catch of female flies was recorded on the inside of the screens than the outside, indicating that flies were being killed that could have returned to be caught by the trap. This is under the assumption that all flies approached and left the trap at a height not greater than that of the screens. Under the assumptions on which the technique is based, more flies should be caught on the outside than the inside because the inside should be catching the same proportion as the outside, but from a smaller population of flies within the ring. This

could provide further increases in the catches of *G. longipennis*.

CHAPTER FIVE

THE ACTIVITY PATTERN OF *G. LONGIPENNIS*

5.1. INTRODUCTION.

The daily activity of tsetse flies, as measured by the flight time, is limited to relatively short periods within each day (Randolph and Rogers, 1978; Bursell and Taylor, 1980). In the early studies on tsetse behaviour and ecology, it was observed that the known vector species, belonging mainly to the *morsitans* and *palpalis* groups, had a diurnal activity pattern. Detailed laboratory studies have since been carried out on several of these species. Some workers also observed that some less well studied species of the *fusca* group were crepuscular, that is mainly active at dawn and dusk.

Remarks on the crepuscular activity of *fusca* species include those of Lamborn (1912) and Swynnerton (1921) on *G. brevipalpis*, Neave (1912) and Lewis (1942) on *G. longipennis*, and Chapman (1950) and Page (1959) on *G. fusca*. The few reports giving some information on the activity patterns of the *fusca* species are those of Power (1964) and Owaga (1981) on the activity pattern of *G. longipennis*, Harley (1965) on the activity pattern of *G. brevipalpis* and Kangwagye (1974) on *G. fuscipleuris*.

The lack of adequate sampling techniques has, however, limited such studies. Most of the field studies carried out on

the *palpalis* and *morsitans* groups have relied on the use of traps which have not been used successfully for the *fusca* species. Work on these species has therefore relied on the use of fly rounds (Power, 1964), baited oxen techniques (Harley, 1965; Kangwagye, 1974) and slow moving vehicles (Owaga, 1981). However, all these methods depend on the efficiency of human catchers, which is variable and impossible to standardize. Furthermore, for crepuscular species, the efficiency of fly-rounds drops to zero when it is too dark for the human eye. Power (1964) noted that his catchers were unable to catch flies at very low light intensities, although *G.longipennis* could still be heard buzzing around. It was therefore not possible for him to determine how long the species remained active after dark.

In the present study an electric net (Vale ,1974b), known to kill about 95% of the flies colliding with it, was used to provide a more objective measure of the activity pattern of *G. longipennis* at Nguruman.

Adequate knowledge of the activity patterns of the tsetse species involved in any tsetse trypanosomiasis/system is vital. Firstly, host-vector contact is one of the factors determining the level of trypanosomiasis in any given area. This depends on the fly distribution in relation to the host distribution in both space and time. Avoidance of challenge from *G. longipennis* may be achieved by keeping cattle out of the fly habitat during periods of activity. Secondly,

knowledge of the activity pattern of a species can be exploited in the development of better sampling techniques.

5.2. MATERIALS AND METHODS

5.2.1 The electric screen

The electrocuting device used for the study was designed by Vale (1974b) and is termed the electric net or electric screen. It consisted of a sheet of fine black nylon netting, measuring about 90 cm x 90 cm, suspended vertically from an aluminium frame measuring 110 cm x 120 cm. Blackened fine copper wires 0.22 mm in diameter were strung vertically 0.8 cm apart between the top and bottom of the frame on either side of the net.

When electrified, a voltage differential of about 20 to 30 kV was created between adjacent wires so that the discharge was enough to kill or stun the fly when it touched the wires. Power was obtained from a 12 volt battery delivered through a specially designed high voltage pulse generator. Details of the construction and functioning of the device are provided by Vale (1974b).

The pulse generator and component parts of the electric net were obtained from Zimbabwe and the net was assembled in ICIPE, Nairobi. In the field the system was set up as shown in Figure 5.1, in a glade in woodland. The screen was tied in a vertical position between two metal poles stuck firmly into the ground. To increase the concentration of flies around the electric screen, a 2 m x 1 m piece of black cloth was

stretched adjacent to the electric screen in the position shown in the figure, as advised by Vale (pers. comm.). Stunned or killed flies were recovered in shallow water-filled metal trays placed on the ground on each side of the electric net. A few drops of detergent were added to reduce the surface tension of the water, thus preventing the recovery and escape of stunned flies.

The trays were placed close to the base of electric net to ensure the collection of all dead flies that might slide down the net. To eliminate the possible attractiveness of the shiny metal to flies, the inner surfaces of the trays were painted orange-brown whilst the aluminium frame was painted with black patches. The equipment was left in place throughout the period of investigation. When not in use, the screen was carefully covered with a heavy plastic tarpaulin to prevent it getting wet. The whole set-up was protected from animal damage by a ring of thorny branches of Acacia.

5.2.2. Meteorological data

A Grant's automatic meteorological recorder was set up about 10 metres from the experimental set-up to record air temperature, relative humidity and wind speed when experiments were being run. The probes for these physical factors were mounted on a pole about 1.5 metres above ground level. Light intensity was measured with a Metrawatt (Metrux K) luxmeter which was placed next to the screen on a horizontal wooden plank erected about 1 metre above the ground. Daily notes were

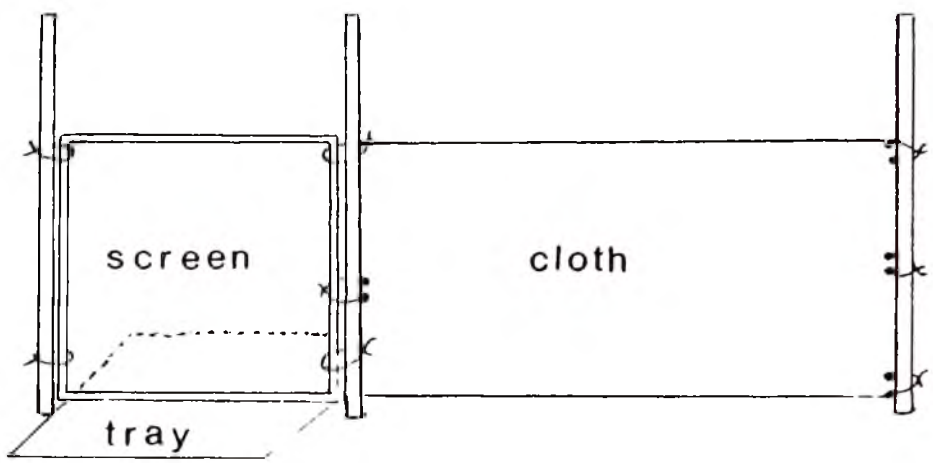


Figure 5.1: Set-up of the electric screen and cloth target used in the study of activity pattern of *G. longipennis*.

kept of the general weather conditions such as cloud cover, the phase of the moon and the times it shone during the experiments. Sunset and sunrise times were also recorded daily.

5.2.3. Activity Period

In a preliminary study, catches were made every hour for two days and two nights. It was observed that most *G. longipennis* were caught in the hour after sunset (1815 h) and the 30 minutes before sunrise (0630 h) whilst activity throughout the rest of the night and day was negligible.

The main investigations were carried out in the dry months of September and October 1987, when it was hoped that there would be no rains to disrupt the experiments. The intention was to collect flies at short time intervals in order to provide a more precise picture of the activity period. Therefore, all experiments were run in the evenings from 1730 h and from 0530 h in the mornings. Flies were collected from the trays at 15-minute intervals until all activity ceased. Light intensity readings were also taken at the beginning of every collection. Two successive records of a zero catch was adopted as the standard to mark the end of fly activity.

A minimum of two people collected flies from each tray and this took 1-2 minutes during which time the screen was switched off. Fly collectors were required to pick out every insect from the tray that was about the size of tsetse. This

was both to hasten the collecting process and to minimize the period of interruption and also to safeguard against the loss of tsetse through misidentification at very low light intensities. To further reduce errors in fly counts for the appropriate time periods and to facilitate the next collection, the trays were cleared of all insects at every collection. The pooled catch for each 15-minute period (from all collectors) was kept separate in an appropriately labelled glass tube.

5.2.3. Experiments

Although the main objective of the investigation was to define the activity pattern of *G. longipennis*, a variety of other factors were tested with the electric screen to assess their effects on catches. These treatments involved materials related to tsetse trapping technology (screen colour and odour baits) which were selected with the view to obtaining information that could be useful in the further improvement of trap efficiency for this species.

Experiment 1:

The attractiveness of blue and black cotton material (the type used in the construction of biconical and NG2B traps; see chapter 4.) was compared. Treatments were alternated from day to day with a 2 m x 1 m piece of the material stretched between two poles adjacent to the screen in the position indicated earlier in Fig 5.1. Cow urine and acetone were dispensed as odour baits; the dispensers were placed next to

the pole between the screen and the cloth. The experiment was run for 10 days (the 9th-19th September 1987) giving 5 morning and 5 evening replicates for each treatment.

Experiment 2:

This was designed to compare the catches with and without the cloth target placed next to the screen. Black cloth was used for the experiment. This was run only in the evenings from the 20th-25th September. Each treatment was thus replicated three times on alternate days.

Experiment 3:

The efficacy of warm cow urine (30 $\pm$ 1°C) was compared with that of urine at ambient morning temperatures (19-22°C). The warm urine was maintained at the desired temperature by immersing a can of urine in water warmed to the required temperature and kept in a polystyrene box as was done in Expt. 14 in Chapter 4. Acetone was dispensed together with both treatments. The experiment was run in the mornings on the same days as experiment 2, giving three replicates for each treatment.

Experiment 4:

A comparison was made between the efficacies of cow urine and a recently developed chemical mixture of paracresol, 1-octen-3-ol and 3n-propyl-phenol (8:4:1 ratio) (Bursell *et al.*, 1988). This was obtained from The Tsetse Research

Laboratories, Bristol, U.K packaged in 150 micron thick porous polythene sachets of total surface area 50cm². According to Hall (pers. comm.) the release rates from these sachets at 27°C with wind speed of 8kph are 9.1, 3.0 and 0.5 mg/day for paracresol, 1-octen-3-ol and 3 n-propylphenol respectively. In the field, these rates will be slightly higher in the afternoon when the temperatures were a little higher than 27°C. Morning temperatures, on the other hand, ranged between 19-22°C which will result in lower release rates. Acetone was dispensed with both treatments. The experiment was run for 6 days (6th-10th October) in the evenings and mornings, giving 3 replicates of each treatment for each time period.

A two way analysis of variance (treatments x time) was carried out on the data from each experiment using a log (N+1) transformation on the numbers caught. When the same experiment was run both in the morning and in the evening the data for these periods were analyzed separately.

5.3 RESULTS

5.3.1. Fly numbers from various treatments

Table 5.1 gives a summary of the results obtained from the various experiments including the fly numbers on each day (males and females pooled), the total catch for each treatment, the F-ratio from the analysis of variance (ANOVA) and the detransformed mean catch/per 15-minute period for each treatment.

Comparing the effects of cloth colours, separate analyses for males and females showed that the treatment effect was

Table 5.1: Numbers of *G. longipennis* caught at the electric screens using various treatments (males and females pooled).

	Daily total					Overall total	Detr.mean per 15-min. period	F-ratio (df)
Evening	1	2	3	4	5			
Blue cloth	41	54	38	51	143	327	7.7	1.22^{ns}
Black cloth	64	70	55	31	31	256	6.3	(1,40)
Cloth	31	51	54	-	-	135	5.2	15.35***
No cloth	9	25	5	-	-	39	1.7	(1,12)
Phenols +Acetone	69	60	46	-	-	157	11.1	5.35*
Cow urine +Acetone	53	11	37	-	-	101	5.7	(1,16)
Morning								
Blue cloth	4	16	24	3	15	62	2.5	0.001^{ns}
Black cloth	17	19	5	4	12	57	2.4	(1,24)
Warm urine	5	21	3	-	-	29	1.8	0.32^{ns}
Ambient	13	5	15	-	-	33	2.4	(1,13)
Phenols +Acetone	19	4	7		-	30	2.0	0.93^{ns}
Cow urine +Acetone	15	1	4	-	-	20	1.2	(1,12)

(*=P<0.05; ***=P<0.001; ^{ns}=not significant).

just significant at the 5% level for males ($F_{(1,40)} = 5.06$) but not for females ($F_{(1,40)} = 0.74$). The blue cloth appeared seemed to catch significantly more males than black, mean catches being 5.5 for blue cloth and 3.5 for black. However, when the pooled data for both sexes were analyzed, there was no significant treatment effect.

The treatment effect in experiment 2, comparing the use of cloth and no cloth, was highly significant ($P<0.001$). The use of cloth increased catches by about 3 times. The analysis was performed on the pooled data for both sexes because the numbers caught without cloth were so few.

There was no significant treatment effect when warm urine and urine at ambient temperature were compared. Therefore, the efficiency of cow urine did not seem to be improved by warming to 30°C. There was a significant difference for the evening catches between the phenol/octenol mixture and cow urine. The latter odour doubled the catch over the former. The effect was not significant for the morning catches but the phenol/octenol mixture still nearly doubled the catch.

5.3.2. The daily activity pattern

Having established that there was little effect of cloth colour on catches, the pooled data from experiment 1 over the 10-day period were used to describe the activity pattern of *G.longpennis*. Tables 5.2 and 5.3 show the daily catches at different times for the evening and morning activity periods respectively. Fig. 5.2 shows the relative levels of activity

between the morning and evening periods and Fig. 5.3 focuses on the main activity pattern in the evening.

Taking sunset at 1815 h (local time = GMT + 3h) as the reference point for evening activity, significant levels of activity were observed by 1745-1800 h, and one or two males were occasionally recorded earlier than this time. Male catches increased gradually to a peak by 1815-1845 h. Thereafter, a gradual decline followed till 1900 h followed by a sharp drop to zero catch by 1915-1930h. Females on the other hand were regularly recorded only after sunset, with the exception of one very cloudy day (later on followed by rain) when two females were caught just before sunset. A rapid rise in catches from 1815 h to 1845 h followed by an equally rapid drop thereafter, often produced a sharp female peak at 1830-1845 h. On one day (11th September) a broad peak extended from 1845 h -1900 h and on another day (15th September) the peak catch was recorded at the earlier time of 1815-1830 h and catches remained high until 1845-1900 h (see discussion for possible reasons). On most days, male and female activity stopped at the same time but one female was recorded on each of two occasions at 1930 h. Although there was very bright moonlight on some days this did not seem to influence the time when activity stopped.

Table 5.2: Catch per 15 minutes, total catch and the percentage of female *G. longipennis* caught at the electric screen during evening activity period.

		Collection Time (h)										
		1730	1745	1800	1815	1830	1845	1900	1915	1930	TOT.	%Female
Day	Sex											
1	M	0	0	0	3	8	9	8	1	0	29	
	F	0	0	0	0	1	7	3	0	1	12	29.3
2	M	0	0	0	1	10	4	13	2	0	30	
	F	0	0	0	0	3	12	18	0	1	34	53.1
3	M	0	2	1	5	7	14	3	1	0	33	
	F	0	0	0	0	3	17	1	0	0	21	38.9
4	M	0	1	1	1	12	9	10	1	0	35	
	F	0	0	0	0	3	20	11	1	0	35	50.0
5	M	0	0	1	3	2	10	7	1	0	24	
	F	0	0	0	0	1	10	3	0	0	14	36.8
6	M	0	0	0	0	11	9	5	1	0	26	
	F	0	0	0	0	12	11	6	0	0	29	52.7
7	M	0	1	1	3	4	13	7	0	0	29	
	F	0	0	1	0	1	17	2	1	0	22	42.1
8	M	0	0	0	5	5	3	4	0	0	17	
	F	0	0	0	0	0	11	3	0	0	14	45.3
9	M	1	0	0	14	30	21	7	0	Rain	73	
	F	0	0	0	2	8	55	3	2	Rain	70	48.9
10	M	0	0	0	1	5	7	1	1	0	15	
	F	0	0	0	1	4	9	2	0	0	16	51.6
Tot.	M	1	4	4	36	94	99	65	8	0	311	
	F	0	0	1	3	36	169	52	4	2	267	46.2

Table 5.3: Catch per 15 minutes, total catch and the percentage of female *G. longipennis* caught at the electric screen during morning activity period.

		Collection Time (h)								
Day	Sex	0545	0600	0615	0630	0645	0700	0715	TOT.	%Female
1	M	0	1	1	0	0	0	0	2	
	F	0	2	0	1	0	0	0	3	60.0
2	M	0	4	1	1	0	0	0	6	
	F	0	5	6	0	0	0	0	11	64.7
3	M	1	9	4	0	0	0	0	14	
	F	0	2	0	0	0	0	0	2	12.5
4	M	1	2	2	1	0	0	0	6	
	F	0	10	3	0	0	0	0	13	68.4
5	M	1	12	3	0	0	0	0	16	
	F	0	2	5	1	0	0	0	8	33.3
6	M	0	2	1	0	0	0	0	3	
	F	0	2	0	0	0	0	0	2	40.0
7	M	0	1	0	0	0	0	0	1	
	F	0	0	1	1	0	0	0	2	66.6
8	M	0	2	0	1	0	0	0	3	
	F	0	0	1	0	0	0	0	1	25.0
9	M	0	6	2	1	0	0	0	9	
	F	0	4	2	0	0	0	0	6	40.0
10	M	0	2	4	0	0	0	0	6	
	F	1	3	1	1	0	0	0	6	50.0
Tot.	M	2	41	18	4	0	0	0	66	
	F	1	30	19	4	0	0	0	54	45.0

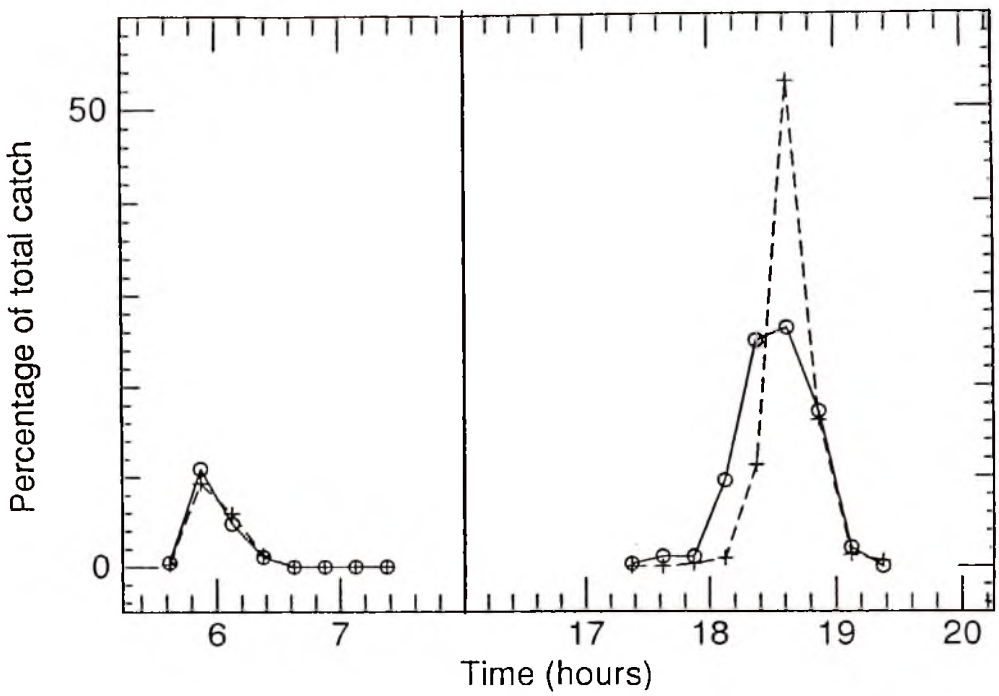


Figure 5.2: The relative levels of activity of *G. longipennis* in the morning and in the evening. (____ males; ..χ..females)

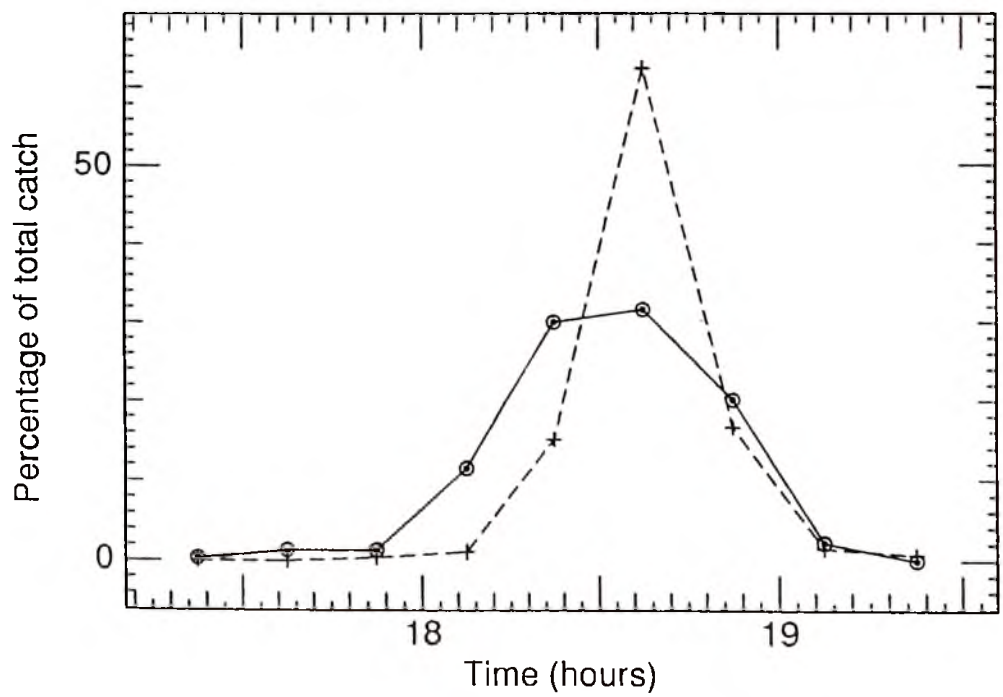


Figure 5.3: Activity patterns of male(____) and female (..χ..) g. longipennis in the evening

In general, less activity was observed in the mornings than in the evenings and the morning activity period was much shorter than the evening one. Over the ten days an average of 58 flies/day were caught during the evening activity as against 12 flies/day in the morning. Pronounced morning activity was observed only after 0545 h although the occasional male was caught before then. Most flies were regularly caught between 0545 h and 0615 h (sunrise at 0630h) with the peak catches usually occurring between 0545 h and 0600 h. By 0630 h only single flies were caught on a few days but only rarely were any flies caught after this time. Given the short period of morning activity, there was no significant difference between the male and female activity pattern in the morning.

5.3. Activity and physical factors.

For each day, the number of flies caught in each 15-minute period was expressed as the proportion of the total catch for the day and used as an index of activity for that time period. Separate plots were then made of the activity against temperature, relative humidity and light intensity recorded at the corresponding periods. The arcsine $\{P + 0.5$ transformation was used on the proportions to normalize the data. In order to avoid the many zero catches recorded in the very early and very late periods, the analysis was limited to catches made from 1800 h (for males) and from 1815 h (for females) to 1900h.

Among the physical factors that were considered, only light intensity showed any significant relationship with activity. Figures 5.4A and 5.4B show the plots of activity against light intensity for males and females respectively. For both sexes the relationship between activity (Y) and light intensity (X) was best described by the fitted parabola with the following functions:

$Y = 1.03 + 0.23X - 0.08X^2$ ($r^2 = 33\%$) for the males

and

$Y = 0.99 + 0.23X - 0.09X^2$ ($r^2 = 67\%$) for the females.

In both cases activity is seen to increase with decreasing light intensity up to a peak at about 100 lux. Activity then decreased with further decrease in light intensity. As can be observed from the figure the relationship was stronger for females than it was for males. Thus 67% of the variability in female catch and 33% of the male catch in the different time periods is explained by the above relationships.

For the morning activity the distinction in the onset of male and female activity was less clear and the sexes were pooled in order to avoid the many zero catches recorded for some periods. No significant relationship was however observed when the above analysis was carried out.

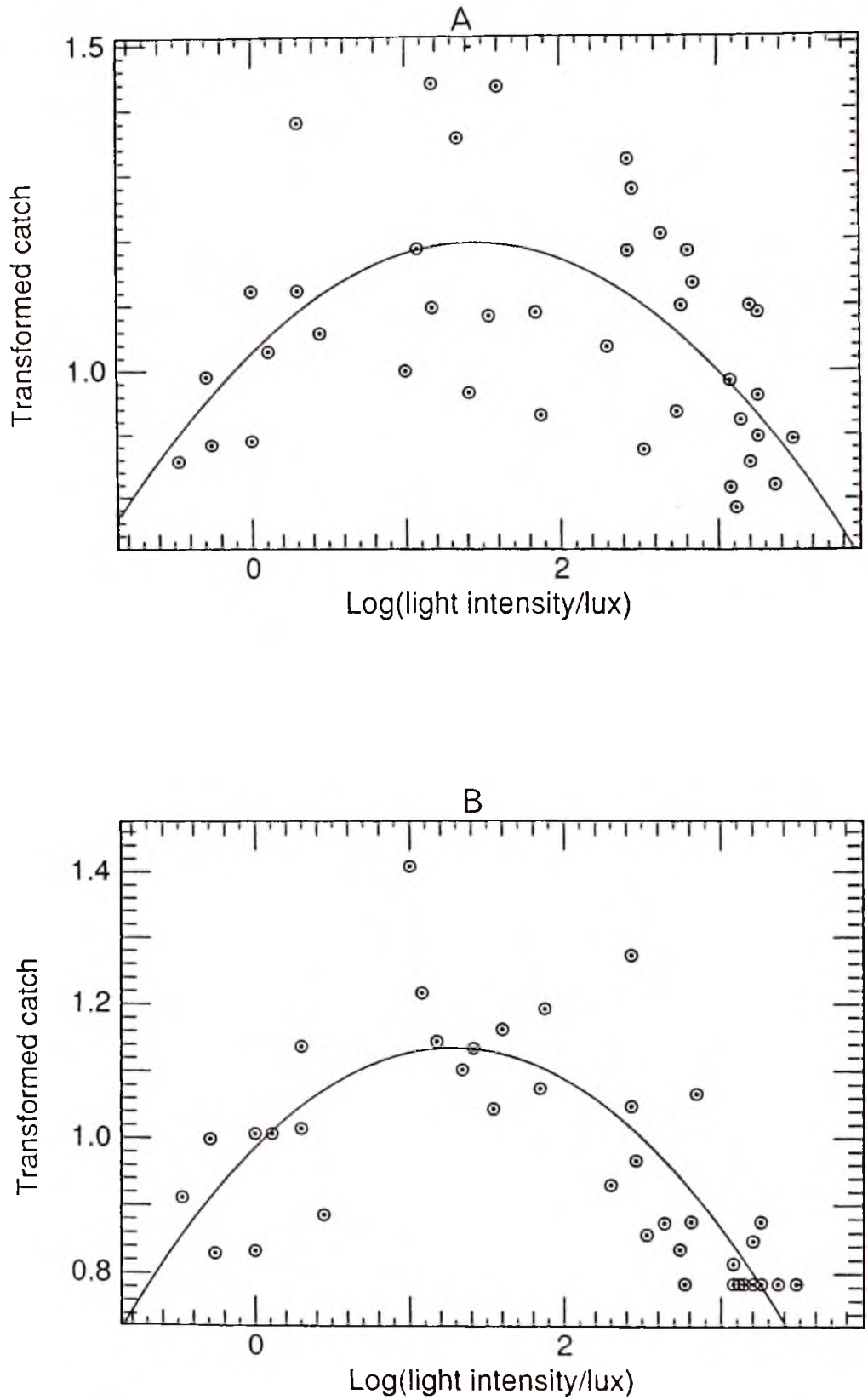


Figure 5.4: The relationship between activity and light intensity.(For males (A), $Y = 1.03 + 0.23X - 0.08X^2$; $r^2 = 33\%$ and for females (B), $Y = 0.99 + 0.23X - 0.09X^2$; $r^2 = 67\%$)

5.4. DISCUSSION

The comparisons among various treatment factors bring out several important points that could be useful in the development of traps for *G. longipennis* and for tsetse control in general. Assuming that the screen killed 95% of the flies colliding with it, as estimated by Vale (1974b), the differences in catches observed between treatments were due to differences in their effectiveness in attracting flies to the screen.

Blue cloth appears to be more attractive than black cloth to male *G.longipennis*. This could be due to the brighter colour of the blue and better contrast with the background. This brightness factor would be more pronounced during the male activity period when there is still sufficient illumination. It was, probably, less important during female activity due to the very low light intensity. Although the overall effect was not significant, it is worth noting the colour combinations when designing traps for *G. longipennis*. The proportion of blue to black could have an effect on the sex ratio.

It was observed that the presence of both odour and visual attraction are required for optimum catches. Visual attraction in host finding should be less important for crepuscular species than for diurnal species but the significant reduction in catch when no cloth was used emphasizes the importance of visual attraction for *G. longipennis*.

The increase in catches when traps were baited using the mixture of phenols and octenol as compared to cow urine could be due to the phenols being superior to the cow urine. The phenols in the mixture are supposed to be the most attractive components occurring naturally in cow urine. The poorer performance of the crude cow urine may be due to the presence of other compounds in the urine which are known to have repellent effects on tsetse (Bursell *et al.*, 1988).

The presence of octenol in the mixture is however a more likely reason for the significant difference in the catch. Brightwell *et al.*(1989) have recently shown that if octenol is dispensed together with crude cow urine and acetone a 2-4 times increase in catch is realized for *G. longipennis*. This supports the idea that the difference in catch obtained in the present investigation was mainly due to the presence of the octenol in the mixture of phenolic compounds.

Although differences in levels of catches were observed between some treatment factors, the onset and end of activity were not altered by these treatments. Basically, the various attractants were effective only when the fly became active. According to Brady (1972, 1973) and Brady and Crump (1978), tsetse generally exhibit spontaneous activity which is controlled by an endogenous rhythm, that may be influenced by some physical factors. Many field workers on diurnal *Glossina* species have observed that the daily activity patterns were dependent on the temperature profile (Challier, 1973; Turner, 1980 and Turner, 1987).

The little earlier work on crepuscular *fusca* species, however, indicated that light intensity was the major factor influencing activity patterns. Power (1964) observed that male *G.longipennis* (near Lake Jipe, Kenya) exhibited an activity pattern similar to that observed in this study. Similar patterns of activity were also observed by Harley (1965) for *G. brevipalpis* in Uganda. Both authors noted the close relationship between the onset of morning and evening activity and sunrise and sunset, respectively. They considered light intensity to be the major factor determining the pattern of activity. Although Power (1964) established a partial regression connecting fly catch with light intensity and relative humidity, he concluded that light intensity appeared to trigger the onset of activity.

The results from the present study also indicate that light intensity was the major factor influencing the activity of *G.longipennis* at Nguruman. Considering the steady decline in light intensity around dusk, the sudden burst of activity, especially of the females, strongly suggests a "trigger" or threshold. The fact that the onset of activity and the timing of peak catches usually occurred at the same time might indicate an entirely endogenous rhythm. However, it was observed that on a few very cloudy days, when the light intensities declined somewhat faster than usual, the peak catches occurred correspondingly earlier in the evening. On clear sunny days on the other hand, the peak was recorded correspondingly later as light intensities fell more slowly.

This suggested that if the threshold level of light intensity occurs at any time during the day, flies may be triggered into activity.

Taking the threshold level as the light intensity at which the sudden rise in catch started, males and females show different threshold levels. From figure 4.3 the threshold level for males was 1,600 lux whilst that for the females was 250 lux.

This can be converted into physical units of illumination energy (Watts/square meter), which according to Young and Gibson (1987) is a more objective measure of light intensity from the insects' point of view. Using their conversion factor of 1 Wm^2 = 355 lux, the threshold levels become 4,507 mWm^2 for males and 704 mWm^2 for females. The peak catch for both sexes occurred at about 100lux,which works out to 281 mWm^2. Quoting light intensity in Zeiss units, Power (1964) recorded peak catches at 4 Zeiss units. Other than the fact that he mentioned that this occurred after sunset, it is not possible to compare this value with that obtained in the present study because the photometer was not calibrated on the bench and the Zeiss unit is not a recognized standard unit for measuring light intensity.

From laboratory studies on *G. morsitans*, Brady (1987) inferred that the short burst of activity observed in many diurnal tsetse species when they change resting sites at dawn and dusk was controlled by light intensity. It is quite possible that the activity in crepuscular species is an

extended form of the above phenomena in diurnal species. This could be an adaptation in crepuscular species, making it possible for them to use the same time for feeding and for changing resting sites as well. Brady (1987) observed that the mean threshold light intensity for take off was 350 mW/m^2. This is quite close to the value obtained at peak activity in this study, soon after which *G. longipennis* retreats. The activity involved in Brady's laboratory study took very short periods which were thought to reflect what happens in the field during the change of resting sites in diurnal species. Compared to the diurnal species, *G. longipennis* appears to take off at a much higher light intensity in order to feed but withdraws to probably change resting sites at about the same time as in diurnal species.

Temperature and relative humidity did not appear to be factors that were likely to determine the pattern of activity. In the first place, the change in the levels of these factors from one collection period to the other were so small that they were not likely to cause the observed changes in catches with time. Moreover, temperatures and relative humidities during morning peak activity differed greatly from those during evening peak activity. Light intensities, on the other hand, were within the same range during both morning and evening peak activities. It is therefore more logical to relate activity to light intensity rather than with temperature and relative humidity. Power (1964), however, suggested that the generally low dawn temperatures might have

an inhibitory effect in the morning. In the months that this study was conducted, morning temperatures ranged between 19°C and 22°C, quite close to critical temperature of 18°C at which tsetse are generally thought to be inactive (Glasgow, 1963). It would, however, be desirable to conduct experiments at other times of the year, when morning temperatures are lower or higher, to find out if the level of dawn activity would be any different from what has been reported here.

CHAPTER SIX

POPULATION DYNAMICS OF *GLOSSINA LONGIPENNIS*: I. APPARENT DENSITIES AND MORTALITY RATES

6.1. INTRODUCTION

Adequate knowledge of a given tsetse population is essential for understanding its involvement in disease transmission and for the development of appropriate control strategies. The main index of the performance of a given animal population is the population size which is determined by four primary parameters: the birth rate, death rate, immigration rate and emigration rate.

In the simplest terms, births and immigration lead to increases in population size whilst deaths and emigration result in decrease in population size. In nature, a combination of these factors act on the population at the same time. Studies of the changes in these parameters, and the underlying causes of these changes, form the basis of population dynamics.

Changes in tsetse population size are influenced by both abiotic and biotic factors. Of the abiotic climatic factors, temperature and relative humidity have long been shown to influence tsetse population sizes through their effect on birth and death rates. The importance of climate for the survival of tsetse in the field was first shown by Nash (1937)

and Nash and Page (1953) who established significant correlations between the population size and meteorological data for *G. tachinoides* and *G. m. submorsitans* populations in northern Nigeria. More recently, Gouteux and Buckland (1984) also showed significant relationships between temperature and relative humidity and the apparent population densities of *G. p. palpalis*, *G. pallicera* and *G. nigrofusca* in Cote d'Ivoire. Other workers have shown significant relationships between mortality rates and climatic factors. e.g. Rogers (1979), Gouteux and Laveissiere (1982) and Rogers *et al.* (1984b). These climatic factors act in a density independent way and therefore cannot regulate populations.

Long term records, however, mainly from fly round data, show that tsetse numbers fluctuate around characteristic population levels (Glasgow and Welch, 1962; Fairbain and Culwick, 1950; Onyiah, 1978), indicating that the populations are subject to tight regulation. Some workers in the past were of the opinion that this was determined by climatic factors. It is now widely accepted that only density dependent-factors can regulate animal populations. Rogers and Randolph (1984, 1985) have shown that density-dependent factors are mainly biotic (e.g. predation, parasitism etc.) and these regulate the populations through feedback mechanisms. In their review on tsetse ecology, Rogers and Randolph (1985) gave direct and indirect evidences of density-dependent regulation in tsetse populations and pointed out that in most cases the causes of

population regulation are difficult to determine. Rogers (1974) thinks that pupal and adult predation are density-dependent. Feeding success (Vale, 1977) and fly movement (Rogers et *al.*, 1984; Turner and Brightwell, 1986) have also been postulated as being regulatory.

The performance of a given population over time is assessed by estimating the various demographic parameters. The size of a given population can be estimated in relative terms (as indices of abundance in one place or at one time relative to another) or in absolute terms (as the actual numbers in a given area at a given time). Detailed reviews of the methods used for both type of population size estimates are given by Southwood (1978) and Seber (1973) provides mathematical details for these methods. Generally, relative methods provide quicker estimates of population size and are more often used but for some purposes absolute estimates may be required.

For *G. longipennis* at Nguruman, traps were used to obtain relative population estimates expressed as catch per trap per day. The recently developed NG2B trap which had been shown to be more effective than the biconical trap (see chapter 4) was the main trap used. However, to provide a standard for comparison, data was also collected from similarly baited biconical traps which were in use by the ICIPE research team for sampling *G. pallidipes*. Absolute population estimates were obtained through mark-release-recapture (see Chapter 8).

Various methods have also been developed to estimate population mortality rates using data obtained from samples

taken from the populations. These include the use of population age structure and the use of change in fly numbers from one sampling period to the next. Details of the above techniques and methods of estimating population parameters are given in the sections that follow.

Finally, attempts were made to explain the causes of the observed changes in some the population parameters by relating them to various climatic factors that were measured during the study period.

6.2. MATERIALS AND METHODS

6.2.1. Field Studies

The field studies consisted of regular monthly sampling of the fly population using NG2B and biconical traps, set in defined positions within the study area. Sampling was carried out during the first week of every month. For effective sampling, the traps were distributed over as much of the area as possible so as to include each of the main vegetation types. Figure 6.1 is a map of the main study area, showing the various vegetation types and the transects in the main study area where sampling was carried out.

A set of five biconical traps was set in the main study area along transect 1 (TR1) which runs from the Ewaso Ngiro river in the east to the base of the escarpment in the west. As can be seen in Figure 6.1., the transect cuts across the

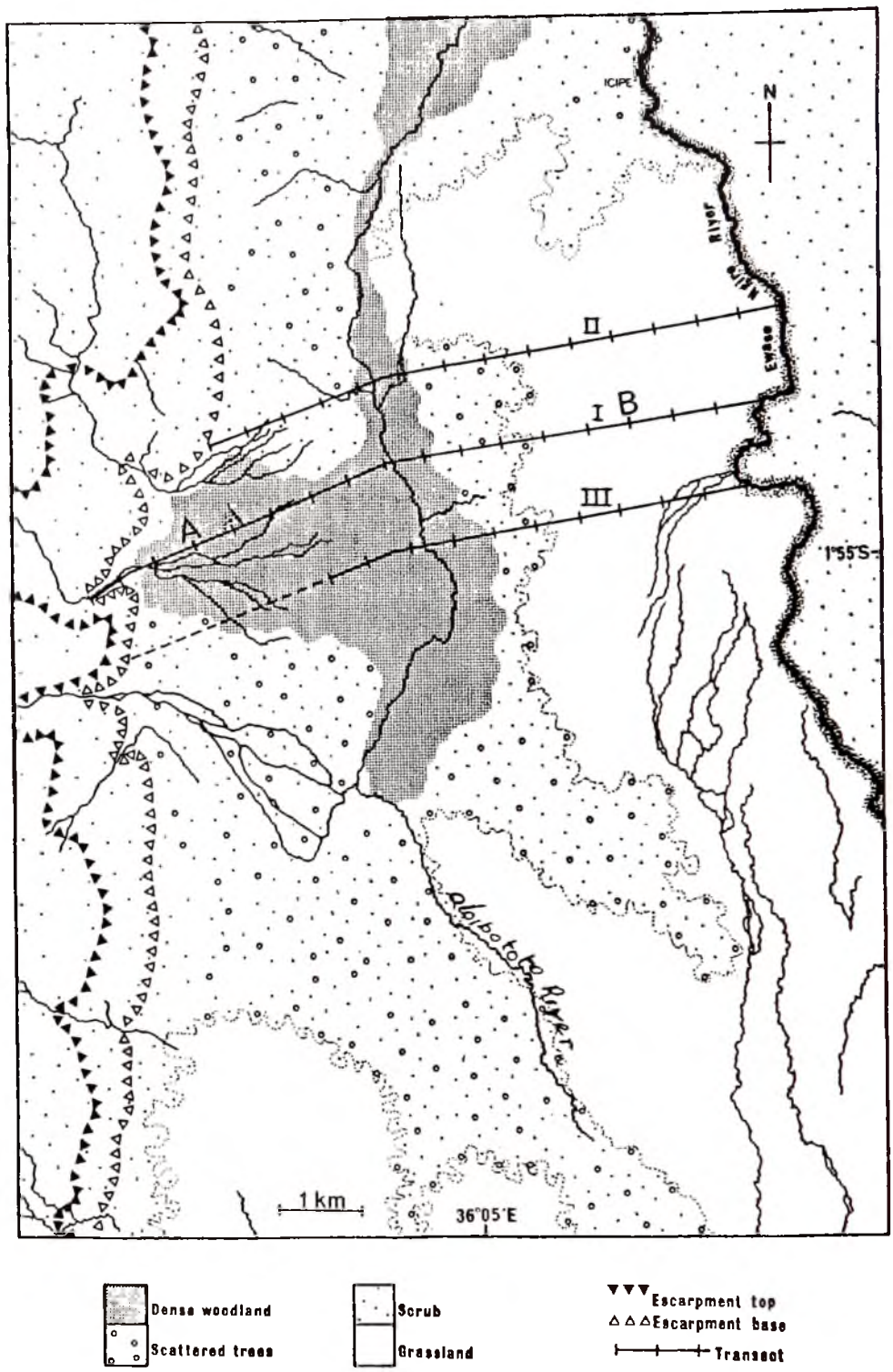


Figure 6.1: Map of transect 1 area showing the different vegetation types and the transect along which biconical and Ng2B traps were set (between point A and B).

four main vegetation types in the area. These are the open plains (PLNS), the acacia woodland (ACWD), a thick lower woodland (LOWD) and a more open upper woodland (UPWD) occurring in this sequence from east to west. One trap was set in each vegetation type except in the lower woodland, where two traps were set. This set of traps, (TR1 biconical traps) were set for the last 3 days of each trip and catches were also collected at 24-hour intervals. Data from these traps cover the period of August 1985 to December 1987.

Sampling with the NG2B traps began in June 1986. Five NG2B traps were set alternating with the TR1 biconical traps along the transect, such that one NG2B trap was also located in each of the different vegetation types (two in the lower woodland). Sampling with the NG2B traps only took place for the last three days of the monthly trip. Since these traps were used only for sampling *G. longipennis*, collecting cages were put on at about 1815 h and catches collected at about 0715 h the following morning. This time period limit included the activity period of *G. longipennis* but was outside the most active periods of *G. pallidipes* to avoid overcrowding of flies in cages.

A set of five biconical traps were also sited about 1 km apart along the bed of the Oloibototo river which runs from north to south through the thickest section of woodland. This set of traps (henceforth termed the river traps) was always put out on the first day of each six-day monthly trip and catches collected every 24 hrs for 6 days. Sampling with the

river traps was carried out from August 1985 till December 1987.

In August 1986, another transect (transect 4) was established in an area about 7 km to the north of the main study area. A similar sampling programme was started in this new area with five baited biconical traps and five baited NG2B traps set along the transect and three biconical traps set along the river. In the dry season, the main connection for possible fly movement between the two areas is maintained by a narrow strip of vegetation along the Oloibototo river bed which runs through both areas. During the rainy season, the flies spread out more so the chance of movement of flies between the two areas is higher. Figure 6.2 shows both the main study area and the transect 4 area and the location of the river biconical traps in both areas (R1-R5 belong to transect 1 and R6-R8 belong to transect 4).

All traps were baited with cow urine dispensed at *c.* 1000mg/h and acetone at *c.* 2500mg/h. These were dispensed from glass jars with aperture diameters of 4.5 cm and 2.2 cm respectively. The cow urine was aged for about 3 weeks in stoppered bottles at ambient temperatures, prior to use. When set in operation, all odour baits were sheltered from sun and rain by covers as described earlier in Chapter 4.

Before the collecting cages were put in place, a careful check for holes in the cage was carried out. A piece of wet cotton wool was then put in each cage to increase humidity to improve the survival of flies in the cages before catches were

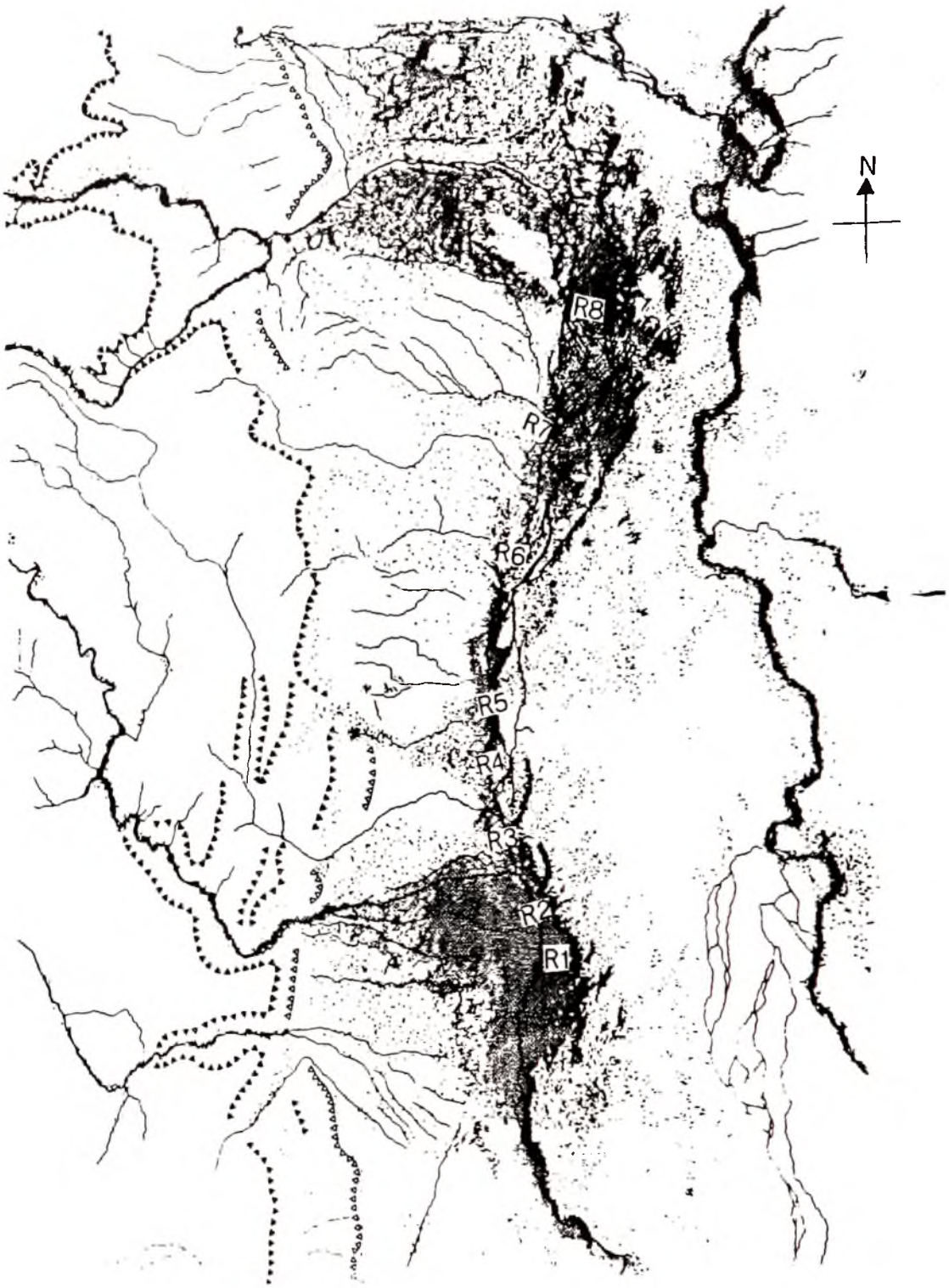


Figure 6.2: Map showing both transect 1 and 4 areas and the location of the River biconical traps along the Oloibototo river in both areas.

collected. When the catches were being collected the cages were again inspected for holes that could have let flies escape. On collection, each cage of flies was labelled and then immediately put under the cover of a wet black cloth. This minimized fly movement in the cages and prevented additional wear and tear on the wings that would give rise to errors in wing fray aging of flies.

After arrival at the camp site, the flies were killed with chloroform and then sexed and counted. All female flies from the NG2B traps were sealed in polythene sachets and immediately preserved in liquid nitrogen according to the preservation method recommended by Minter and Goedbloed (1971). These were later taken to the laboratory in Nairobi for ovarian and wing-fray aging.

6.2.2. Laboratory Studies

Female flies were dissected for ovarian age. When taken out from liquid nitrogen, flies were immediately transferred to the freezing compartment of a refrigerator to prevent a sudden rise in temperature which normally results in the disintegration of fly tissues. After about 30 minutes, when the specimens were sufficiently thawed, they were removed one at a time and dissected under a Wild dissection microscope.

Prior to dissection, the wing on the right side of each fly was transferred on to a drop of glycerine on a microscope slide. Sets of 14 wings were arranged on the slide and then pressed between two slides held together with cellotape. The

wings, thus collected, were later on used to determine the age of flies according to the wing fray method proposed by Jackson (1946). By this method, flies were ascribed to age classes 1 to 6, whereby 1 was for the youngest flies and 6 for the oldest flies based on the degree of wear on the trailing wing margin.

The ovaries of each fly were dissected out to determine the ovarian age according to the method proposed by Saunders (1960) and improved by Challier (1965). The method depends on the cyclical development of tsetse ovarioles which enables eight ovarian age categories to be recognized on dissection. This is based on the relative positions of the sequentially developing follicles and the presence or absence of follicular relics attached to the developing eggs. Flies in the first four categories (designated 0, 1, 2 and 3) can be aged accurately. In these categories the largest developing egg is found in one of four different positions with no follicular relic attached to it. Category 0 flies are nulliparous (not ovulated) and include two subcategories OA and OB. Flies in subgroup OA have not had a blood meal and no egg development is seen in the first follicle in the sequence. Flies of the OB subgroup have had a blood meal and the first egg is in some stage of development. The last four categories (designated 4 + 4n, 5 + 4n, 6 + 4n and 7 + 4n are composite categories from which it is not possible to determine whether a fly is in its 4th, 8th, 12th ..., 5th, 9th, 13th ...; etc. ovarian cycle. This is because, unlike in mosquitoes, only one relic is

normally found attached to the next developing follicle although there might have been several ovulations from that ovariole.

6.2.3. Analysis of Data

6.2.3.1. Fly numbers and sex ratio

The fly numbers from each monthly sampling were pooled for each set of sampling traps and the apparent population density estimated by calculating the arithmetic mean catch per trap per day. This gives an unbiased estimate of the population size; standard errors can be obtained by taking {N (Williams *et al.*, in press). These were first plotted to show the monthly changes in apparent densities. To show major trends in relative population densities over time, male and female catches were then plotted on a log scale and the curve smoothed by taking three monthly running means.

To determine the monthly changes in fly distribution within the different vegetation types, the percentage catches by traps within the vegetation were calculated. Averages were taken of the percentages of the biconical and the NG2B traps that were sited in the same vegetation type.

The monthly percentage female catches were also calculated for the different sets of sampling traps. These data over the whole sampling period were then subjected to an analysis of variance following an arcsine p transformation. This was to determine if there were any significant

differences in sex ratio between trap types and between months.

6.2.3.2. Estimation of mortality rates from ovarian age distribution

The monthly ovarian age distributions were used to estimate mortality rates. In a review of the various methods used to estimate mortality rates from tsetse age distribution data, Rogers *et al.* (1984) pointed out that the age distribution can only reflect real mortality when the population is stable. However, they considered that changes in age structure can provide information on changes in mortality rate from one sample to the next. But Dransfield *et al.* (1986a) observed that this is not strictly valid when the adult recruitment rate is not constant. In this study two methods were used to estimate mortality rates; the first is that method proposed by Rogers *et al.* (1984) and modified by Dransfield *et al.* (1986a). The modified method excludes category 0 (nulliparous) flies which are not sampled at the same efficiency as the other age categories. Data on later

categories only were therefore used and an inter-larval period of 9 days was assumed. According to the method the proportion of parous flies in Category 1 (P1) is given by

$$P1 = (1-e^{-9m})$$

where 'm' is the mortality rate.

Similarly, for the other age categories

$$P2 = e^{-9m}(1-e^{-9m})$$

$$P3 = e^{-18m}(1-e^{-9m})$$

$$P4+ = e^{-27m}(1-e^{-9m})$$

$$P5+ = Re^{-36m}$$

$$P6+ = Re^{-45m}$$

$$P7+ = Re^{-54m}$$

where

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

A non-linear least squares fit method was then used to estimate 'm'.

The second method is the Robson-Chapman survival method which was first applied on fish by Chapman (1965) and recently applied to tsetse by Dransfield *et al.* (1986a). Category 0 flies were also excluded from the analysis. The method is based on three assumptions:

1. S, the proportion of a given age-group surviving from one age-group to the next, is the same for each age-group and remains constant over time.
2. N_x, the number of animals of age x in the population at the time of reproduction is constant from one period to the next and N_o is the birth-rate. (per 9 days in the case of tsetse).

3. Sampling from the population is random with respect to age.

From assumption (2) the number of animals N_x growing out of age x will be balanced by the number $SN_{(x-1)}$ growing into this age-group.

Hence

$$N_x = SN_{x-1} = S_x N_o \qquad (1)$$

and

$$N = \sum N_x = N_o(1+S+S^2 \ldots) \qquad (2)$$

Since the sum of the infinite series in brackets = $1/(1-S)$

$$N = N_o/(1-S); \qquad (3)$$

Therefore substituting for N_o in (1),

$$N_x = (1-S)\, S^x N \qquad (4)$$

and the proportion in each age group is given by

$$N_x/N = (1-S)\, S^x \qquad (5)$$

Based on assumption (1) Robson and Chapman showed that a minimum-variance unbiased estimate of S is given by

$$S = X/(n+X-1) \qquad (6)$$

where $n = (\sum n_x)$ is a random sample in which n_x are observed to be of age x; (x = 0,1, 2...r) and

$$X = \sum x n_x \qquad (7)$$

When older age-groups are being pooled the formula is modified. Supposing that all animals y+1 years old and above are pooled.Let

$$n_y = \sum n_x \qquad (8)$$

and

$$X = \sum x n_x + (y+1)\, n_y \qquad (9)$$

then the maximum-likelihood estimate of S is now

$$S_{pool} = X/(n - n_y + X) \qquad (10)$$

In this study the age-groups pooled were 4+ to 7+. Assuming a 9 day inter-larval period, S_{pool} the survival rate is equal to e^{-9m} so

$$m = - \ln (S_{pool})/9. \qquad (11)$$

6.2.3.3. Estimation of mortality rates from Moran curves

Rogers (1979) proposed a method for estimating the overall density-independent mortality rate of the population from the change in apparent density from one sampling occasion to the other using Moran curves. To obtain the Moran curve, the log densities in one month were plotted against those in the previous month. A boundary line was then fitted for the maximum growth rate of the population which for tsetse, in the absence of any mortalities, would be doubling per month. Assuming an exponential population growth, the relationship between densities in succeeding months remains linear (after the log transformation) until density-dependent mortalities set in; the curve then bends towards an equilibrium level given by the 45° line through the origin where rate of

increase should be zero and densities in succeeding months are the same. Thus, in any one month the difference between the expected density and the observed density gives the density-independent mortality rate for that month. This may be estimated directly from the plot, as the distance of the observed log density below the maximum growth rate curve.

Mortalities obtained by this method are the overall or generation mortality rates as opposed to those from ovarian age data which estimate adult mortality rates. Because of the population suppression exercise that was going on in the TR1 area at the time, only the data from TR4 which was outside the suppression area were used for the analysis.

6.3. RESULTS

6.3.1. Apparent densities

Monthly changes in apparent densities (log catch/trap/day) of *G. longipennis* in the biconical and NG2B traps set along transect 1 in the main study area are shown in Figures 6.3A and 6.3B. To bring out the major trends, the curves have been subjected to a three-point smoothing and the two trap types superimposed for males and females. Generally, both sexes showed similar trends for each trap type. Peak catches following the long rainy season of 1986 were observed in June/July in both the biconical and the NG2B traps. Peak catches during the short rains were recorded in November/December with both trap types but the biconical traps showed peak catches which were about 3X lower than the peaks

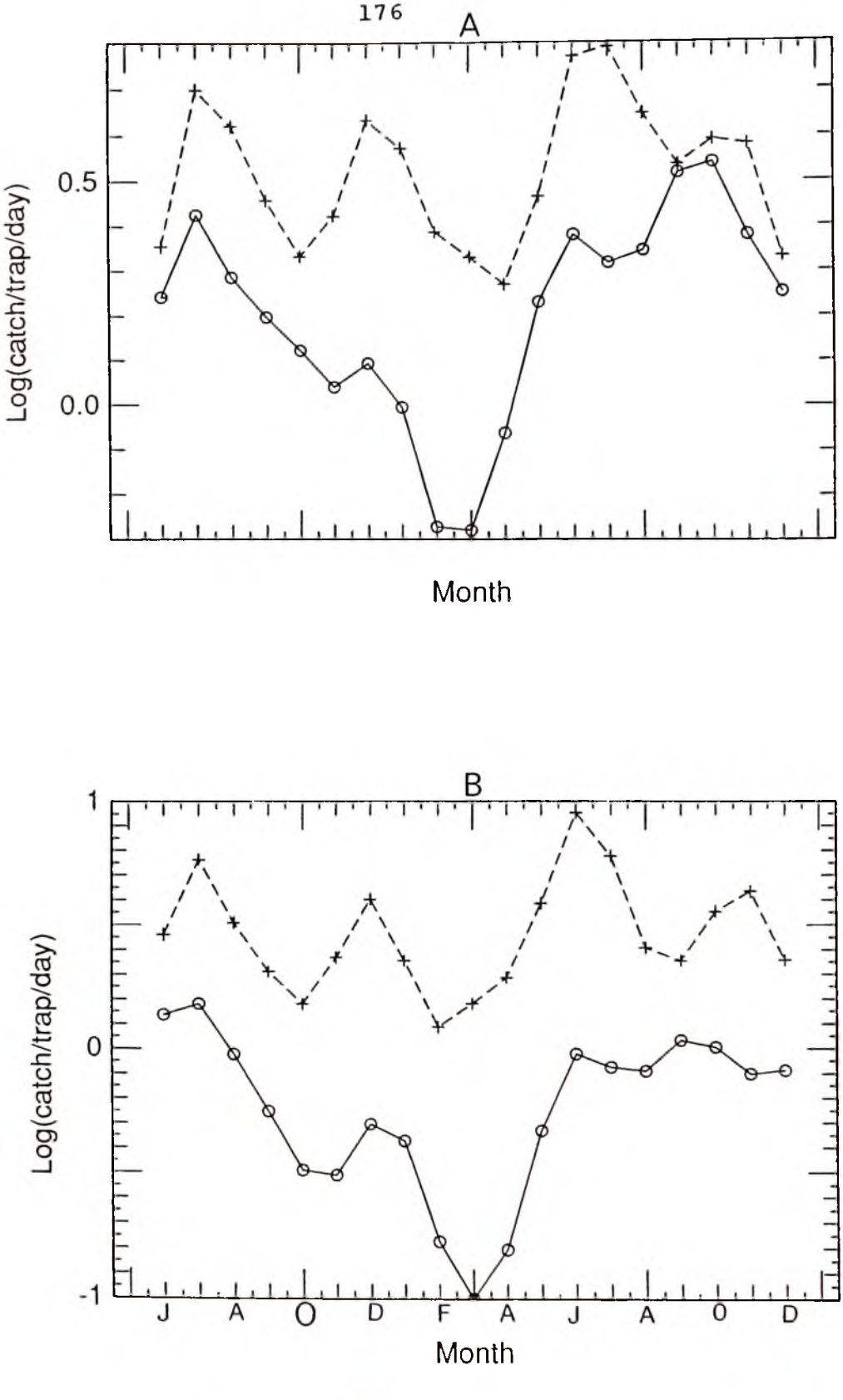


Figure 6.3: Monthly changes in the apparent densities of male (A) and female (B) *G. longipennis* in the biconical (____) and NG2B (χ..χ) traps set along Transect 1.

catches recorded after the long rains whilst the NG2B recorded similar apparent densities in both seasons. The lowest catches were recorded in February/March/April in both trap types. In 1987 a lower peak was recorded at the end of the long rainy season than during the short rainy season with the biconical traps whilst it was the reverse with the NG2B traps. Furthermore, these peaks were recorded about a month earlier with the biconical traps in both seasons.

The monthly catches in the river biconical traps are given in Figure 6.4A and 6.4B. for males and females respectively. To better compare trends in these traps with those set along the transect, the plots of catches by the transect biconical traps are superimposed on those of the river biconical traps. Generally, the highest catches in the river biconical traps were observed in the hottest and driest periods of the year and rainy season catches were rather low. For example, marked peaks were observed in August-October in the river biconical traps when catches in the traps along the transect were on the decline. These trends were similar for both sexes.

Changes in the apparent densities recorded by the traps set along the transect 4 are shown in Figures 6.5A and 6.5B. Generally, peak catches here were also observed towards the end of the dry season and that of the rainy season but the peaks on TR4 preceded those of TR1 by one month. For example, the dry season peaks in 1986 and 1987 occurred in September-October on TR4 but in November-December on TR1. The rainy

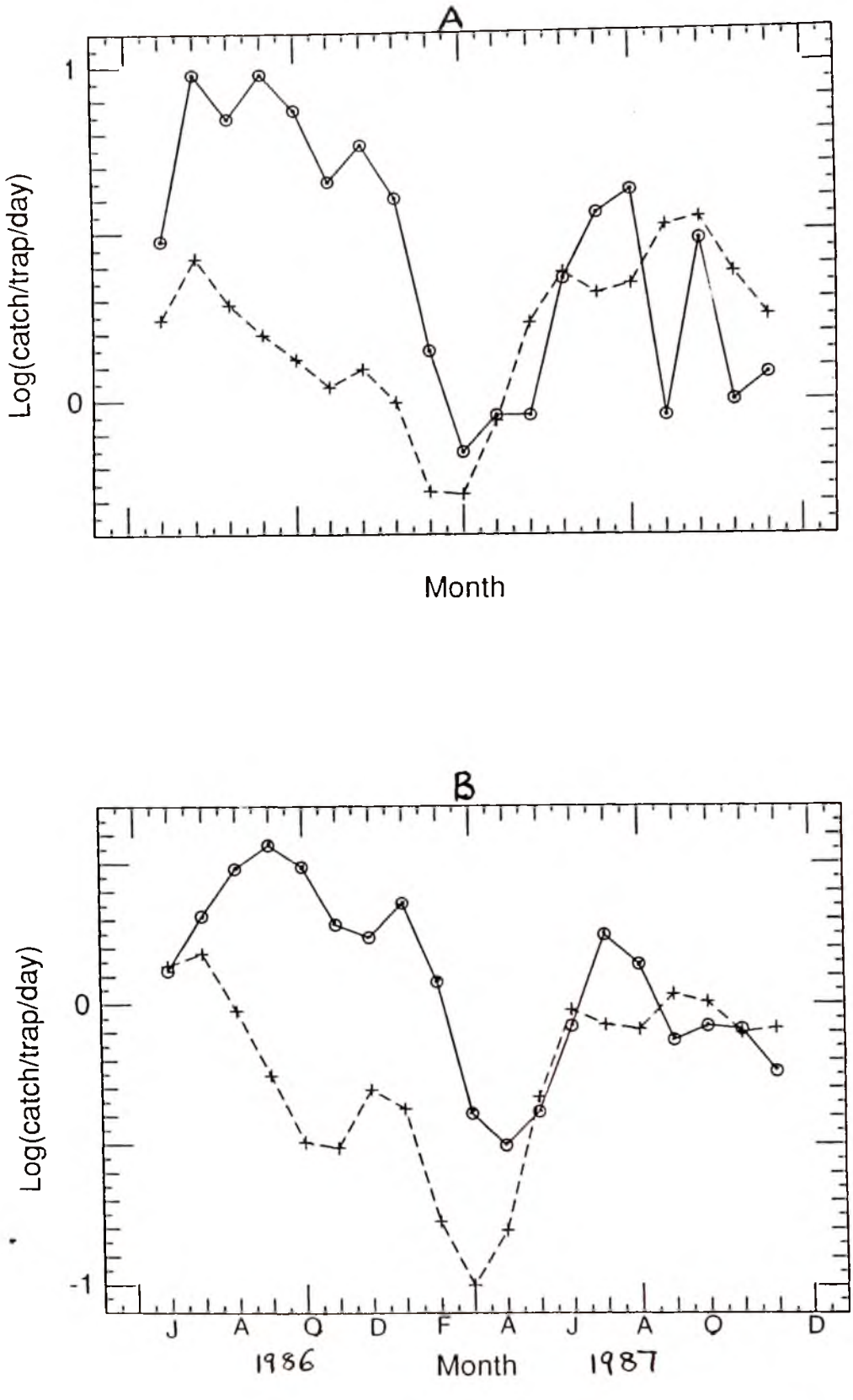


Figure 6.4: Monthly changes in the apparent densities of male (A) and female (B) *G. longipennis* in the transect biconical (____) and the river biconical traps (x..x) of transect 1 area.

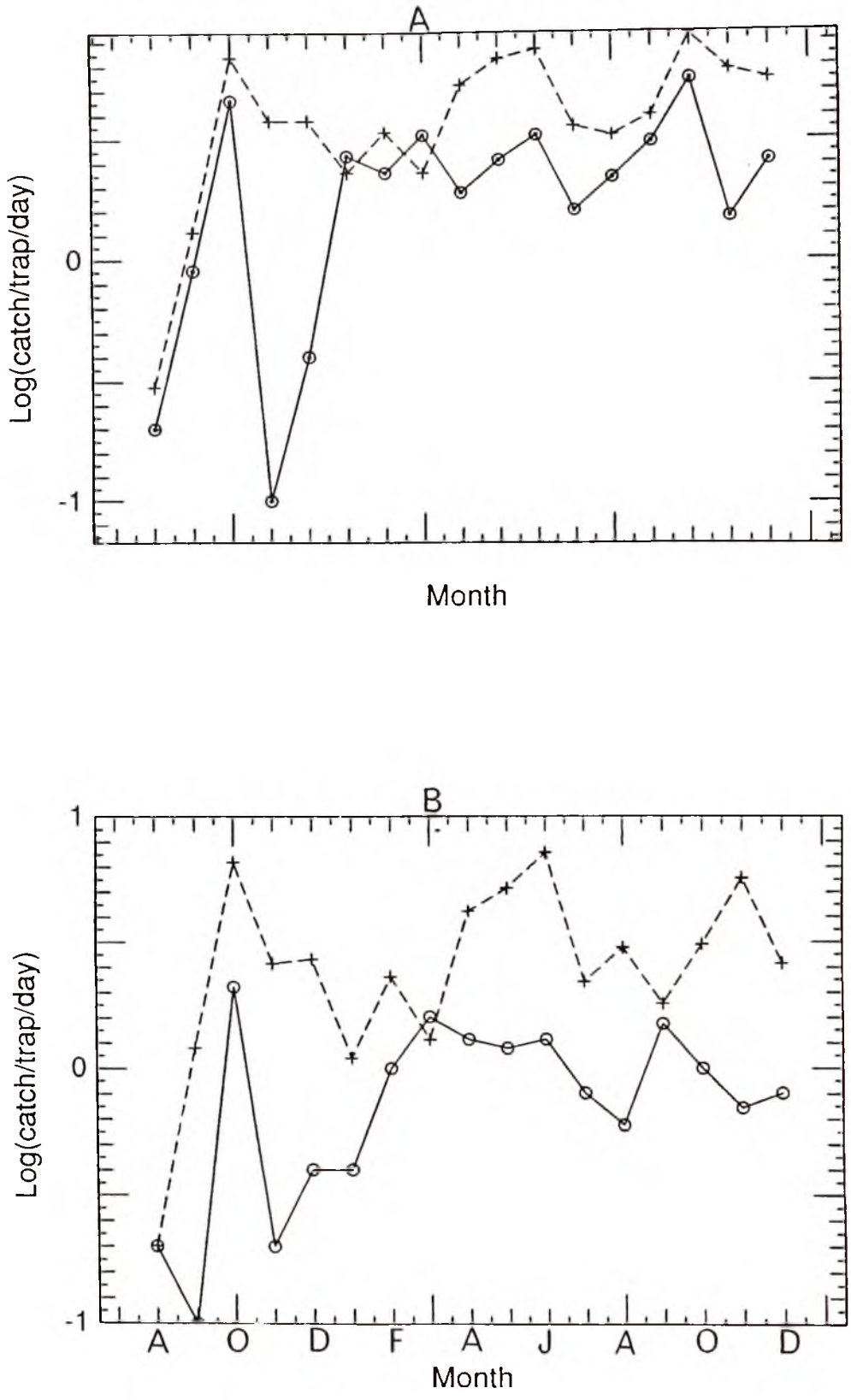


Figure 6.5: Monthly changes in the apparent densities of male (A) and female (B) *G. longipennis* in the biconical (____) and NG2B (x..x) traps set along Transect 4.

season peak occurred in May-June on TR4 but it was observed in June-July on TR1. Whereas very low catches were recorded in February-March on TR1, catches were on the rise on TR4 in these months, this difference being more pronounced between the biconical traps of the two transects.

Catches in the river biconical traps of TR4 are given in Figure 6.6 (males and females together). The trends in these appear to reflect aspects of the trends in both TR1 and TR4. Increases in these traps started earlier than they did on TR1 but at the same time as on TR4. However, these traps showed broad peaks that covered the months in which peak catches occurred on both transects. The low catches observed in February and March with these traps are characteristic of trends in TR1 traps. This is because two of the river traps ascribed to TR4 are actually sited in a stretch of vegetation between the central part of TR4 and TR1. Thus, the intermediary position of the trends shown by these traps may be reflecting movement of flies between the two transects.(see Discussion).

When the monthly mean catch per trap per day in the NG2B and biconical traps are compared, a number of observations can be made with regards to the sampling efficiencies of the two trap types. Generally, catches in the NG2B traps were higher than those in the biconical traps. On TR1 for instance, the average mean catches/trap/day $\pm$ 1 s.e. over the sampling

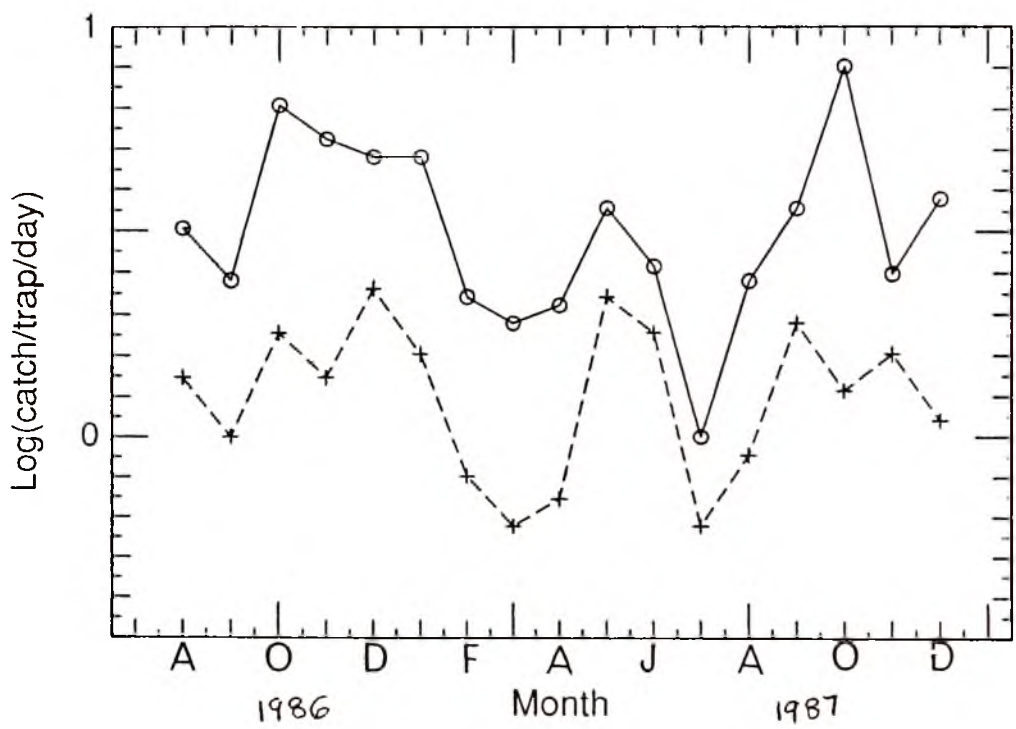


Figure 6.6: Monthly changes in the apparent densities of male (____) and female (x..x) G. longipennis in the river biconical traps of transect 4 area.

period were 5.3 ± 0.3 males and 2.3 ± 0.06 females in the NG2B traps compared to 1.2 ± 0.03 males and 0.6 ± 0.02 females in the biconical traps.

The monthly mean percentages of females caught in the transect 1 biconical and NG2B traps are shown in Figure 6.7 and 6.8 respectively. Generally, the proportion of females in the catch seemed to follow the same trends as the apparent densities with peaks towards the end of the dry and the rainy seasons. The highest percentage of females was recorded in July and the lowest at the beginning of the dry season in August and at the beginning of the rainy season in April. The trends were similar in both the biconical traps and the NG2B traps.

The overall mean female percentages were 46.7 ± 3.4% for the NG2B traps, 27.1% ± 2.3 for the TR1 biconical traps and 31.5% ± 2.5 for TR1 River traps . An analysis of variance performed on the monthly female percentages (following an arcsine {P transformation) showed that there were significant differences between female percentages in the three trap sets. Comparing the means using the Duncan's Multiple Range Test, the mean percentage of females caught in the set of NG2B traps was significantly higher than those in the transect and river biconical traps but those from the latter two sets of traps did not differ significantly.

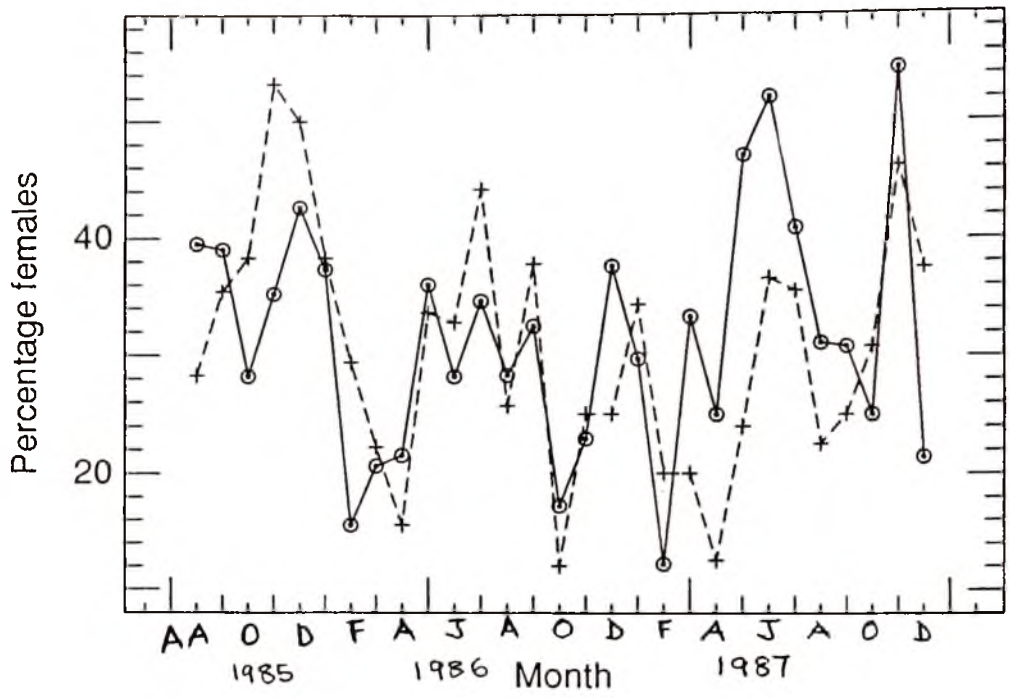


Figure 6.7: Monthly changes in the percentage of females caught by the biconical traps.

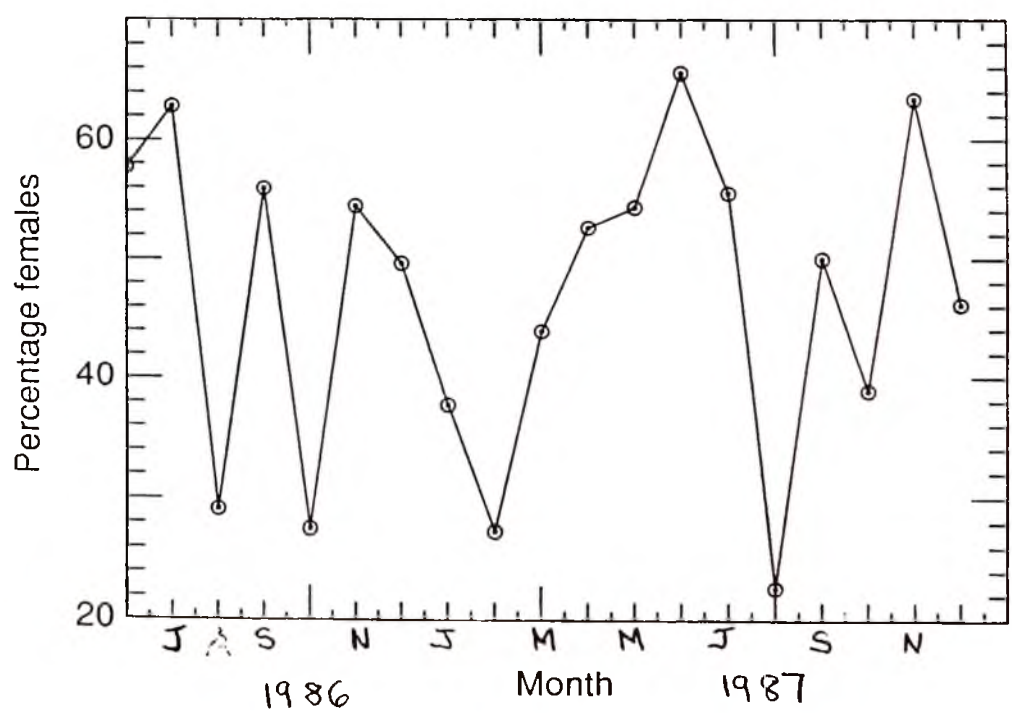


Figure 6.8: Monthly changes in the mean percentage of females caught by the NG2B traps.

6.3.2. Fly distribution in different vegetation types.

Changes in the relative distribution of *G. longipennis* in the different vegetation types in the TR1 area are shown in Figs. 6.9A and 6.9B for males and females respectively. These figures were produced from the averages taken of the data grouped into sets of three months to roughly correspond with the different annual seasons in the study area: July-September (cold dry season), October-December (short rains), January to March (hot dry season) and April to June (long rains). Generally, the highest percentage catches were recorded in the lower and upper woodlands and the lowest in the open plains. In the cooler wet seasons a more even distribution was observed as flies tended to spread into all vegetation types. In the dry seasons, however, flies became concentrated in the dense vegetation (riverine thicket and lower woodland). Both sexes followed similar trends of movement in relation to seasons. It is clear from the figures that flies concentrated more in the riverine thickets in the hot dry season (January-March) of 1986 than they did in the same season of 1987. This is probably because it was cooler during this season in 1986 than in 1987, the average maximum temperature for these 3 months in 1986 being 37.9°C as against 36.3°C for 1987.

The relative distributions in the River traps are shown in Fig. 6.10A for males and Fig. 6.10B for females. The data were again grouped into seasons as described above. It should be pointed out that although all the River traps were

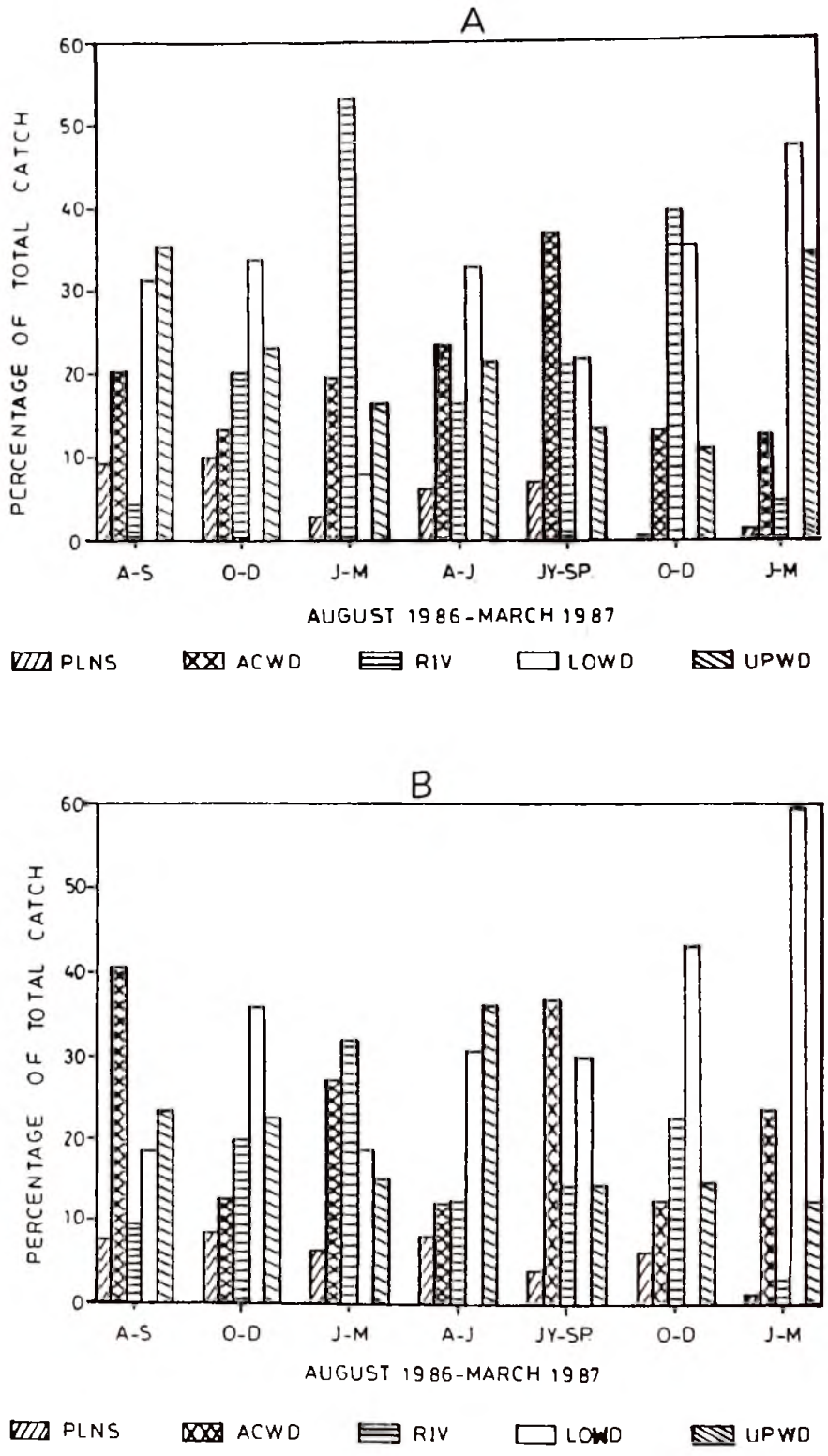


Figure 6.9: Monthly changes in the relative distribution of male (A) and female (B) *G. longipennis* in different vegetation types along transect 1.

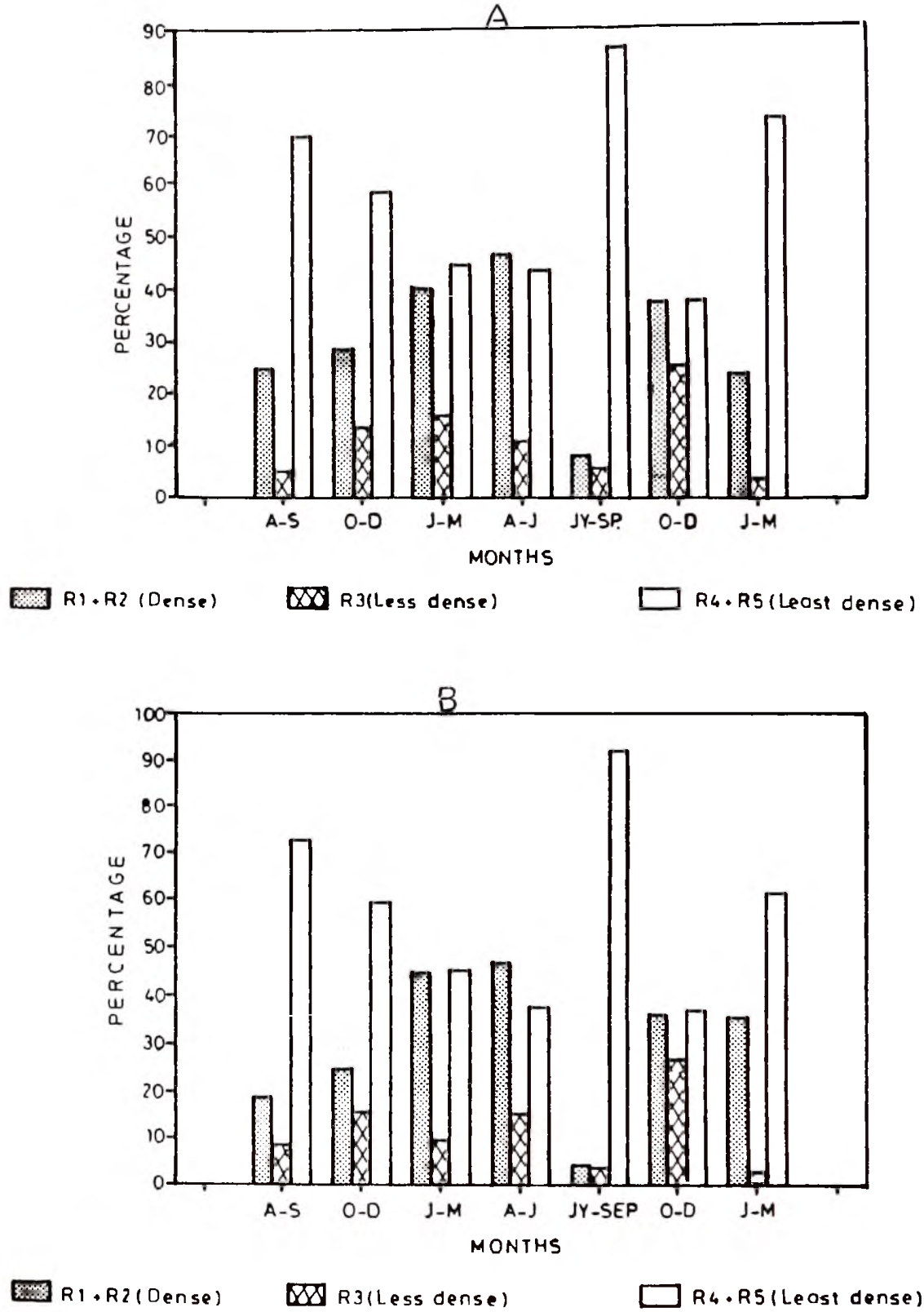


Figure 6.10: Monthly changes in the relative distribution of male (A) and female (B) *G. longipennis* in different vegetation types along the river bed of transect 1 area.

generally located in the thickest section of the habitat (along the river bed), there were local differences between the trap sites with respect to vegetation cover. Traps R1 and R2 were located in relatively dense woodland to the south of R3 which itself was in a less dense site, whilst R4 and R5 were in more open sites to the north of R3.

The relative percentage catches in these traps show that flies also showed preference for different vegetation cover in different seasons in a manner similar to that along the transect. Generally, flies were abundant in the more open woodland (R4 and R5) in the cool dry season and apparently moving into the denser vegetation in the hot dry and becoming more evenly distributed in the rainy seasons. The lesser concentration in the denser woodland in the January-March of 1987 compared to 1986 can also be observed here for the reason suggested above. These trends were similar for both males and females.

Figures 6.11A and 6.11B show the monthly percentage distribution of catches in river traps of TR4 for males and females respectively. The figures do suggest a seasonal movement of flies between R6 (nearest trap to TR1) and R8 (in the centre of TR4). The catches in R8 rose steadily as the dry season progressed from July to October 1986 and decreased during the short rains in November-December. A steady increase is again observed in R8 during the hot dry season from January to March, followed by a gradual decline during the long rains. This pattern of fly movement between TR1 and TR4 deduced from

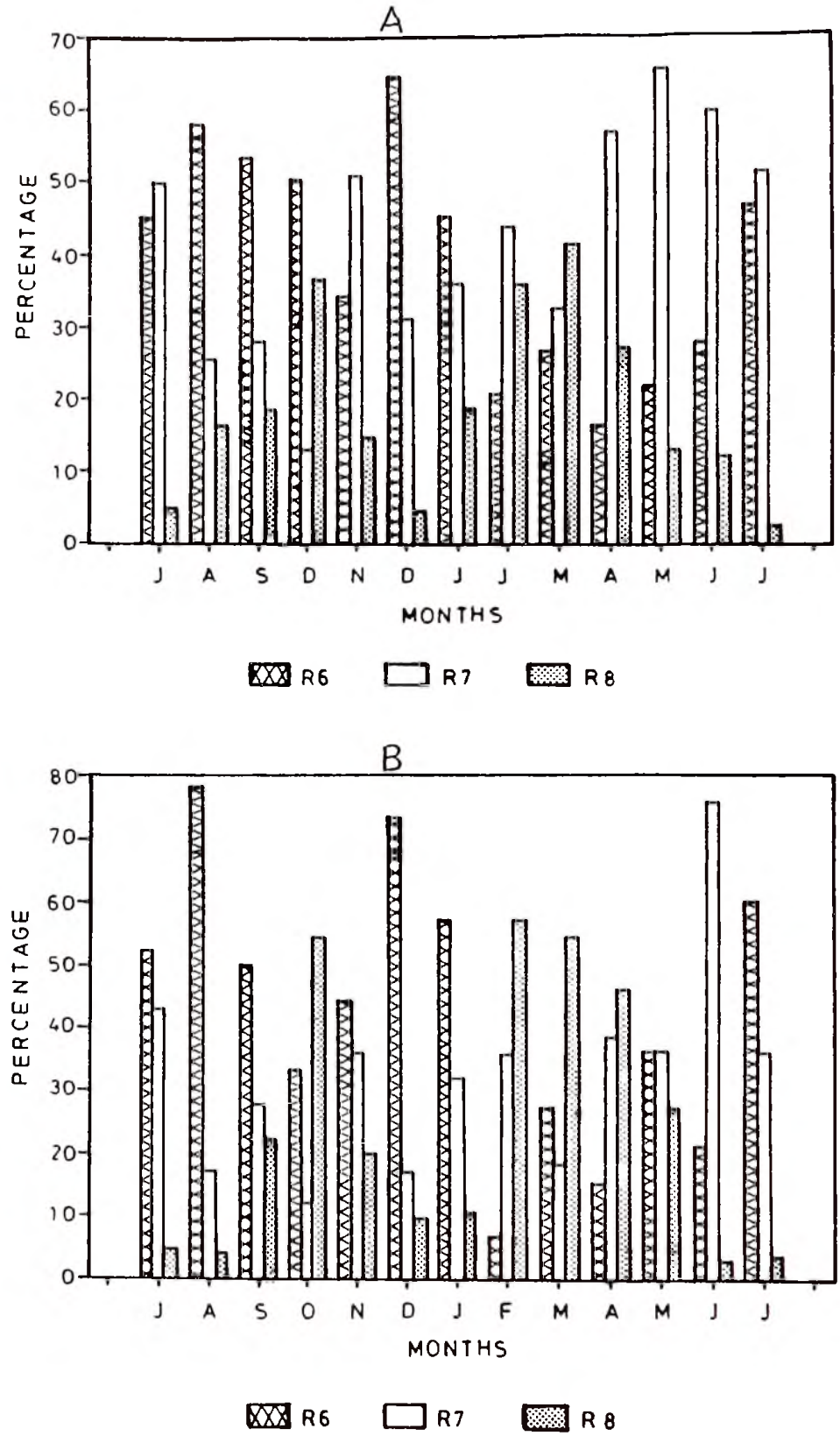


Figure 6.11: Monthly changes in the relative distribution of male (A) and female (B) *G. longipennis* in the river traps of transect 4 area.

the relative percentage catches in traps R6, R7 and R8 could also result from the search for different vegetation cover in the two areas at different times of the year.

6.3.3. Age structure

The age distribution of female *G. longipennis* caught by the NG2B traps are shown in Figures 6.12 and 6.13 for transects 1 and 4 respectively. From June 1986 to January 1987, when the population was not being suppressed (see chapter 9) there was a relatively low percentage of category O flies. This observation is true for both transects except when the sample size was very small as in the case of October 1986 (on TR1) and January 1987 (on TR4). As already reported earlier, the NG2B trap shows a bias for older flies when compared to the biconical trap (see chapter 4).

Soon after the start of the suppression programme, there was a considerable increase in the proportion of young flies especially those belonging to category O and a corresponding reduction in the proportion of older flies. Although the suppression exercise was being carried out in the transect 1 (with barrier traps between TR1 and TR4) the above change in age composition was also noticeable in the transect 4 samples. This implies that the population of flies in the latter area was also being affected by the suppression operation, which is expected if there is considerable movement of flies between

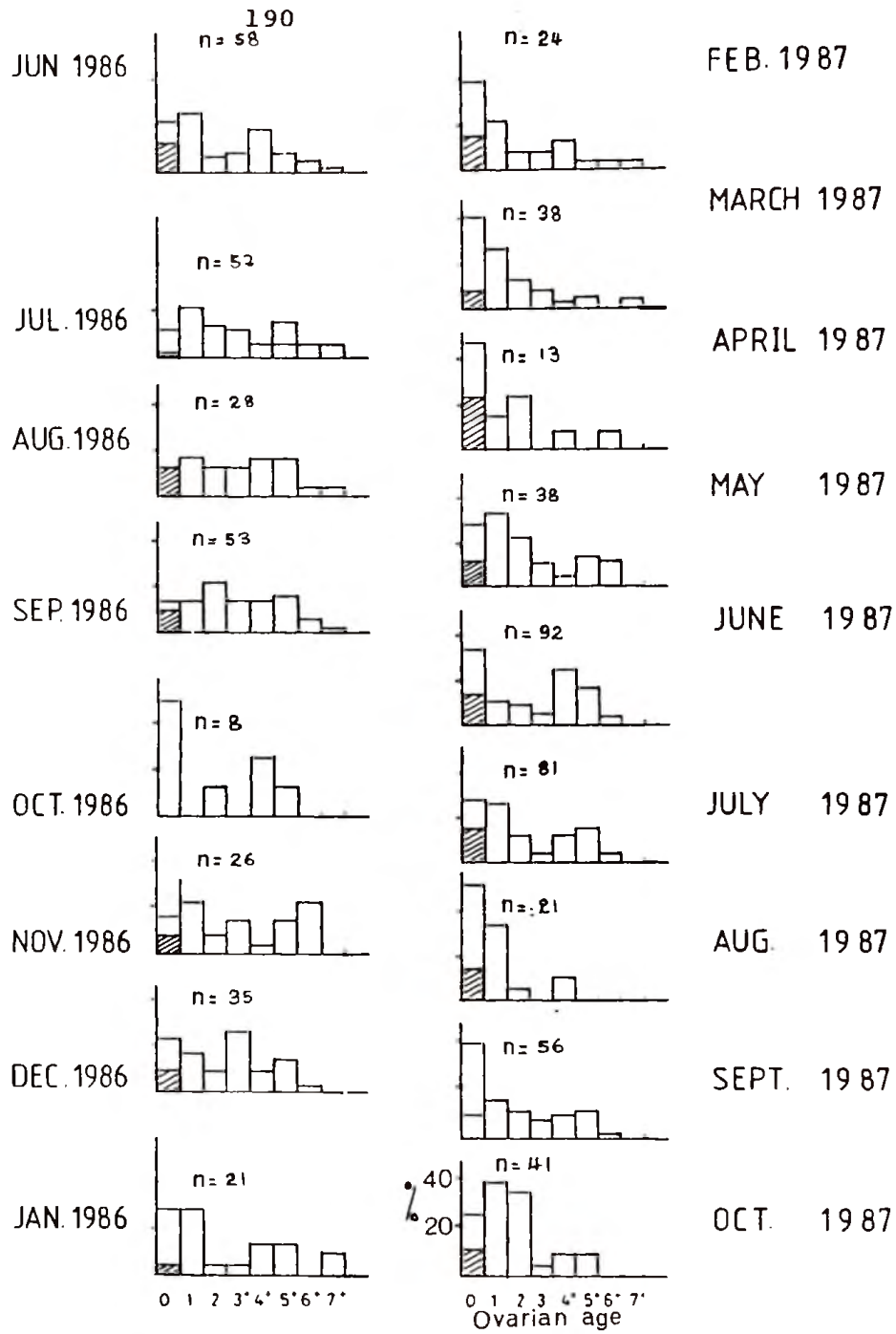


Figure 6.12: The age distribution of female *G. longipennis* caught by the NG2B traps of transect 1 area.

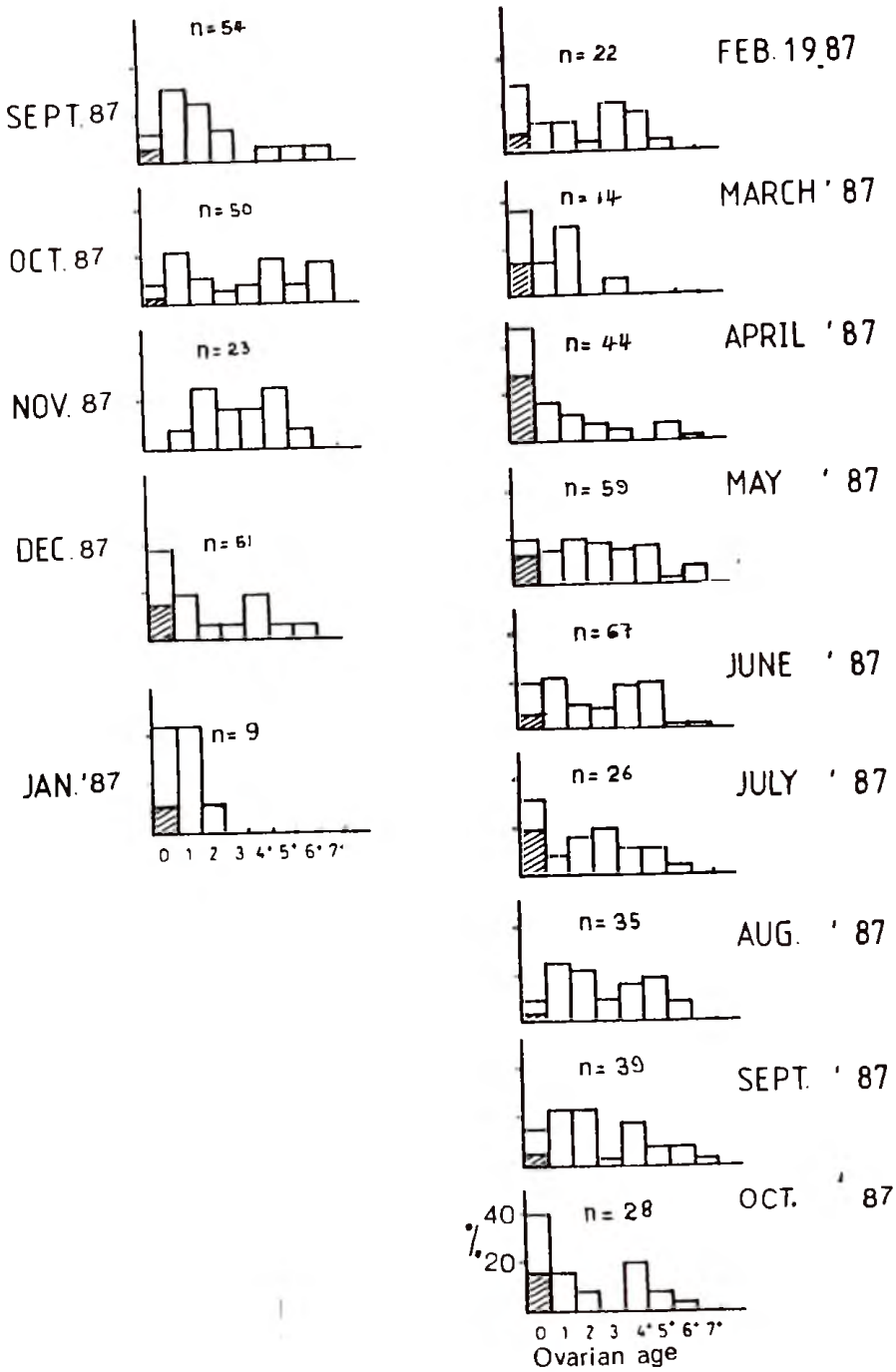


Figure 6.13: The age distribution of female *G. longipennis* caught by the NG2B traps of transect 4 area.

the two areas. Therefore flies migrating from TR4 (which are more likely to be old flies) are not likely to return as they will get trapped in TR1.

However, from May 1987 up to July 1987 the proportion of older flies is seen to increase again in the main study area which was partly due to heavy immigration into the suppression zone and partly to the suppression traps being less effective. The above period is just after the rains when there is abundant vegetation cover and flies spread out into more open areas where the density of suppression traps is very low. The months of August to October are drier months when flies tend to withdraw into the thicker woodlands and one can see the reduction again in the proportion of older flies in these months as the control traps become more effective and immigration is reduced. This latter effect was not immediately noticeable in the Transect 4 where the proportion of old flies remain relatively high until October (see chapter 9 for more details).

The ovarian aging method was compared to the wing fray method by plotting the ovarian age against wing fray. Figures 6.14 and 6.15 show the relationships between ovarian age and the wing fray for samples from TR1 and TR4 respectively. The analysis was limited to flies in ovarian age categories 0 to III because of the uncertainty in aging flies above age group III. The following estimates of the calendar ages (in days) of

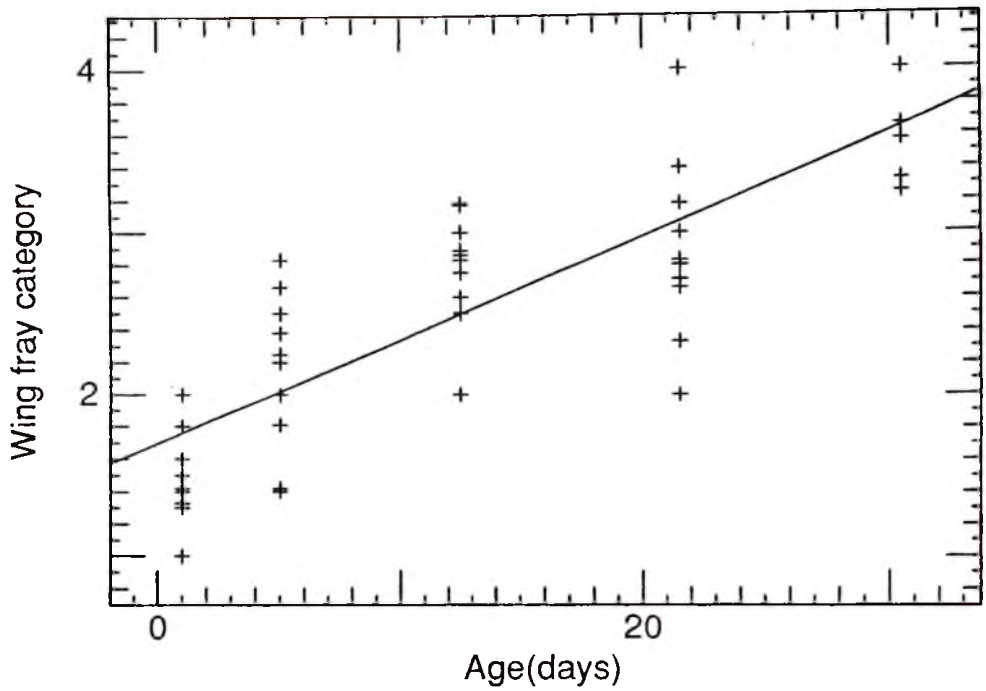


Figure 6.14: The relationship between ovarian wing-fray age and ovarian age of female G. longipennis from transect 1 area (Y = 1.70 + 0.064X; r = 0.0844, P<0.001).

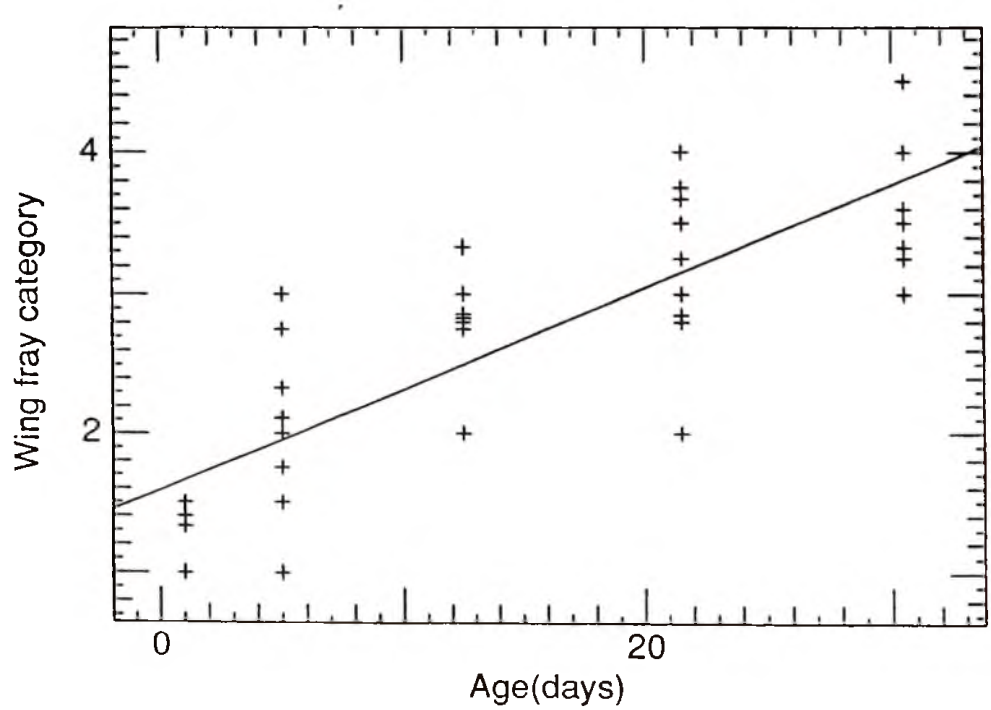


Figure 6.15: The relationship between wing-fray age and ovarian age of female *G. longipennis* from transect 4 area (Y = 1.59 + 0.073X; r = 0.0815, P<0.001).

the various ovarian age categories were used for the analysis: 1 day for category Oa flies, 5 days for Ob, 12.5 for category I, 21.5 days for II and 30.5 days for category III flies. The regressions of wing fray category on ovarian age were significant for samples from both transects;

$Y = 1.70+0.064X$, ($r = 0.844$, $P<0.001$) for TR1

and

$Y = 1.59+0.073X$ ($r = 0.0.815$, $P<0.001$) for TR4.

An analysis was then carried out to determine if there was any difference in the rate of wing fray between the flies from two transects. Following the method used by Ryan *et al.* (1980) and Rogers (1984), the slope of a regression of wing fray on ovarian age should give an estimate of the rate of wing fray of the population. The slopes ($\pm$ 1 s.e) of the regressions line were 0.064 $\pm$ 0.0055 for TR1 and 0.072 $\pm$ 0.0070 for TR4. A t-test showed that there was no significant difference between the slopes and hence the rate of wing fray between flies from the two transects ($t = 0.23$, $P>0.05$). Considering the evidence that there is some movement of flies between the two transects the above finding supports the view that the same population is actually being sampled in both sites.

The data were next examined to find out if there were any significant relationships between the rate of wing fray and climatic factors (temperature and relative humidity). This was done by determining the rates of wing fray for each month and then carrying out a correlation analysis of these with maximum

temperature and minimum relative humidity. Since sampling was usually carried out in the first week of every month it was assumed that flies experienced environmental conditions of the previous month and of the month of sampling. Therefore means of these monthly temperatures and relative humidities of these two months were taken for the analysis. However no significant association was found between the rate of wing fray and these climatic factors.

6.3.4. Mortality rates from ovarian age distribution.

Figs. 6.16 and 6.17 show the monthly changes in adult mortality rates on TR1 and TR4 respectively, estimated from the ovarian age distribution. The estimates were made from bimonthly running sums of ovarian age distributions to avoid the problem of very small samples in some months. Both figures include mortality rates estimated by the two methods described in section 2.3 (Rogers *et al.*, 1984 and Dransfield *et al.*, 1986a). Both methods gave very similar values of mortality rates ranging from 0.022-0.059 per day.

On TR1 the mortality rates rose towards the end of the cold dry season from October to a peak in February-March with a small drop between December and January. On TR4 mortality rate also increased from October but reached a much higher peak in December than it did on TR1, declined to its lowest level peak in January-February and rose again to a smaller peak in March. Following the February peak, there was a decline on both transects which stopped in April on TR1 to be

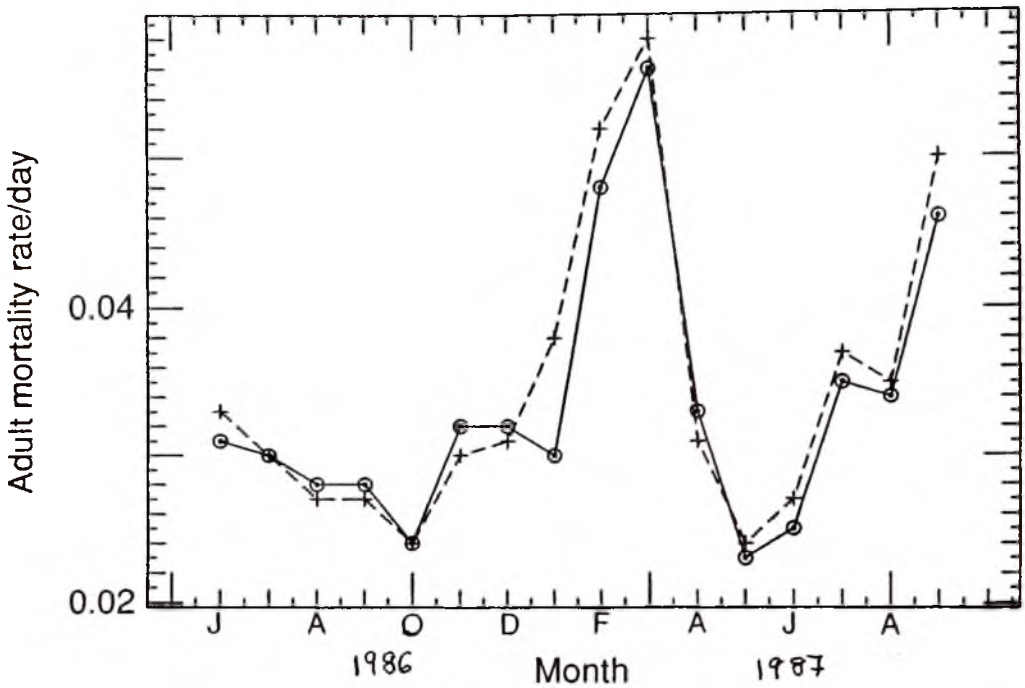


Figure 6.16: Monthly changes in adult mortality rate estimated from ovarian age structure on transect 1.

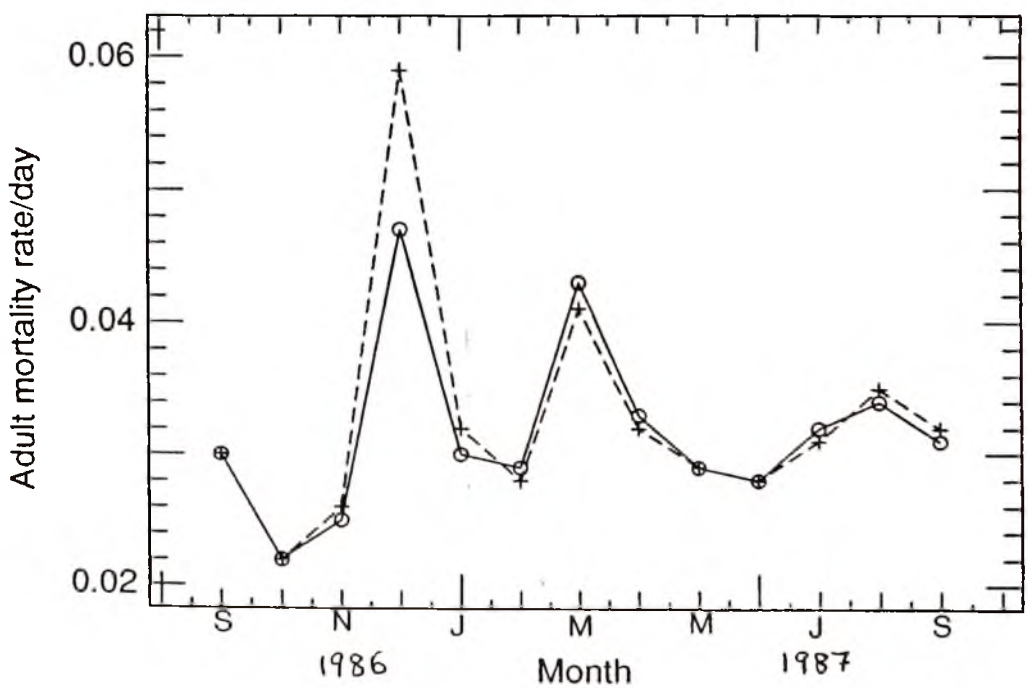


Figure 6.17: Monthly changes in adult mortality rate estimated from ovarian age structure on transect 4. (____method 1; x—xmethod 2).

followed by a sharp rise until August. On TR4 the decline continued until May and was then followed by a rise at a lower level. This difference in levels of mortality rates between the two transects which show up after February probably reflects an additional mortality arising from the population suppression operation (using odour baited traps) which was started in February 1987 in the transect 1 area.

Comparing the trends in apparent mortalities to those in apparent densities on the two transects, some general observations can be made. On both transects, periods of low mortalities seem to be followed by a rise in apparent densities in subsequent months and vice versa. For instance, on TR1, the low mortalities from June to September were followed by rises in apparent densities from October to December. Then the high mortalities from December to February were followed by decline in apparent densities from January to April. Low mortalities from March till May were followed by rises in apparent densities from April to June. However, correlations between apparent mortality in one month and the apparent density in the next month were not significant.

Analyses were carried out to determine the relationship between adult mortality rate and climatic factors. With the data from TR1, a significant positive correlation was observed between mortality rate and the maximum temperature (Fig. 6.18). The regression equation of mortality rate against temperature was:

$$Y = -0.114+0.004X \quad (r = 0.83,\ P<0.001,\ n = 15)$$

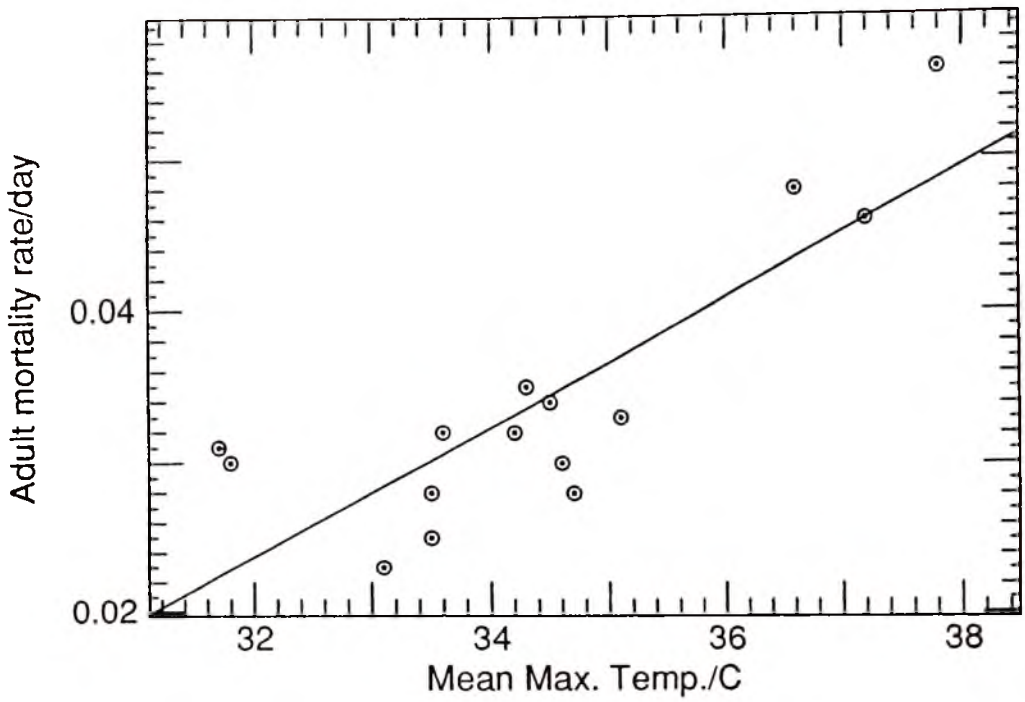


Figure 6.18: The relationship between adult mortality rate on transect 1 and the mean monthly maximum temperature (Y = -0.114 + 0.004X; r =0.83, P<0.001, n = 15).

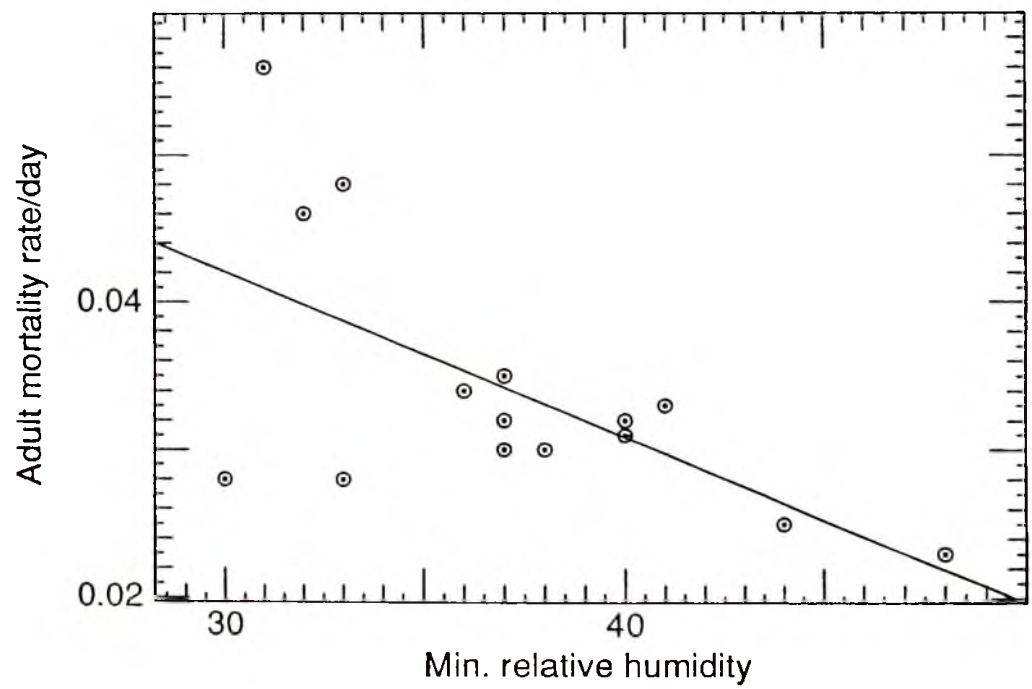


Figure 6.19: The relationship between adult mortality rate on transect 1 and the mean monthly minimum relative humidity (Y = 0.074 - 0.001X; r = -0.54, P<0.05, n = 15).

A weaker but still significant relationship was shown between mortality rate and relative humidity (Fig. 6.19). The regression equation was:

$Y = 0.074-0.001X$ ($r = 0.54$, $P<0.05$ $n = 15$)

Weaker relationships were observed between the mortality rates on TR4 and the climatic factors. The relationship with temperature was just significant at the 5% level ($r = 0.64$, $n = 12$) (Fig. 6.20). The correlation with relative humidity was not significant (Fig. 6.21).

When the data on TR1 was re-analyzed just for the period before the population suppression operation, the strength of the relationships was reduced to the same levels as for those for TR4. The correlation with maximum temperature was still significant ($r = 0.64$, $P<0.05$, $n = 9$) but that with relative humidity was not. The implication is that the additional mortality due to the traps during the population suppression was strongly correlated with climatic factors especially temperature (see Discussion for more details). The data for October were excluded from the above analysis because of the very small sample size of flies dissected for that month.

6.3.5. Mortality rates from Moran Curves

Figures 6.22A and 6.22B show the plots on the Moran curves from which generation mortality rates were estimated and Fig. 6.23 shows the monthly changes in mortality rates. Like the mortality rate estimates from ovarian age data, high mortalities were generally observed in the hot dry and cold

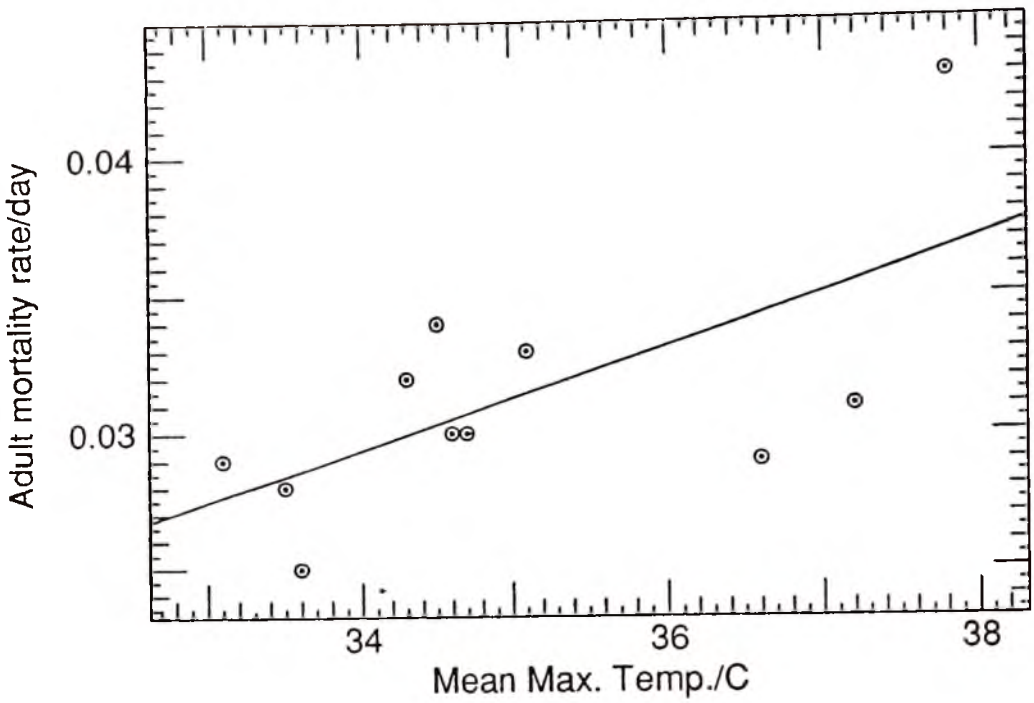


Figure 6.20: The relationship between adult mortality rate on transect 4 and the mean monthly maximum temperature (Y = -0.114 + 0.004X; r =0.83, P<0.001, n = 15).

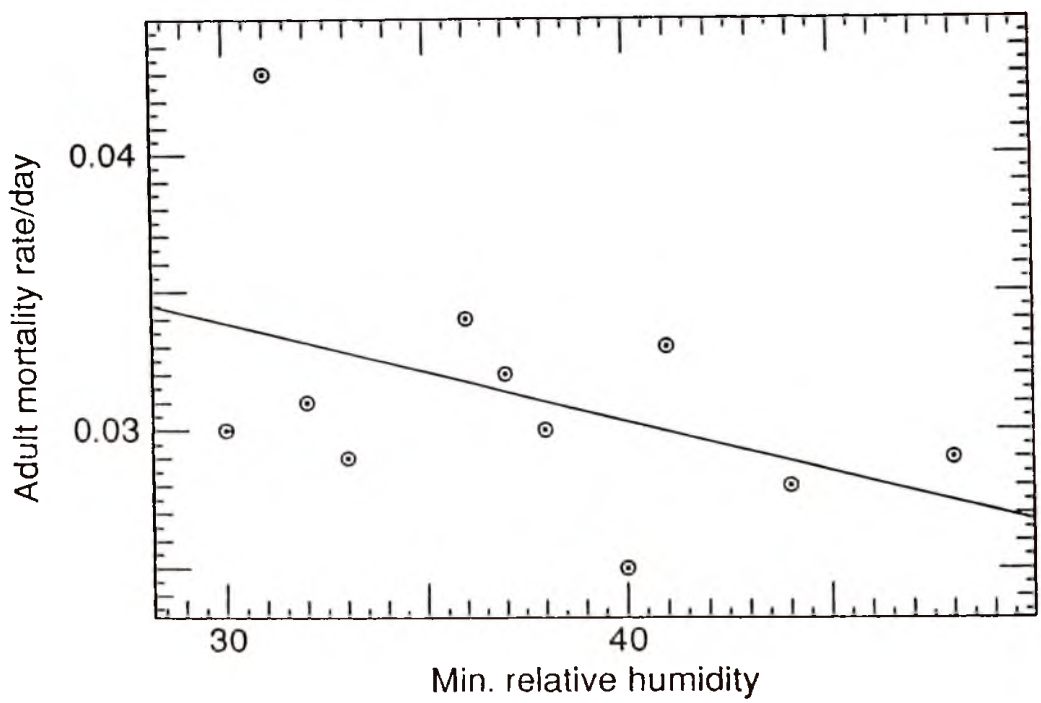


Figure 6.21: The relationship between adult mortality rate on transect 4 and the mean monthly minimum relative humidity (Y = 0.074 - 0.001X; r = -0.54, P<0.05, n = 15).

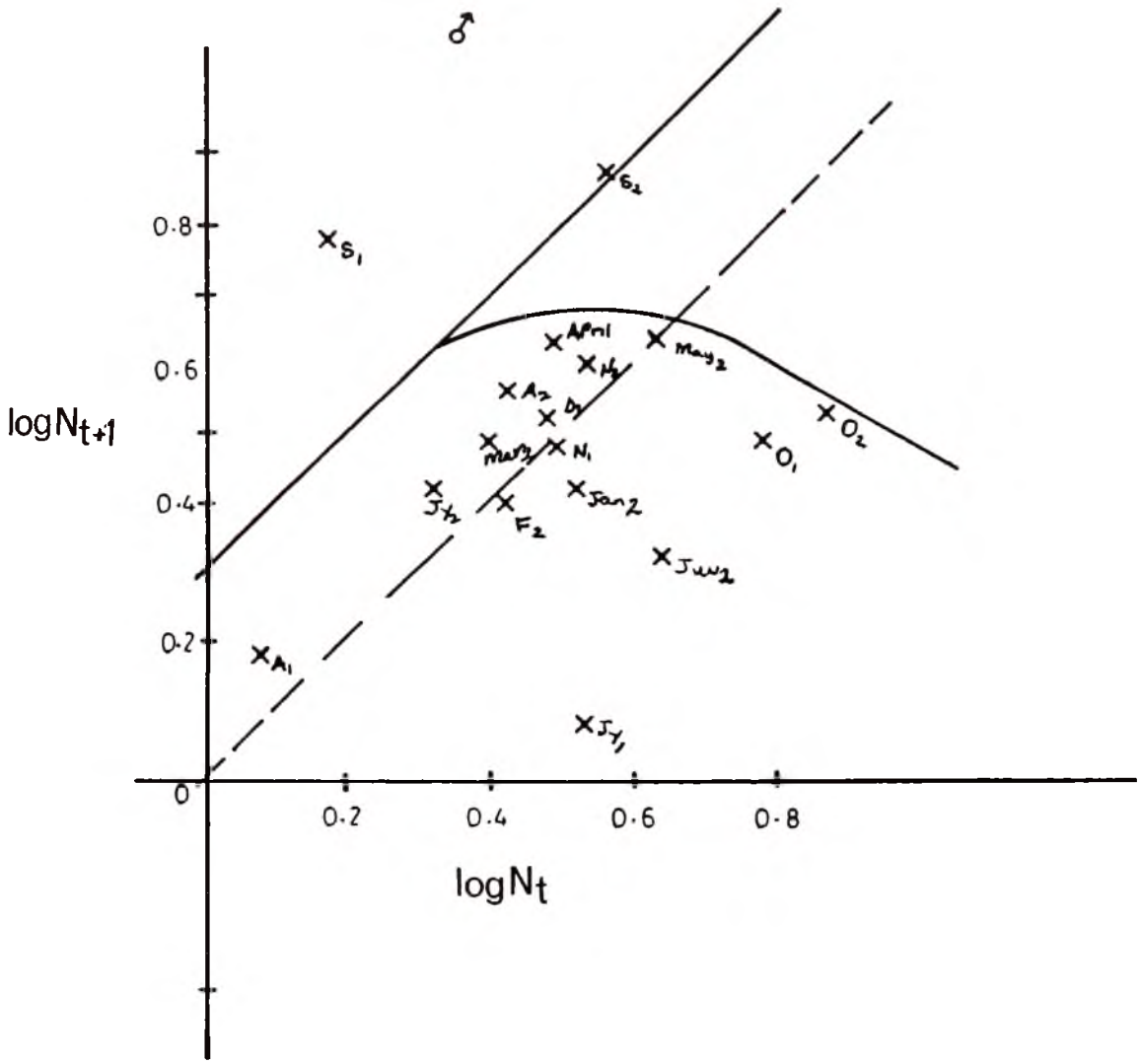


Figure 6.22A: Scatterplots of male apparent densities from transect 4 and the fitted Moran curves.

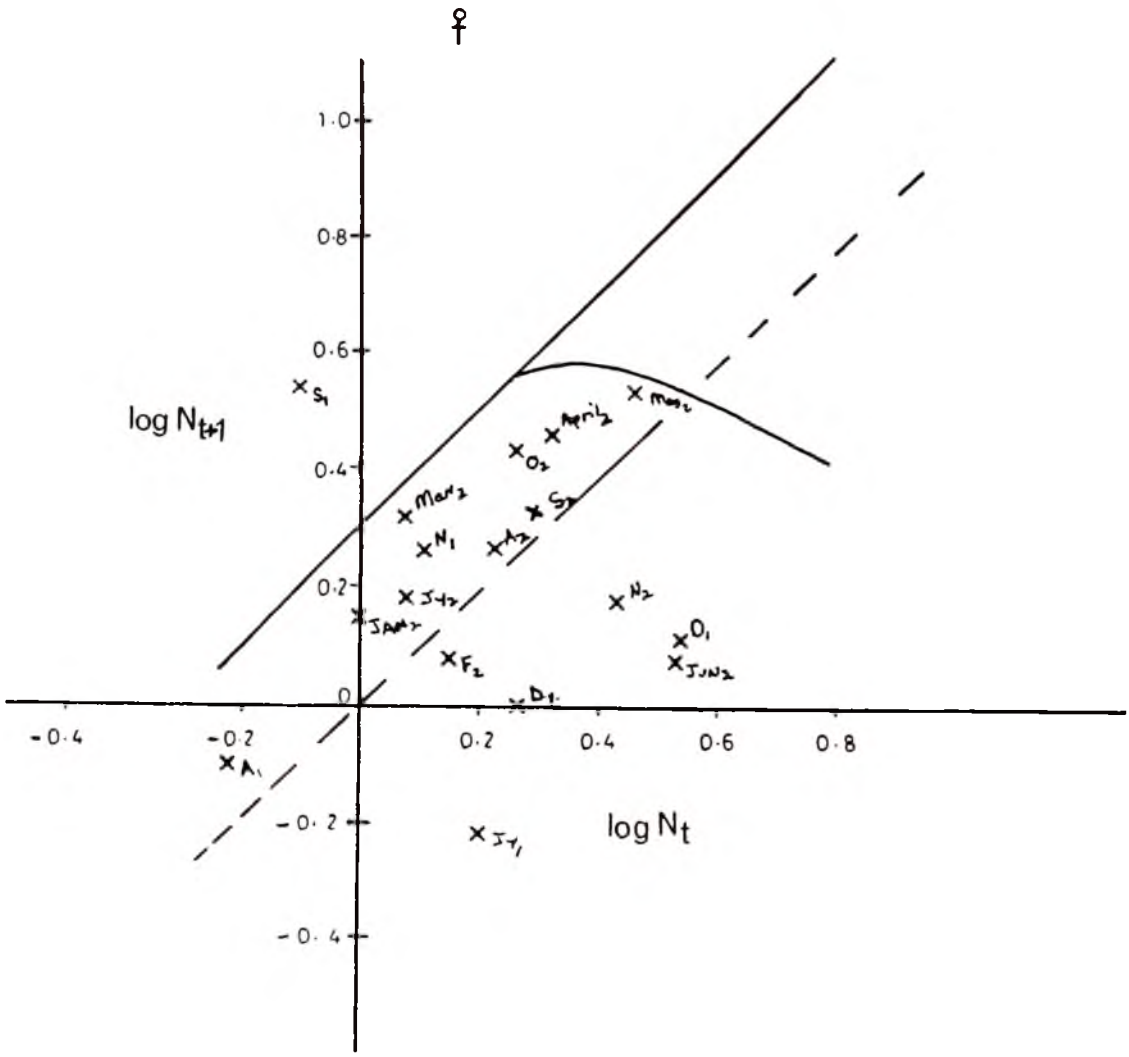


Figure 6.22B: Scatterplots of female apparent densities from transect 4 and the fitted Moran curves.

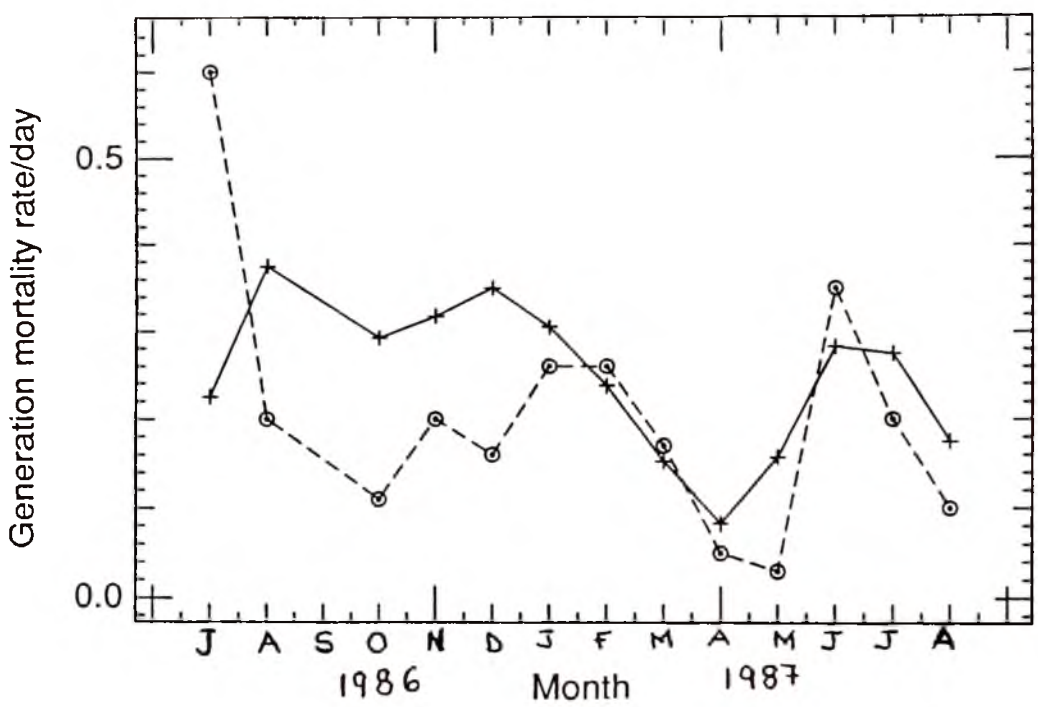


Figure 6.23: Monthly changes in generation mortality rate estimated from Moran curves (____males ; x.-.x.females).

dry seasons which declined in the long rainy season (March, April and May). However, there was no significant correlation between the generation mortality rate and the adult mortality rate from the ovarian aging. Furthermore, there were no significant correlations between the mortality rates from the Moran curves and climatic factors (temperature and relative humidity). Because of the problem of immigration, these mortality rates may be less reliable than those estimated from the ovarian age structure (see Discussion).

6.3.6. Mortality rates and changes in the percentage of nulliparous flies.

The monthly changes in the percentage of nulliparous flies are shown in figures 6.24 and 6.25 for TR1 and TR4 respectively. When the changes in adult mortality rates (estimates from ovarian age structure) are compared with those in the percentage of nulliparous flies, some general trends can be observed. A higher percentage of nulliparous flies follows periods of very high or very low mortalities. On TR1 the low mortalities from June to October are immediately followed by an increase in percentage of nulliparous flies from September to October. The rise in mortalities from November to a peak in February-March is also followed by a corresponding rise in the percentage of nulliparous flies with a peak in March-April. Similar trends occur on TR4.

Normally low mortality rates should result in low percentages of nulliparous flies since parous flies would be

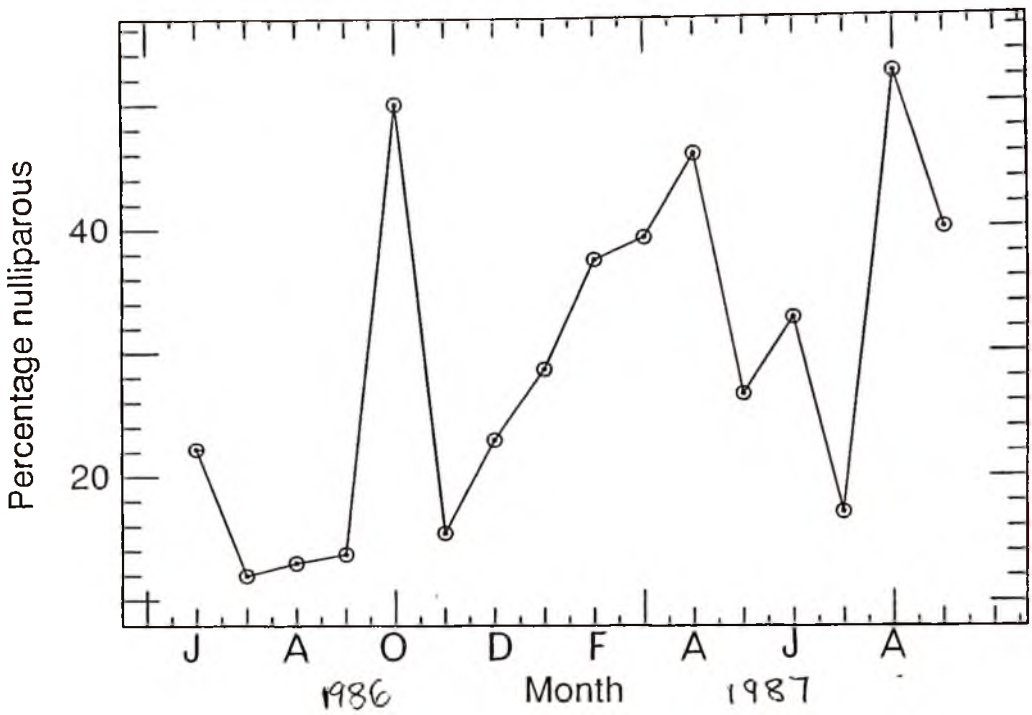


Figure 6.24: Monthly changes in the percentage of nulliparous flies in the transect 1 area.

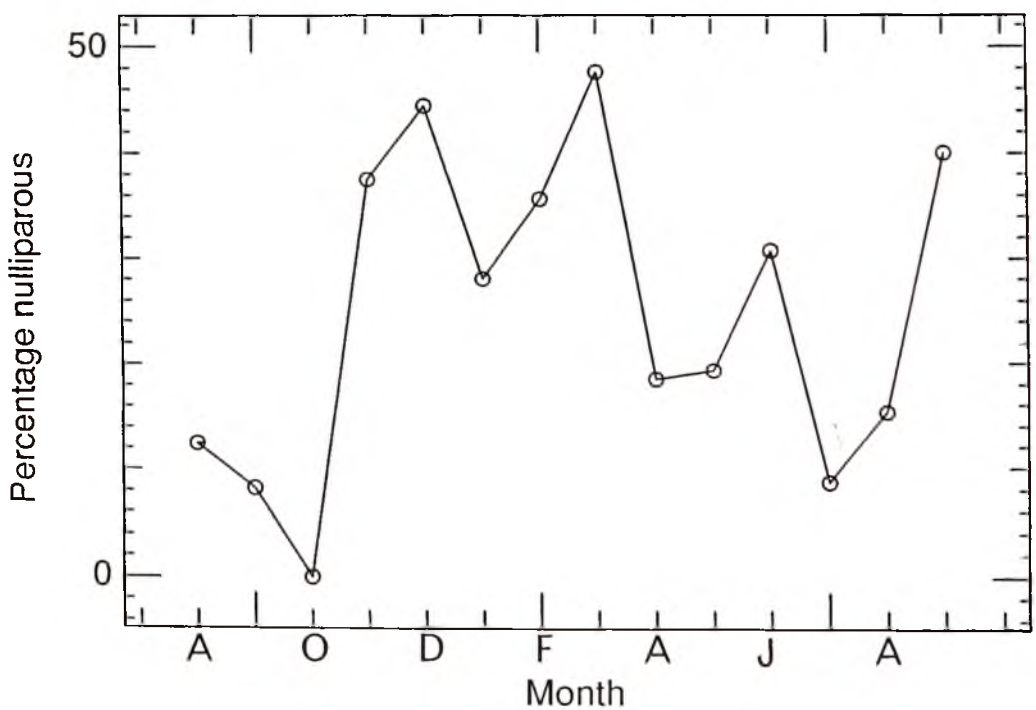


Figure 6.25: Monthly changes in the percentage of nulliparous flies in the transect 4 area.

living longer and vice versa. But according to Rogers *et al.* (1984) the high percentage of young flies occurring when mortalities are low implies an expanding population or an emigration of older flies from the trapping area.

Recalling the patterns of fly movement between the two transects suggested in section 6.3.2, emigration may partially explain the changes in percentage young flies. Peak percentages of nulliparous flies seem to correspond to periods of emigration from the respective areas. For instance the movement of flies from TR1 to TR4 from August to October is associated with a rise in the percentage of young flies on TR1 and low percentages of young flies on TR4. The movement in the opposite direction, from October to December, reverses these changes on the two transects. The net movement of flies to TR4 from December to March results in a rise in nulliparous flies on TR1 as expected but the percentage of nulliparous flies on TR4 remained relatively high. This implies that young flies were being recruited to this population

The gradual decline in the percentage nulliparous flies from May to June on TR1 can be explained by net immigration into the area during this period. However, on TR4 where there was apparent emigration during this period, the percentage of nulliparous flies was on the decline which can be explained by the generally low mortality rates during these months so that parous flies lived longer.

6.4. DISCUSSION

Although trapping is now the preferred technique for sampling tsetse populations, the method is still not successful for some species. The success of using acetone and cow urine to bait the traps for sampling *G. longipennis* in the same locality in which past attempts have failed, clearly demonstrates the advantage of employing an effective odour bait. Unbaited traps were previously found to be ineffective (Owaga, 1980).

Since effective sampling requires more than just catching large numbers of flies, the two trap types were used simultaneously to compare their efficiencies for sampling. Although similar trends in apparent densities were recorded by both traps, some important differences in the samples taken by the two trap types are worth noting. Firstly, higher fly numbers were generally recorded by the NG2B traps than the biconical traps, in agreement with previous findings. Thus, in situations of very low population densities, the biconical trap may not catch any flies at all and will therefore be inadequate for sampling. Secondly, a higher percentage of females was obtained with the NG2B trap than with the biconical trap. Going by the expected percentage of 70%-80% females in a wild population (Jackson, 1949), the female percentages recorded in this study were generally below the expected value. Therefore, although both traps were probably under-estimating the female population, this was more so with the biconical trap.

This underlines the observation made by Rogers (1984) that all traps are biased in one way or the other and that these biases should be quantified if population characteristics are to be deduced from trap catches. Trap biases may be quantified by using the model proposed by Rogers (1984) based on the feeding cycle of the species involved, although this is still unknown for *G. longipennis*. Alternatively, trap catches could be compared to absolute population estimates from mark-release-recapture methods made at the same time as the sampling took place to determine the relationship between apparent and absolute estimates (see chapter 9).

In the absence of such correction factors, the question arises as to whether these changes reflect actual changes in the population size or if they are due to fly activity and hence availability. In this study, both trap types showed similar trends in population changes (despite the disparity in relative numbers) and, assuming that the very short flight period of *G. longipennis* does not change throughout the year, the observed changes probably indicate changes in the population size rather than fly availability.

Assuming the above assumptions hold, it can be concluded that the population of *G. longipennis* increased to a major peak towards the end of the long rainy season, declined in the dry season, and rose to a smaller peak during the short rainy

season. Similar trends were observed by Dransfield et al.(1986a) for the *G. pallidipes* population in the same study site over the same period.

Looking at other *fusca* species, Kangwagye (1974) recorded peak catches of *G. fuscipleuris* towards the end of the rains in western Uganda. In Cote d'Ivoire, Gouteux and Buckland (1984) observed major peak catches of *G. nigrofusca* at the end of the rainy season and a smaller peak towards the end of the dry season. They attributed the small dry season peak to the emergence of pupae deposited by flies during peak densities at the end of the rains. Challier (1982) reviewed a wide range of population fluctuation patterns recorded by various workers in different localities. He observed that fluctuation patterns in tsetse populations are roughly related to the rainfall distribution throughout the year with the basic feature being an increase during the rains and a decrease during the dry season. However the general pattern may be modified by the amount and monthly distribution of the rains. Vale et al. (1985) attributed the decline in the dry season to the fact that female flies do not live long enough to produce replacement offspring.

The observed seasonal changes in the relative distribution of *G. longipennis* between the different vegetation types has been reported by a number of workers for other tsetse species. In the same study area Dransfield et al. (1986a) observed that *G. pallidipes* also tended to spread out during the rains and contracted into the more dense vegetation

during the hot and dry seasons. A similar observation was reported on *G. m. submorsitans* by Dransfield *et al.* (1982) in northern Nigeria with flies spreading out into the more open woodland in the rainy season but concentrating in the forest in the dry season. According to this author, the tsetse habitat may be described as a patchwork of areas with seasonally changing probabilities of survival and reproductive success; hence flies tend to concentrate in the most suitable habitat.

Habitat suitability may be determined by both abiotic and biotic factors. Concentration of flies in the thicker vegetation during the hot and dry seasons may serve to avoid lethal levels of temperature and humidity. At the same time it could be that flies are following their hosts which would tend to frequent the thicker vegetation in search of food which would be more available here than in the more open parts of the habitat during the dry season.

Whatever the reasons may be, the differences in catches between the various vegetation types demonstrate the importance of sampling over the full range of the distribution of a "population" of tsetse when carrying out population dynamics studies (Gruvel,1975; Hargrove and Vale, 1980; Dransfield *et al.*, 1986a). The latter authors remarked that a wrong picture may be obtained if sampling is not done over all the vegetation types.

The apparent lag in phase between population changes on the two transects could be due to movement of flies between

them. A net movement of flies from one area to the other would account for the subsequent rise in apparent densities in the latter and a corresponding decline in the former. From the above argument, the trends in apparent densities seem to show a net movement of flies from TR1 to TR4 from August to October and in the reverse direction from October to December. Again there was an apparent net movement of flies into TR4 from January to March and back to TR1 from March till July.

The adverse effect of climatic factors on adult survival is shown by the significant positive correlation between mortality rate from ovarian aging and the maximum temperature experienced by flies. A weaker relationship was shown between mortality rate and minimum relative humidity. This suggest that higher environmental temperatures are more lethal to *G. longipennis* than environmental dryness. The fact that the fly limits its activity to dawn and dusk is probably an adaptation to avoid lethal levels of these factors. During the rest of the day it may be that the fly is able to seek out micro-habitats that are humid enough, but less able to avoid lethal high temperatures. It should be noted, however, that low humidities may well have sublethal effects on *G. longipennis* (see Chapter 7).

The stronger relationship between adult mortality rate and these climatic factors observed on TR1 when the data included the months of population suppression may be an artefact created by the mortality due to the trapping. In deploying traps for the population suppression operation most

of the traps were located in the thicker woodland (see chapter 9), where flies normally concentrate when it is very hot or very dry. Thus it is likely that adult mortality rate due to the suppression operation in this area was higher during these periods. This could then result in the strong correlation between adult mortality and temperature. When the analysis was limited to only natural mortalities by excluding the months of population suppression the relationships were comparable to those of TR4 which was outside the suppression zone.

The lack of correlation between the mortality rate estimates from Moran curves and those from the ovarian age structure implies some inaccuracies in the estimates by one of the methods or both. Both methods are subject to errors when flies are migrating into the sampling area, but the ovarian age method may still be reliable if the immigrant flies have the same age distribution as the resident population. Since immigrant flies are more likely to be old flies (excluding category O flies) and the mortality rate estimates in this study excluded category O flies, the estimates could be reliable.

The Moran curve method, on the other hand, will certainly be rendered inaccurate by immigration. Rogers (1979) observed that points that lay outside the realistic range of reproductive rate in the Moran plot were associated with periods of immigration into the sampling area or were due to sampling errors. In the present study, there was evidence of immigration from the Moran plots. Outlying points were

observed for the month of September 1986 for both sexes and September 1987 for the males only. From the suggested pattern of fly movement, there was movement of flies into TR4 from September to October. The zero mortality rates recorded in September for both 1986 and 1987 were therefore due to the effect of immigration.

Rogers (1979) also remarked that Moran curves give more reliable results for data collected over a longer period of time. In view of this, the present data set is probably too small for the accurate identification of the key density independent factors. Considering the above, the mortality rate estimates from ovarian age structure may be more reliable than those from the Moran curves. This is supported by the fact that estimates by the ovarian age method show significant relationships with the climatic factors whilst those from the Moran curves do not.

The relationship between climatic factors and tsetse populations has been investigated by a number of workers. For example, a significant relationship between adult mortality rate and maximum temperature was observed for *G. palpalis* by Rogers *et al.* (1984). However, the latter authors only established significant negative correlations between apparent density and the mortality rate of the previous month in some sampling areas but not others. It was realized that the areas for which there were lack of significant correlations were subject to constant immigration pressure. A similar explanation could account for the non-significant correlation

between mortality rate and apparent densities observed in this study.

Apart from the movement of flies between the two sampling areas (suggested earlier), there is also evidence from other studies, carried out in the study area (Dransfield *et al.*, unpublished), that flies do migrate from the top of the escarpment into the sampling area. With immigration, the effect of mortalities experienced by parent flies may not be significantly reflected in the subsequent samples since immigrant flies would also be contributing to the changes in the population levels.

Although the analyses presented here have provided information on the density independent mortality factors, they have shed little light on the nature of the density dependent losses which regulate the population size. From the Moran curves, such losses would appear to be operating primarily in the months of October and May/June. The high mobility of the flies suggests that, at least at a local level, movement may be an important regulatory factor. Studies at Nguruman on *G. pallidipes* have also suggested that pupal losses and predation of the adults could be important, and more work needs to be carried out on *G. longipennis* on these aspects.

CHAPTER SEVEN

POPULATION DYNAMICS OF *GLOSSINA LONGIPENNIS*: II. REPRODUCTION AND SIZE

7.1. INTRODUCTION

In the absence of immigration, tsetse populations are dependent on the reproductive rate to balance the mortality rates considered in the previous chapter. The first factor affecting this is the insemination rate which is influenced by the male insemination capacity and the female receptivity. Various workers, reviewed by Challier (1982), have shown that the timing of insemination varies with different species.

The other factor affecting reproductive rate is the duration and survival rate of the larva stage in utero. The inter-larval period has been shown to be dependent on temperature (Glasgow, 1970, Challier, 1973). Certain reproductive abnormalities have been observed by Challier (1973) in *G. p. gambiensis* which resulted in delay in reproductive cycle, degeneration of eggs, non-viable larvae and abortions. He and other investigators (e.g. Madubunyi, 1978; Turner and Snow, 1984) are of the opinion that abortions are the main source of reproductive loss and Jordan (1962b) suggested that they may play a significant role in keeping tsetse populations at low densities. This was based on a very high mean abortion rate of about 60% observed in a population of *G. palpalis* in midwestern Nigeria. Other workers

have, however, reported rather low abortion rates (below 10% on average) in various tsetse populations (Okiwellu, 1976, 1977; Madubunyi, 1975, 1988; Dransfield *et al.*, 1986a). Hence, Madubunyi (1988) expressed doubts as to whether abortions can significantly affect tsetse population levels. However, it has been suggested (Dransfield *et al.*, in press) that abortions may only represent a small percentage of reproductive loss. Production of undersized larvae resulting from parental stress may result in subsequent losses at the pupal and emergent adult stages.

This loss may be investigated by monitoring the size of the adults. It has been shown for some species that fly size as indicated by wing vein length is influenced primarily by the environmental conditions experienced by the parent during pregnancy (although temperature at the pupal stage can also have an effect; Bursell and Taylor, 1960). Jackson (1953a) established significant negative correlations between the monthly mean size of male *G. pallidipes*, *G. swynnertoni* and *G. morsitans* in Tanzania and saturation deficit and maximum temperatures experienced by the parent females. At Nguruman, Dransfield *et al.*, (1988 in press) found similar correlations. There is evidence that very small flies are at a disadvantage when they emerge. Phelps and Clarke (1974) estimated that up to 75.5% of *G. m. morsitans* population was lost at emergence due to small size in the hot dry season. Dransfield *et al.* (1988, in press) also found size dependent mortality of *G. pallidipes* at emergence. A first indication of whether such

mortality could be occurring in *G. longipennis* populations would be to establish whether size of adults of this species does vary seasonally and whether such changes are indeed correlated with environmental conditions.

Another point of interest is whether wing vein length of the progeny can be used as a simple index of the parental density-independent mortality rate. Dransfield et al. (1988, in press) suggest that this may hold true for *G. pallidipes*, which could be of use when determining the additional levels of mortality needed from trapping to suppress a tsetse population

In the light of the above, studies were carried out to determine the changes in the monthly insemination and abortion rates and in the size of both adult and immature stages of *G. longipennis*. Investigations were carried further to determine the influence of climatic factors on the changes in these population parameters.

7.2. MATERIALS AND METHODS

All data were collected from the same samples that were dissected for ovarian age determination (see Chapter 6). Following age categorization, the uterine content of each fly (empty, egg, 1st, 2nd, or 3rd instar larva) was recorded. All flies belonging to category Oa or Ob were examined for the presence of sperm in the spermathecae. Measurements were then taken of the length of uterine content and the length of the largest developing follicle.

Adult fly size was estimated according to the method proposed by Jackson (1949). This is by measuring the length of the middle part of the fourth longitudinal vein of the wing. These measurements were taken of the same wings that were collected prior to ovarian age dissection and used for wing fray aging as described in Chapter 6. All measurements of wing vein length, uterine content and follicular length were made using a pre-calibrated eye piece graticule.

7.3. RESULTS

7.3.1. Insemination rate

The insemination rate of *nulliparous G. longipennis* was observed to be very high. Throughout the study period, all flies of the Ob category were found to be inseminated. The insemination rate for category Oa flies was also 100% in all months except in June 1986, April 1987 and May, 1987 when the insemination rates were 85, 66 and 75% respectively.

7.3.2. Abortion rate

The percentage distribution of intra-uterine contents recorded from routine dissections of female flies caught by the NG2B traps on TR1 and TR4 are given in tables 7.1 and 7.2 respectively. The tables also show the monthly changes in the percentage of empty uteri (assumed to be mainly abortions) for the two transects (also shown in Fig.7.1). The values recorded here are most likely higher than actually occurring in nature since trap-induced abortions could not be distinguished from

natural abortions. The estimates for October 1986 (for TR1) and January 1987 (TR4) are especially high and may be unreliable due to the very small sample sizes.

However, assuming trap induced abortions affected the values for all months in the same way, some information can still be gained from the relative monthly abortion frequencies. Generally, the percentage of empty uteri was higher in the cold dry and hot dry seasons than in the other months of the year. However, there were slight differences in the trends on the two transects. Whereas on TR1 the percentage of abortions declined from October to zero in December, the percentage of abortions was on the rise on TR4 during this period and reached a peak in December-January (although the January sample was very small). The mean abortion rates on the two transects were 7.7 and 11.1% for TR1 and TR4 respectively which did not differ significantly by the chi-squared test.

Relationships between monthly abortion rate and maximum temperature and minimum relative humidity were examined through correlation analysis, after pooling data from both transects. There was a significant negative correlation (Fig.7.2) between the percentage empty uteri and minimum relative humidity. The regression equation of percentage empty uteri (Y) on minimum relative humidity (X) was:

$$Y = 30 - 0.64X \quad (r = -0.53, P<0.05)$$

There was no significant correlation between percentage empty uteri and maximum or mean temperature.

7.3.3. Frequency distribution and size of immature stages

Tables 7.1 and 7.2 also show the monthly percentage distribution of the different pregnancy stages of flies from the two transects. Flies with the egg-stage were generally most abundant followed by those with first instar larva. There was no consistent difference between the frequencies of the second and third instar larvae. The mean percentages for the different stages taken over the whole sampling period were similar on both transects.

Table 7.3 gives the monthly mean lengths of the four developmental stages recorded from the uteri. Data from the two transects were pooled and averages taken because of the very small sample sizes in each category. No obvious seasonal trends can be observed in the variation of the uterine content length.

Taking the averages for the two transects, the relative percentages ($\pm$ 1 S.E) obtained for the four pregnancy stages and the mean lengths (mm $\pm$ SE) for the developmental stages are given together in Table 7.4.

The mean lengths of the egg follicule next in ovulation sequence or largest developing follicle at the various pregnancy stage are given in Table 7.5. These are taken for the whole sampling period and for the two transects.
It can be observed that the mean size of the largest developing follicule at the LIII stage is very close in value to the mean egg-measurement in the uterus indicating that the egg is ready to be ovulated soon after deposition of the

Table 7.1: Percentage distribution of uterine contents in monthly samples of *G longipennis* with the NG2B traps on TR1.

MONTH	UTERINE CONTENT					N
	EMPTY	EGG	LARVA I	LARVA II	LARVA III	
1986						
June	2.3	45.2	26.1	8.5	16.6	54
July	4.8	53.6	9.7	26.8	4.8	50
August	15.0	40.0	15.0	20.0	10.0	23
September	13.6	34.0	27.2	11.3	13.6	51
October	75.0	25.0	0.0	0.0	0.0	8
November	8.0	56.0	8.0	4.0	24.0	24
December	0.0	29.6	22.2	25.9	22.2	35
1987						
January	0.0	28.5	14.2	21.4	35.7	21
February	20.0	33.3	33.3	6.6	6.6	24
March	4.3	30.4	34.7	8.6	21.7	38
April	0.0	37.5	50.0	12.2	0.0	14
May	3.9	49.0	21.5	11.7	13.7	51
June	1.8	40.0	15.0	15.0 1	8.8	92
July	8.5	40.0	25.7	2.8	22.8	83
August	3.2	38.7	0.0	32.2	25.8	33
Sept.	6.4	38.7	16.1	9.3	19.3	33
October	3.3	50.0	30.0	13.3	3.3	41
MEAN	7.0	40.8	21.7	15.0	16.2	
S.E.	1.9	2.2	2.6	2.3	2.3	

Table 7.2: Percentage distribution of uterine contents in monthly samples of *G longipennis* with the NG2B traps on TR4.

MONTH	UTERINE CONTENT					N
	EMPTY	EGG	LARVA I	LARVA II	LARVA III	
1986						
September	7.1	14.2	35.7	35.7	7.1	16
October	2.7	43.2	29.7	13.5	10.8	36
November	25.0	41.6	8.3	8.3	16.6	12
December	20.0	40.0	20.0	0.0	20.0	16
1987						
January	60.0	20.0	0.0	20.0	0.0	12
February	5.5	38.8	22.2	16.6	16.6	25
March	11.1	33.3	33.3	0.0	22.2	14
April	4.3	34.7	47.8	4.3	8.6	44
May	3.9	49.0	21.5	11.7	13.7	59
June	0.0	54.7	22.0	13.5	18.6	67
July	11.1	44.4	16.6	11.1	16.6	26
August	3.2	38.7	0.0	32.2	25.8	35
Sept.	2.9	44.1	17.6	17.6	17.6	39
October	0.0	47.0	29.4	5.8	17.6	28
MEAN	11.2	38.2	21.1	13.6	15.1	
S.E	1.1	1.5	4.2	2.7	1.6	

Table 7.3: Monthly means of uterine content lengths (mm) for *G.longipennis* (Jan.-Sept. 1987)

	UTERINE CONTENT LENGTH (mm)			
	EGG	LARVA I	LARVA II	LARVA III
MONTH				
January	1.91	2.32	4.48	-
February	2.01	2.28	4.24	5.44
March	1.85	2.60	4.30	5.19
April	1.99	2.78	3.84	5.45
May	1.99	2.54	4.29	5.73
June	2.00	2.07	3.17	5.43
July	2.00	2.64	3.25	5.01
August	-	-	-	-
Sept.	1.99	2.11	3.50	5.21
October	2.00	2.30	3.23	5.40
MEAN	2.00	2.35	3.31	5.20
S.E	0.01	0.19	0.23	0.23
N	203	106	62	68

Table 7.4: Mean percentages (± 1 S.E) and lengths of uterine contents (mm ± 1 S.E.) at the four pregnancy stages.

Pregancy stage	Percentage	Mean length
Empty Uteri	8.6	-
Egg stage	40.0 ± 1.5	1.97 ± 0.02
LarvaI	21.4 ± 2.6	2.40 ± 0.19
LarvaII	14.3 ± 2.3	3.81 ± 0.23
LarvaIII	15.7 ± 2.3	5.35 ± 0.25

7.5: Mean length of the largest developing follicule at the different pregnancy stages.

Pregnancy stage	Sample size	Mean length(mm)	Standard error	95% confidence limits
E	192	0.93	0.03	0.87-0.99
LI	108	1.48	0.05	1.38-1.58
LII	59	1.85	0.04	1.77-1.93
LIII	58	1.96	0.02	1.92-2.00

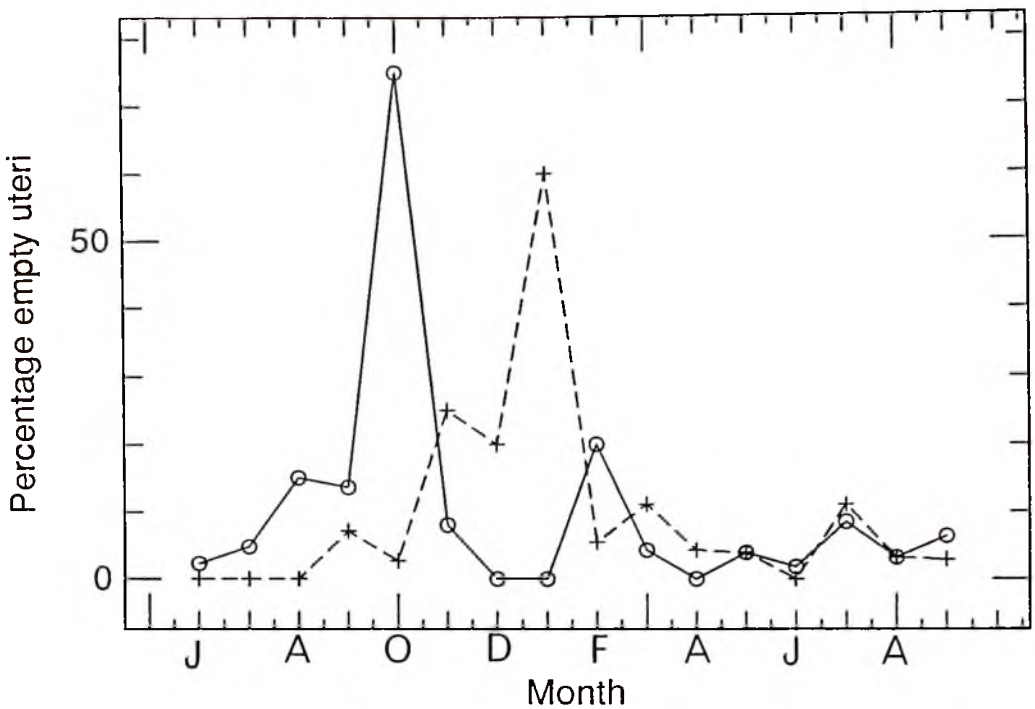


Figure 7.1: Monthly changes in the apparent abortion rate. (____ transect 1; x..x transect 4).

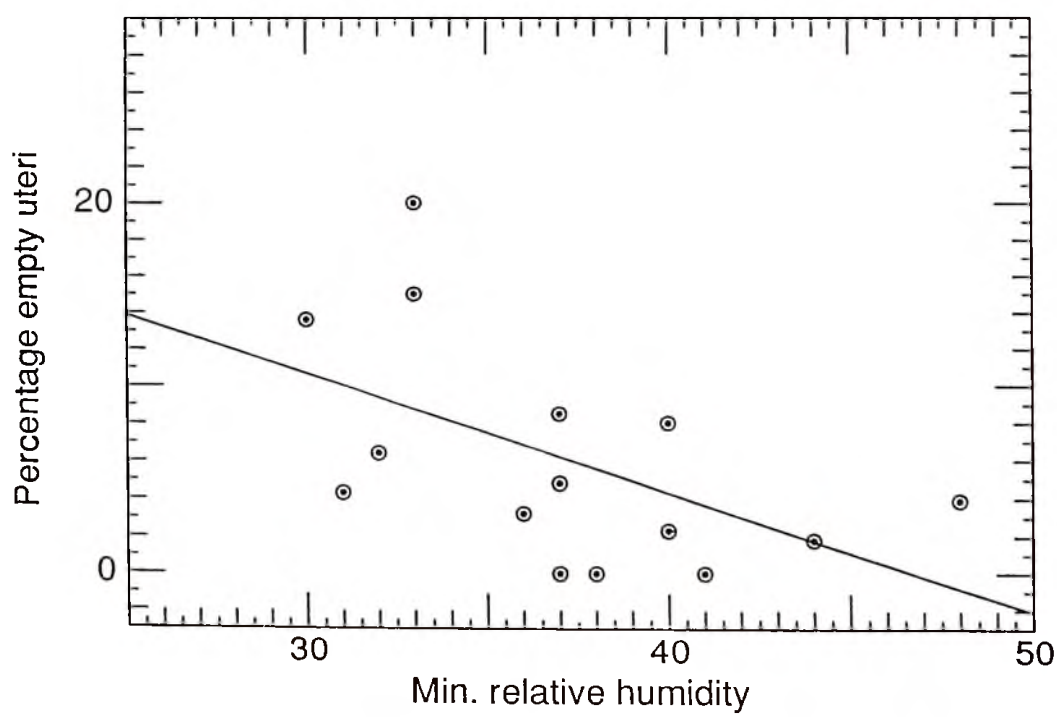


Figure 7.2: The relationship between monthly abortion rate and minimum relative humidity (Y = 30 - 0.64X; r = -0.53, P<0.05).

larva. The largest follicule of nulliparous flies in ovarian age category Oa measured 0.82 ± 0.01mm and those of Ob flies measured 1.67 ± 0.02mm.

The rate of growth of the follicle between pregnancy stages may be roughly estimated by taking the differences between two successive stages and dividing by the corresponding developmental period between the two pregnancy stages. Recalling the developmental duration of the different pregnancy stages (3.5 days for egg, 1.5 days for larva I, 2 days for larva II and 2 days for Larva III), the growth rate of the follicule was estimated as follows: 0.16mm/day between egg and larva I, 0.25mm/day between larva I and larva II and 0.06mm/day between larva II and larva III. The growth rate of follicle is therefore slow in the beginning, accelerating later on and slowing down again towards the end. The observed trend in the growth rate of the follicle agrees with the trend of follicular growth in tsetse proposed by Saunders (1960) and also observed by Madubunyi (1978) for *G. m. morsitans* in Zambia.

7.3.4. Size of adult flies

Fig. 7.3 shows the monthly changes in mean wing vein length of female flies on the two transects. The changes in the wing vein length followed similar trends on both transects with quite close corresponding values. Mean wing vein length range from 2.201 mm to 2.257 mm on TR1 and 2.205 mm to 2.275 mm on TR4.

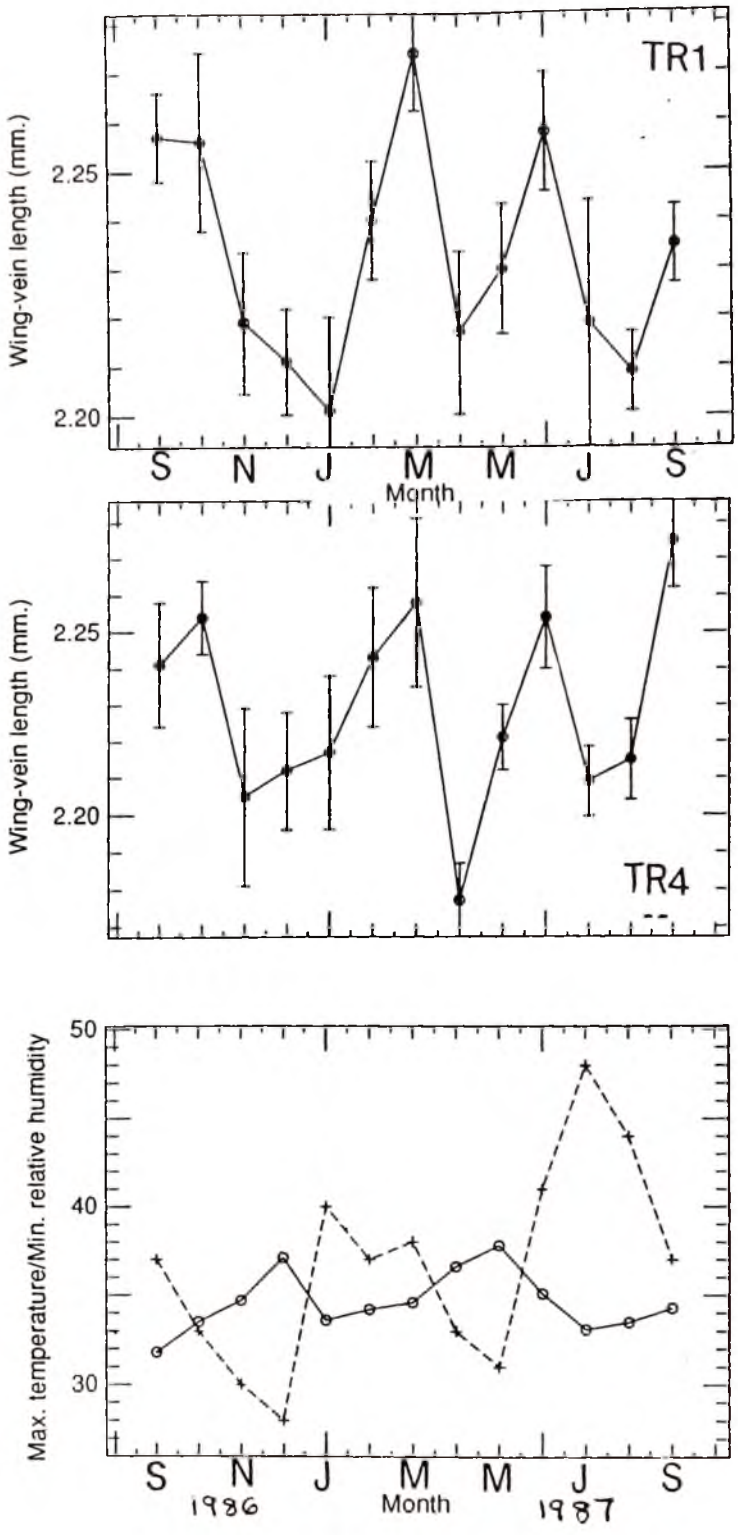


Figure 7.3: Monthly changes in the wing vein length on transects 1 and 4 in relation to changes in mean monthly minimum and maximum temperature and relative humidity.

The effect of climatic factors (temperature and relative humidity) on fly size was examined. Changes in these factors are also shown in Figure 7.3. On examining the changes in wing vein length and those of temperature and relative humidity there are some apparent related trends. Periods of high relative humidity (and of low temperature) seemed to be followed (about two months later) by increases in wing vein length. Relationships were thus investigated by plotting the wing vein length against minimum relative humidity of the previous month but one. Figures 7.4A and 7.5A show the scatterplots for TR1 and TR4 respectively. A linear fit showed no significant relationship. The function best describing the relation is a parabola in each case. The function indicates that below relative humidity of 40% the wing vein length increases with increasing relative humidity but above 40%, the wing vein length decreases. The breakdown of the linear relationship was possibly due to invasion of the area by flies which are smaller. These periods obviously occur during the long rains and short rains when there is every evidence that fly movement is very high (see discussion for more details). When the points for these months are removed from the plot, significant linear relationships are shown on both transects (Figs. 7.4B and 7.5B). The regression equations of wing vein length on minimum relative humidity below 40% were:

$Y = 1.78 + 0.004X$ ($r = 0.75$, $P<0.01$) for TR1

and

$Y = 2.06 + 0.005X$ ($r = 0.82$, $P<0.01$) for TR4.

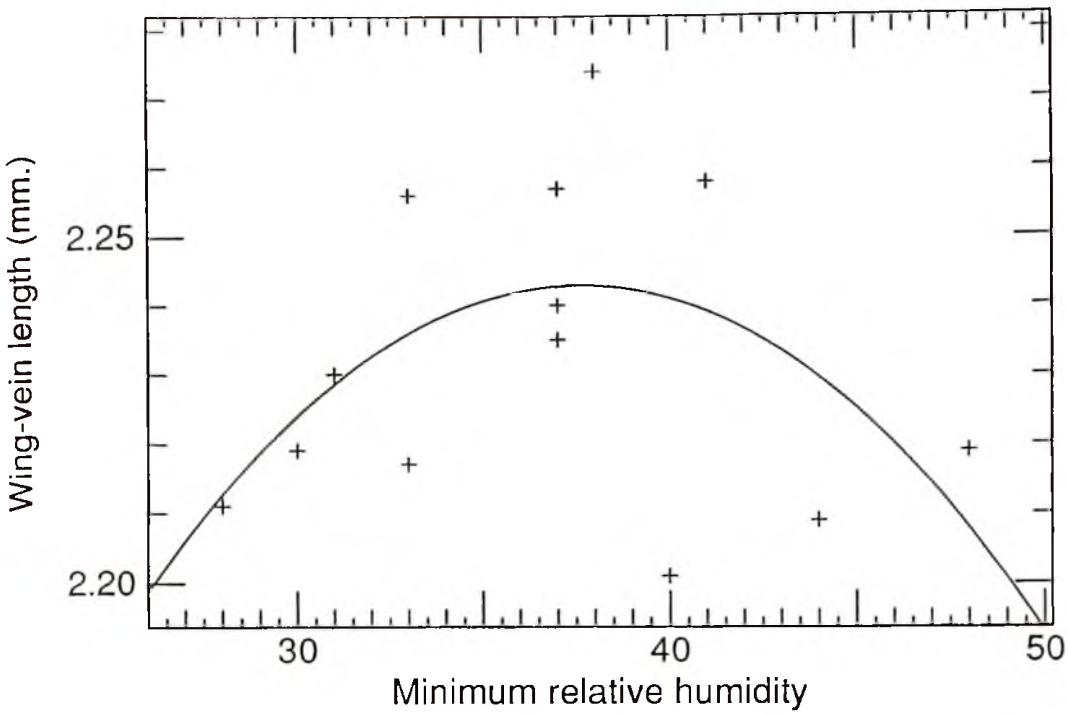


Figure 7.4A: The relationship between the wing vein length in one month on transect 1 and the minimum relative humidity of the previous month but one.

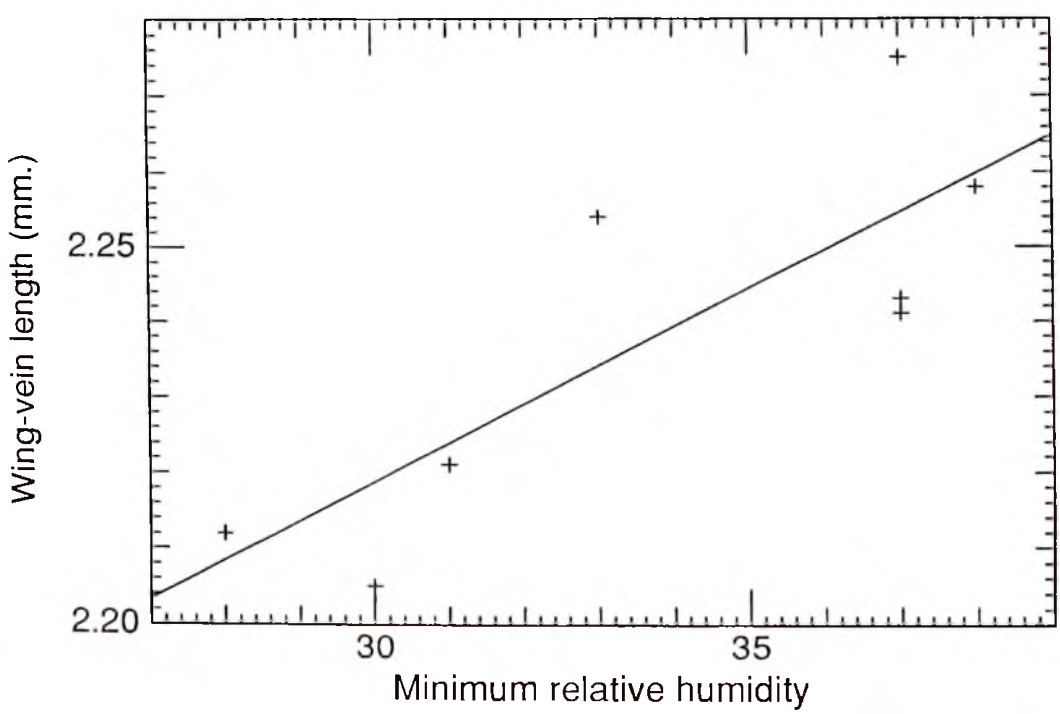


Figure 7.4B: Linear relationship without data points for months of suspected fly immigration to transect 1 (Y = 1.78 + 0.004X; r = 0.75, P<0.01).

A larger data set of wing vein length measurements collected from the study area from June 1983 to October 1986 (courtesy Dransfield et al.,unpublished) was also subjected to the analysis described above. A significant, though still weak, positive linear correlation was observed between the wing vein length and the minimum relative humidity of the previous month but one. The regression of wing vein length (Y) on relative humidity (X) was as follows;

$Y = 2.206 + 0.001X$; ($r = 0.35$, $P<0.05$)

The possible association between mortality of the parental generation and the size of the progeny was also examined. Correlations were carried out between the mean wing vein length and mortality rates (both from ovarian aging and Moran curves) of the previous month but one, but no significant relationship was established.

4. DISCUSSION

The observed rates of insemination are much higher than those observed for *G. pallidipes* in the same study site (Chaudhury, pers. comm.). He observed that very few of Oa (1-3 days old) female *G. pallidipes* were inseminated compared with about 88% of the Ob (4-8 days old) flies. Vale *et al.*(1976) observed that no *G. pallidipes* females were inseminated before they had fed. Compared to *G. pallidipes*, higher insemination rates were recorded for teneral *G. m. morsitans* (Okiwellu, 1977) and *G. p. gambiensis* (Challier, 1973).

The higher insemination rate observed in young flies, as in the case of *G. longipennis* implies, that the species mates not long after emergence as opposed to *G. pallidipes* which is reported to mate only after 4 to 6 days following emergence (Snow, 1980). Mating in *G. longipennis* may be taking place either at the breeding site or at the host during the first blood meal. It was a common sight in the study area, to observe mating pairs of *G. longipennis* coming to and getting caught in traps or electric screens. The apparent decrease in the insemination rate during the rainy season may be due to the fact that fly contact is reduced by dispersal of the population during this period.

The occurrence of peak abortion rate at different time periods on the two transects could imply significant differences between the microclimates of the two areas during this period. Looking back at the suggested pattern of fly movement between the two areas based on Figs. 6.11A and B, flies appear to be moving out of TR4 from October to December (at the time percentage abortions are increasing on this transect). On the other hand there was apparent movement towards TR1 during these months when abortions were on the decline in this area. This probably indicates that flies tended to move away from areas where the microclimate was unfavourable at one time (as indicated by increased abortions) to where the microclimate was more favourable. The fly movement and difference in peak abortion rate could also be partially associated with host movement between the two

transects. Flies moving from one area to the other during the above mentioned periods may be following hosts. Since malnutrition is regarded as a major cause of abortion the decrease in host population in one area could therefore result in an increase in the abortion rate in that area and vice versa.

The relationship between abortion rate and climatic factors indicated that atmospheric dryness appears to adversely affect the pregnancy more than high temperatures, although the two factors are often closely linked. Low relative humidity could be having a direct physical stress on the flies. On the other hand it could again be an indirect relationship associated with the weather and hence vegetation changes that bring about the movement of host form the study area as a whole.

Most of the work on tsetse reproduction both in the laboratory and in the field indicates a 9-10 day reproductive cycle with the duration of the egg and the three larval stages being 3-4, 1-1.5, 2.5 and 2 days respectively. If a 9-day cycle is also assumed for *G. longipennis*, the duration of the egg and larval stages can be fixed at 3.5 days (egg), 1.5 days (first instar), 2 days (second instar) and 2 days (third instar). If the probability of capturing a female in one pregnancy stage is proportional to the duration of each stage, then these probabilities should be 0.389, 0.167, 0.222 and 0.222. Comparing the proportions obtained in this study to these expected values, there is some degree of agreement. The

observed value for the egg-stage (40%) is quite close to the expected value. However, the larva I stage is over-represented (21.4%) whilst larva II and III stages are under-represented (14.3 and 15.7% respectively) This might mean that the assumed duration of larval stages for *G. longipennis* are incorrect. An alternative explanation is that trap induced abortions are more likely to occur in flies bearing later instar larvae than in those bearing early instar larvae. Thus, some of the flies which would have been classified under abortions on dissection would have actually been trapped as second or third instar stage flies. This would therefore lower the observed frequencies of these categories of flies. The high value for flies bearing first instar larvae could have arisen because there were occasions during dissection when it was quite difficult to distinguish between first and second instar larvae. This could account for the apparent reversal in the expected values for these two categories of flies.

The average percentage flies bearing third instar larvae recorded in this study is markedly higher than those recorded for *G. pallidipes* at Nguruman in the same type of traps (Dransfield *pers comm.*) and in Lambwe Valley, Kenya (Turner 1987). On average about 5% of *G. pallidipes* caught in the NG2B traps are in the 3rd instar stage. Even lower percentages are recorded in biconical traps. In this study, only 9% of *G. longipennis* caught in the biconical traps had third instar larvae which is still higher than that for *G. pallidipes* (1%). The results from studies on other tsetse species indicate

flies bearing third instar larvae do not actively seek blood meals and are thus not readily caught in traps (which are known to attract mainly host-seeking flies). The results of this study suggests that *G. longipennis* still feeds readily during the 3rd instar stage or that the female flies are attracted to the trap for purposes other than host-seeking. Consequently, trap samples of *G. longipennis* are less biased with respect to the pregnancy stage than is the case for several other species.

A significant correlation between wing vein length and relative humidity has been observed for a number of tsetse populations by previous workers. Jackson (1953a) working in Tanzania found that *G. pallidipes* showed the greatest variation in wing vein length with seasons and *G. swynnertoni* the least. He suggested as a result that the latter species might be better adapted to the habitat than the former. In this study, the relationship observed for *G. longipennis* was weaker than that found for *G. pallidipes* by Dransfield et al. (1988, in press). They, however, used the wing vein lengths of only ovarian age category O flies whereas in this case the mean age of the whole monthly sample was used (the numbers of category O flies for *G. longipennis* were too low to be considered separately). It was therefore not possible to accurately define the exact period when the fly would have been *in utero* in the parent female, and hence the period to take for climatic data. Another explanation for the weaker relationship is that a higher proportion of the population may

have been composed of immigrants from top of the escarpment where climatic conditions are quite different.

The latter speculation is supported by the observation that the apparent outliers to a significant linear relationship (months with over 40% relative humidity) are data points for the cool months during which immigration rate is high. The reduction in mean wing vein length could mean that immigrant flies are smaller implying their origin from a habitat with quite different environmental conditions. The most immediate source of such a habitat for which there is evidence of invasion is the top of the escarpment where temperatures are much lower than in the study area. Lower temperatures certainly results in longer developmental periods (Glasgow, 1963), but whether this results in smaller flies is not certain. This requires a separate study, that involves monitoring the changes in fly size with time in comparison to that of surrounding fly populations.

The seasonal variation in size of *G. longipennis* and its correlation with environmental factors, does suggest that size dependent mortality may be occurring at emergence for this species as has been found for other species. Whether such mortality does occur, should be established in future by comparing the size of flies emerging from field collected pupae with the size of tenerals caught in the field at the same time.

CHAPTER EIGHT

MARK RELEASE RECAPTURE STUDIES

8.1. INTRODUCTION

Mark release recapture (MRR) is widely used for estimating the population size of mobile animals such as insects. Le Cren (1965) traced the technique back to Petersen in 1886 who used the recapture technique to calculate the mortality rate in fish. Lincoln (1930) used it to estimate the population size of a species of North American duck.

The method is based on the following principles. A number of animals 'r' are captured, marked and released. After a period, when these have re-mixed with the rest of the population, a further sample 'n' is captured and the number of marked individuals in the latter sample (m) noted. i.e. an unknown fraction of the population is first marked and on the second occasion a sample of this fraction is taken. Provided the effect of sampling error is negligible 'N' the population size can be estimated by $\hat{N}$ in the following formula:

$$r/\hat{N} = m/n$$

and

$$\hat{N} = rn/m$$

Where $\hat{N}$ is an estimate of the true population size N.

This formula is variously referred to as the 'Petersen estimate' or 'Lincoln index'.

If $\hat{N}$ is to be a suitable estimate of N the following assumptions must hold:

1. The population should be closed i.e there must be no addition of individuals (birth or immigration) to the population between the first and the second capture occasions. Loss from the population will not affect the m/n fraction because marked individuals will die or move out at the same rate as unmarked ones, provided condition (2) is fulfilled.
2. Marked individuals must behave in every respect like unmarked ones. In particular, they must suffer no damage and must not be subject to greater risk of predation or capture than the unmarked. Individuals must also not loose their marks between the first and second capture occasions.
3. Marked individuals must evenly mix with the unmarked population
4. The second sample is a random sample i.e. each individual has an equal chance of being caught; all marks must also be reported on recovery.

Since many animal populations are not closed, a number of workers have developed more complex analyses for mark-release-recapture data to allow for births, deaths and movement of marked individuals, with the underlying principles still based on the Petersen estimate and the rest of the assumptions. Mark release recapture techniques were first used to estimate

tsetse populations by Jackson (1933). Later on Jackson (1937, 1939) extended the analysis to allow for birth rate and death rate and the problem of immigration was considered in Jackson (1941, 1944, 1948). Similar analyses for a series of mark-release-recapture data were developed by Dowdeswell, Fisher and Ford (1940, 1949), Fisher and Ford (1947) and Leslie and Chitty (1951) for various animal populations. Bailey (1951, 1952) examined the precision and biases of population estimates by these methods and developed analyses for calculating standard errors. The estimation of population parameters based on multiple recaptures was independently developed by Seber (1962), Jolly (1965), and Manly and Parr (1968).

The various methods developed for handling mark release recapture data have been reviewed by Southwood (1978)and Begon (1979). Seber (1973) provided the details of the mathematics involved in these methods. The methods for analyzing mark release recapture data have been grouped into five main ones named after the pioneers who developed them. These include the Jackson's positive and negative methods, the Bailey's triple catch method, the Fisher-Ford method,the Joly-Seber stochastic method and the Manly-Parr method. In addition to the general assumptions underlying all mark release recapture operations, each of these methods is based on a number of assumptions peculiar to it. The choice of any of them for application to mark release recapture data is dependent on whether the

underlying conditions have been met. Details of these are provided in the reviews already mentioned above.

8.2. MATERIALS AND METHODS

Mark-release-recapture studies were carried out in two major experiments.

a. In monthly marking experiments, whereby flies were marked on the first day (on Transect 1) and on the second day (on Transect 4) of every 6-day-long monthly visit to the field.

b. In a continuous 7-day mark-release-recapture experiment undertaken once in the course of the study period.

8.2.1. Monthly mark-release-recapture experiments.

These were started in February 1986 in the transect 1 area and in August 1986 in the transect 4 area. On the first and second evening of each monthly visit to the field, a number of odour baited F3 traps were set up in the transect 1 and transect 4 areas respectively and the catches of *G. longipennis* were collected at about 0700h the following morning for marking. Because of the general sampling schedule, flies could not be marked immediately on collection but to minimize stress and improve survival, the flies were always kept cool under moist black cloth for the hour or so before marking took place.

The flies were marked using artist's oil paint (Winsor and Newton), with a different colour of paint used each month.

By using six different colours of paint in a known sequence, a particular colour could only be repeated after six months. It was assumed that this time interval was long enough for flies marked with a given colour to have died.

The main colours of paint used were ultramarine blue, undercoat white, vermillion, red and chrome-yellow. The various colours used for marking were then composed from these by mixing the above in the appropriate proportions. The colours used for marking flies were blue, green, yellow, orange, pink and turquoise. A few drops of linseed oil was used when necessary to bring the paint to a consistency that was neither too thick nor too thin; thick paint marks were likely to flake off whilst very thin paint marks were more likely to smudge.

In both transect 1 and transect 4 areas, marking and release took place in sites that were roughly in the centre of the area. During marking, each fly was carefully removed from the cage, held between the fingers and marked with two distinct spots of the paint on the dorsal side of the mesothorax, care being taken to keep marks as small as possible. This was to ensure that marked individuals were not more conspicuous to predators than unmarked ones. Flies marked on transect 1 had the two spots positioned side by side whilst those marked on transect 4 had their spots positioned one above the other. In both areas, teneral flies were distinguished by a third spot on the scutellum.

Marked flies were immediately transferred to a larger retaining cage of mosquito netting that was kept cool and damp under cover of a wet black cloth. As marking proceeded, batches of marked flies remained in the retaining cages for 15-20 minutes before they were released. This was to allow flies to settle down following handling so as to minimize an escape response. For release, the cage of marked flies was taken into a well shaded thicket by the Oloibototo River and the cage opened for flies to fly out. Flies that failed to fly out of their own accord were considered moribund and were killed.

Recaptures of marked flies were then obtained from catches by all traps that were operating in the study area. Until February 1987, these traps were mainly those used for the 6-day regular population sampling and those being used in experiments that were run within the six days of every monthly trip. From February 1987, a population suppression operation using odour baited NG2B traps was started in the transect 1 area. To monitor the changes in the fly populations during this operation, a continuous sampling programme was started whereby samples were regularly collected from 20 of the control traps. This therefore provided a more extended period of continuous sampling, instead of just five days, after every monthly marking occasion.

8.2.2. Seven-day continuous marking experiment

Because recapture rates for the monthly marking were very low, an experiment was carried out whereby flies were continuously marked and released on a daily basis for seven days from the 28th January to the 3rd February 1987. Date specific marks were obtained by using a different colour each day. In order to distinguish flies marked in this experiment from those marked on the monthly basis, the two spots of paint were applied diagonally on the thorax; one spot in the top right hand corner of the pronotum and the other in the bottom left hand corner of the metanotum. The colours used were blue, green, yellow, orange, pink, turquoise and white.

F3 traps were again used to collect flies each day at about 1730h but in this case the trap catches were collected at 1930h the same evening. The flies were then marked the same evening and retained in a large cage under the cover of damp black cloth to reduce activity and improve survival of flies. At about 0530h the following morning the cages of marked flies were taken to the same site as previously and the cage left open for flies to escape. For every day that flies were being collected for marking, the recaptures of the previous days' marks were recorded. The week of continuous mark-release-recapture was immediately followed by the regular monthly trip for the month of February thus providing another week of daily sampling in which recaptures continued to be recorded. In addition, recaptures were also obtained from the fly samples taken in by the 20 NG2B traps involved in the population

suppression operation which started on the 4th February 1987 (one day after the last marking day in this experiment).

8.2.3. Analysis of data

Because of the low number of recaptures obtained from each of the monthly marking occasions, the data were pooled over several months before any attempts could be made at estimating any population parameters. The data from February 1986 to January 1987 were pooled together because they were obtained before the population suppression operation. During the suppression period, monthly marking occasions from February to May 1987 and June to October 1987 were pooled for males, as were February to October 1987 for females. The data for males and females were always kept separate. Whilst it would have been preferable to analyze months separately, it was felt that the above procedure would at least give average estimates of population size for the different time periods.

An average recapture rate was calculated for each sampling period after marking. To allow for the variation in the samples sizes on the different sampling occasions, the recaptures were corrected according to the method proposed by Jackson (1948). When data for more than one marking occasion are pooled, as in this case, the method is further modified (Rogers and Randolph, 1986) to give the following formula for

average corrected recapture rate (Yn).

$$Yn = \Sigma Rn_i .10^6 / \Sigma Co_i Cn_i$$

where

i ranges from 1 to k marking occasions that are being pooled

Rn_i is the number of flies marked on the ith marking occasion that were recaptured on day n,

Co_i is the number of flies released on day 0 of the ith occasion and

Cn_i is the number of flies caught on day 'n' of the ith occasion

For the 7-day daily marking experiment the data were first grouped into four marking occasions, by considering every two consecutive days of marking as one marking occasion. This yielded 3 pairs of marking occasions for the first six days plus the 7th day taken alone as the fourth. Again, because of very few recaptures, samples taken after marking had to be pooled over a number of days to produce the unit periods after marking, for each of which the average recapture rates were then calculated. The first two periods consisted of 2 days each, days 0 and 1 being the first sampling period after marking and days 2 and 3 forming the second. Periods 3 and above each consisted of data pooled at one weekly intervals. Finally, the average corrected recapture rate for all the four marking occasions was calculated for each period after marking using the same formula as already given above.

Estimation of population size

Given the data obtained from the monthly marking experiments, the method of analysis found most suitable for estimating population sizes was that based on a model suggested by Parker (1955), details of which are given by Seber (1973). In brief the model is applicable when mark release is carried out on a single occasion followed by a series of 'instantaneous'samples (sampling time being negligible) being removed from the population. It is similar to Jackson's positive method described by Begon (1979) and allows variable mortality and recruitment in the population. The model is based on the equation:

$$E\,[m_i/n_i] = M_i/N_i$$

where m_i is the number of marked individuals in the ith sample, n_i is the size of the ith sample, M_i is the size of marked individuals just before the ith sample and N_i is the size of the total population just before the ith sample. i.e. the expected ratio of marked to unmarked individuals in the ith sample is the same as the ratio of all marks in the population just before the ith sample. Thus, if recruitment is taking place, M_i/N_i will decline with time. Parker suggested that if m_i/n_i is plotted against t_i the curve can be extended to $t = 0$, to obtain an estimate M_o/N_o and hence, N_o. It is argued that such a method will always give a graphical estimate of N_o irrespective of the changes that take place in the population and provided there is a reasonable smooth trend in the m_i/n_i and the above equation is valid. When possible a

suitable transformation m_i/n_i may be used to linearize the regression so that N_o may be estimated by least squares method.

In the present experiments the equivalent of m_i/n_i, corrected average recapture rate was plotted against days after marking. The logarithmic transformation of the corrected recapture rate was used in an attempt to stabilize the variance and linearize the regression. A population size estimate was only made if the regression was significant indicating a smooth trend of decline in the corrected recapture rate.

For comparison, the Jackson's positive method was also used to estimate the population from data obtained from the 7-day continuous marking experiment. It is essentially the same as Parker's method except the grouping has been carried out differently, and weighting is used to cope with small numbers of recaptures. In this study the whole 7-day marking was considered as one marking occasion i. e. date specific marks were ignored after the last day of marking and the total number of marked individuals released was adjusted by subtracting all recaptures that were made before the last day of marking. Although samples after marking were obtained from various traps that were emptied at different intervals, all samples were pooled and grouped as if sampling were done at weekly intervals.

According to the method:

if q_i is the proportion of the ith sample that is marked

$$q_i = m_i / n_i$$

where

m_i = the number of marked individuals in the ith sample,

n_i = the size of the ith sample.

This proportion should not be affected by looses from the population since marked individuals are assumed to die and emigrate at the same rate as unmarked ones. If, however, there is recruitment to the population then q_i will decline with time since only unmarked individuals will be added to the population.

The aim is to estimate N_o, the population at the beginning of marking before any additions to it and this can be achieved by estimating q_o the marked proportion of a hypothetical random sample taken on day 0, which should be the same as the marked proportion in the total population:

$q_o = r_o / N_o$,

where r_o is the number of individuals marked and released on day 0.

Therefore

$N_o = r_o / q_o$.

To estimate q_o a birth or gain rate 'b' is defined.

By calculating the proportion of marked and unmarked individuals surviving from one day to the next, it can be shown that:

$$q_i = q_o (1-b)^i \qquad \text{equation (2)}$$

or

$$\ln q_i = i(\ln(1-b)+\ln q_o \qquad \text{equation (3)}$$

this is a regression equation of $\ln q_i$ on i, both of which are known from the data and the regression constants $\ln(1-b)$ and $\ln q_o$ can be calculated.

To take care of less accurate estimates of q_is from small recapture values which are susceptible to chance effects the m_i values can be used as weights to obtain the following equations:

$$\ln(1-b) = \Sigma m_i (\ln q_i - \overline{\ln q})(i-\bar{i})/\Sigma m_i (i-\bar{i})^2 \qquad \text{equation (4)}$$

and

$$\ln q_o = \overline{\ln q} - \ln(1-b)\bar{i}. \qquad \text{equation (5)}$$

8.3. RESULTS

8.3.1. *Monthly marking experiments*

Tables 8.1 and 8.2 summarize the results of the monthly mark release recapture experiments carried out between February 1986 and January 1987 on males and females respectively. The corrected daily recapture rates, shown at the bottom of each table, were then plotted against days after marking to give Fig. 8.1 for the males and Fig. 8.2 for the females.

The male data suggests increases in recapture rate on days 3 and 5 implying increased activity on these days following marking. The plot for the females shows a general decline in the recapture rate with small increases on days 2 and 4.

On population estimates, the regression of male recapture rate against days after marking was not significant mainly because of the enormous increase on the fifth day. No attempt was therefore made to estimate population size for males. For the plot on the female recapture rates, a regression line was fitted to all the points over the five days. The female population size was estimated at 20,892, which represents the average population size from February 1986 to January 1987, since the recaptures rates were averages obtained for the marking in these months. From the slope of the regression line the dilution rate of the population was estimated as 34.5% per day. This, however, is almost certainly an overestimate of the dilution rate since it is affected by fluctuations in the recapture rate due to the feeding cycle.

Table 8.1: Numbers of marked male *G. longipennis* released each month, percentage recaptures within five days, numbers recaptured and total numbers caught on various days after marking in each month from February 1986 to January 1987.

MONTH (i)	NO. RELEASED (Co)	DAYS AFTER MARKING(n=1-5) (Recaptures(Rn) and sample size(Cn)) 1	2	3	4	5
FEB	116	1	1	1	0	2
		172	177	187	136	182
MAR	41	1	0	0	0	0
		59	175	107	159	96
APR	105	3	0	0	0	0
		539	580	451	124	180
MAY	314	3	1	3	0	3
		253	311	177	169	131
JUN	38	0	0	0	0	0
		50	25	50	22	33
JUL	159	0	0	0	0	1
		85	64	85	108	157
AUG	73	0	0	0	0	0
		34	80	104	113	87
SEPT	63	0	0	0	0	0
		54	89	78	136	131
OCT	45	0	0	0	0	0
		37	39	65	52	33
NOV	67	0	0	0	0	0
		19	35	52	44	34
DEC	57	1	0	0	1	0
		68	77	78	106	57
JAN	7	0	0	0	0	0
		13	12	109	49	49

Average corrected recapture rate (CRR) for, i=February 1986-January 1987

Days after marking	1	2	3	4	5
ΣRn_i	9	2	4	1	6
$Rn_i / \Sigma Co_i Cn_i \times 10^6$ (CRR)	48.24	9.20	23.84	7.43	45.43
Log CRR	1.68	0.96	1.38	0.87	1.66

Table 8.2: Numbers of marked female *G. longipennis* released each month, percentage recaptures within five days, numbers recaptured and total numbers caught on various days after marking in each month from February 1986 to January 1987.

MONTH (i)	NO. RELEASED (Co)	DAYS AFTER MARKING(n=1-5) (Recaptures(Rn) and sample size(Cn)) 1	2	3	4	5
FEB	112	0	0	0	0	0
		39	29	60	38	74
MAR	47	0	0	0	0	0
		34	103	70	58	17
APR	120	0	0	0	1	0
		190	483	283	120	108
MAY	472	2	5	1	0	0
		199	203	156	140	158
JUN	39	0	0	0	0	0
		21	4	42	6	36
JUL	177	0	1	0	0	1
		46	51	70	152	188
AUG	168	2	0	0	0	0
		18	51	45	39	69
SEPT	39	0	0	0	0	0
OCT	54	0	0	0	0	0
NOV	97	0	0	0	0	0
DEC	40	0	0	0	0	0
JAN	3	0	0	0	0	0

Average corrected recapture rates (CRR) for, i=February 1986-August 1986

Days after marking	1	2	3	4	5
ΣRn_i	4	6	1	1	1
$Rn_i / \Sigma Co_i Cn_i \times 10^6$ (CRR)	29.65	33.41	7.20	8.25	7.0
Log CRR	1.47	1.52	0.86	0.92	0.85

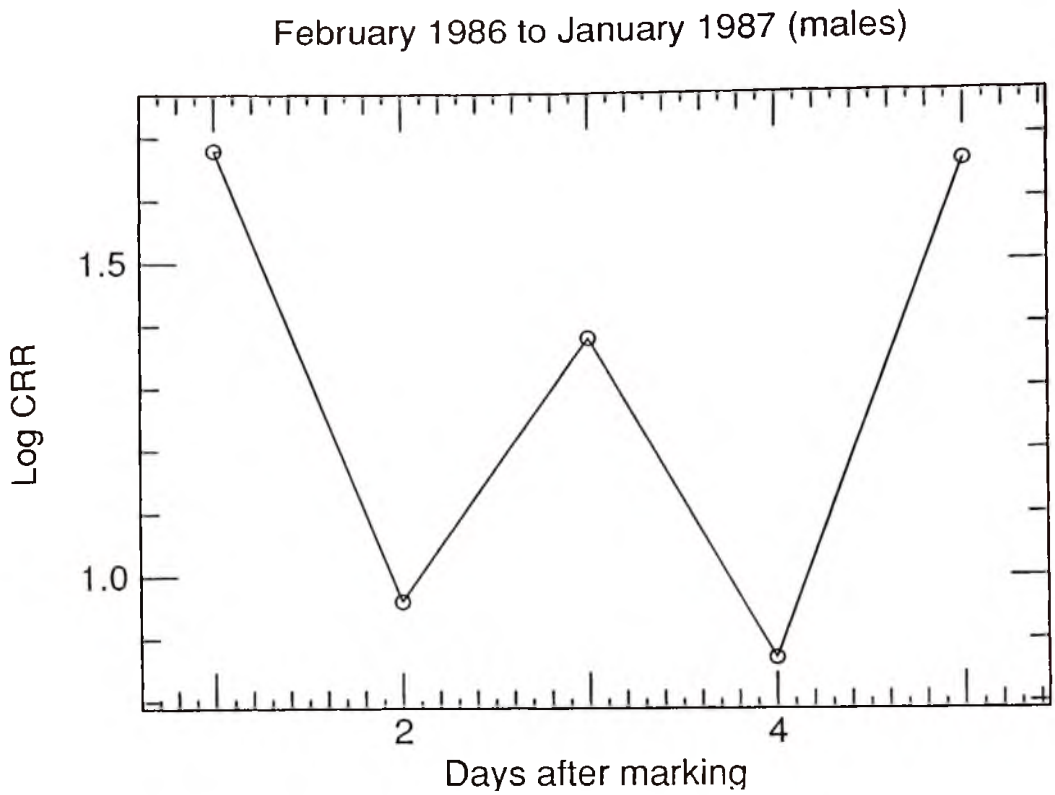


Figure 8.1: Changes in the recapture rate of male *G. longipennis* with days after marking. (February 1986- January 1987)

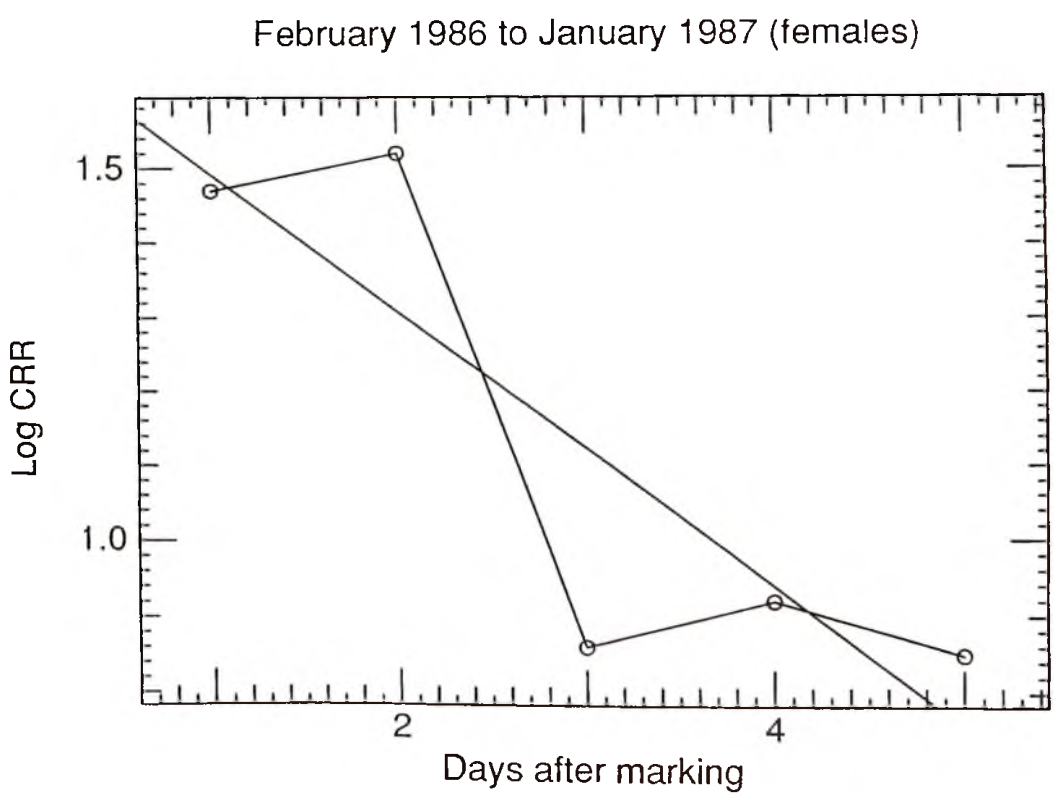


Figure 8.2: Changes in the recapture rate of female *G. longipennis* with days after marking. (February 1986- January 1987), Regression : Y = 1.68 - 0.18X; r = 0.86, P<0.001).

The results for monthly marking starting from February 1987 to October 1987 are given in Tables 8.3 and 8.4 for males and females respectively. Marking in these months, was immediately followed by a continuous regular sampling programme which provided recaptures for more extended periods than just five days within the month of marking. The daily recapture rates were therefore calculated for up to 45 days after marking.

Data for males were pooled into two groups; one group from February to May and the other from June to October. Plots for the average daily corrected recapture rates for the two groups of data are shown in Figs. 8.3 and 8.4 respectively. Since most of the samples were pooled over about 7 days before calculating the recapture rate there are no marked periodic increases in recapture rate shown in these plots that reflect feeding cycles. The population estimates from the regressions were 10,471 males for February to May with a dilution rate of 8.0% per day and 25,703 for June to October 1987 with a dilution rate of 12.9% per day.

Figure 8.5 shows the plot of the daily recapture rate of females against days after marking. Despite the log transformation, the decline in the recapture rate was not linear. Recapture rates were very high the first three days but then dropped rapidly. This implies that the marks were rapidly diluted out. A curvilinear fit was found to be significant and the average population size for February to October 1987 estimated as 15,848.

Table 8.3: Numbers of marked male *G. longipennis* released each month, percentage recaptures within 45 days, numbers recaptured and total numbers caught on various days after marking in each month from February 1987 to October 1987.

MONTH (i)	NO. RELEASED (Co)	PERIODS AFTER MARKING(n=1-8) (Recaptures(R) and sample size(Cn)) 1	2	3	4	5	6	7	8
FEB	85	2	1	1	0	1	0	0	1
		290	166	580	501	560	539	513	184
MAR	23	2	0	0	0	0	0	0	0
		203	179	236	184	427	432	490	436
APR	23	1	1	1	1	0	0	0	0
		152	47	490	436	434	449	590	383
MAY	45	1	0	2	0	0	0	0	0
		206	156	593	383	646	493	763	541
JUN	73	0	0	0	0	0	0	0	0
		372	278	558	363	530			
JUL	66	3	1	0	0	0	0	0	0
		420	235	641	522	645			
AUG	160	4	0	0	1	0	0	0	0
		497	318	522	625	352			
SEPT	223	10	0	1	1	0	0	0	0
		395	169	508	331	362			
OCT	7	1	1	0	0	0	0	0	0
		117	250	350	374	246			

Average corrected recapture (CRR)rates for:
i=February-May

Days after marking	1	3	10	17	24	31	38	45
ΣRn_i	6	2	4	1	1	0	0	1
$Rn_i / \Sigma Co_i Cn_i \times 10^6$ (CRR)	142.6	76.0	43.2	13.5	10.4	0	0	17.0

i=June-October

Days after marking	1	3	10	17
ΣRn_i	18	2	1	2
$Rn_i / \Sigma Co_i Cn_i \times 10^6$ (CRR)	80.6	15.9	3.5	8.4

Table 8.4: Numbers of marked female *G. longipennis* released each month, percentage recaptures within 45 days, numbers recaptured and total numbers caught on various days after marking in each month from February 1987 to October 1987.

MONTH (i)	NO. RELEASED (Co)	PERIODS AFTER MARKING(n=1-8) (Recaptures(Rn) and sample size(Cn))							
		1	2	3	4	5	6	7	8
FEB	95	5	0	0	0	1	1	1	0
		318	116	560	454	413	460	458	533
MAR	38	1	0	0	0	0	0	0	0
		223	183	274	533	308	231	494	349
APR	14	0	0	0	0	0	0	0	0
		103	41	394	349	445	442	665	455
MAY	63	1	0	1	0	0	0	0	1
		222	145	665	455	732	877	1064	545
JUN	157	12	2	1	0	0	1	0	0
		686	376	545	330	572	1114	770	495
JUL	69	4	0	0	0	0	0	0	0
		482	208	770	495	526	527	596	456
AUG	105	1	0	1	0	0	0	0	0
		216	185	456	627	268	328	383	263
SEPT	139	6	2	0	0	0	0	0	0
		274	105	373	263	304	418	440	250
OCT	8	2	0	0	0	0	1	0	0
		112	187	315	355	250	184	644	744

Average corrected recapture (CRR) rates for:
i=February-May

Days after marking	1	3	10	17	24	31	38	45
$\leq Rn_i$	7	0	1	0	1	1	1	1
$Rn_i / \leq Co_i Cn_i \times 10^6$ (CRR)	129.4	0	9.3	0	9.7	8.8	7.2	9.6

i=June-October

Days after marking	1	3	10	17	24	31
$\leq Rn_i$	25	2	1	0	0	1
$Rn_i / \leq Co_i Cn_i \times 10^6$ (CRR)	23.4	18.4	4.2	0	0	3.3

i=February-October

Days after marking	1	3	10	17	24	31	38	45	52	59
$\leq Rn_i$	32	4	3	0	1	3	1	1	1	1
$Rn_i / \leq Co_i Cn_i \times 10^6$ (CRR)	124.6	29.3	8.5	0	3.3	7.2	2.5	3.6	3.8	3.3

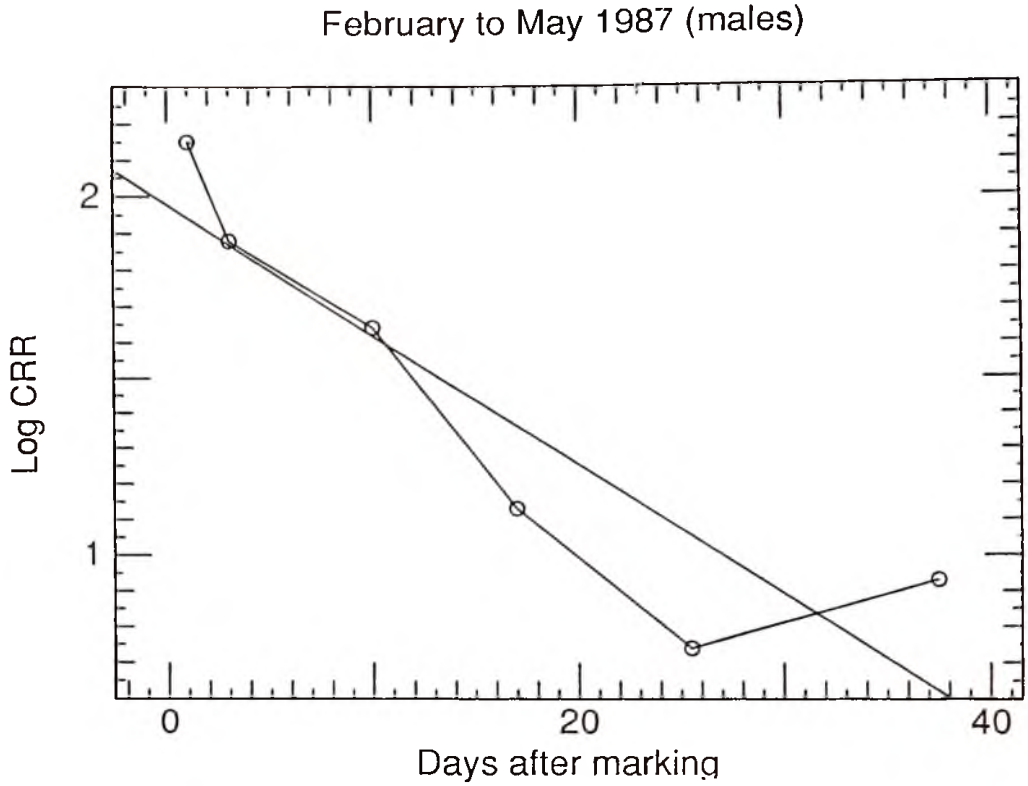


Figure 8.3: Changes in the recapture rate of male *G. longipennis* with days after marking. (February 1987 - May 1987), Regression: Y = 1.98 - 0.036X; r = - 0.90, P< 0.001) dilution rate = 8.0%.

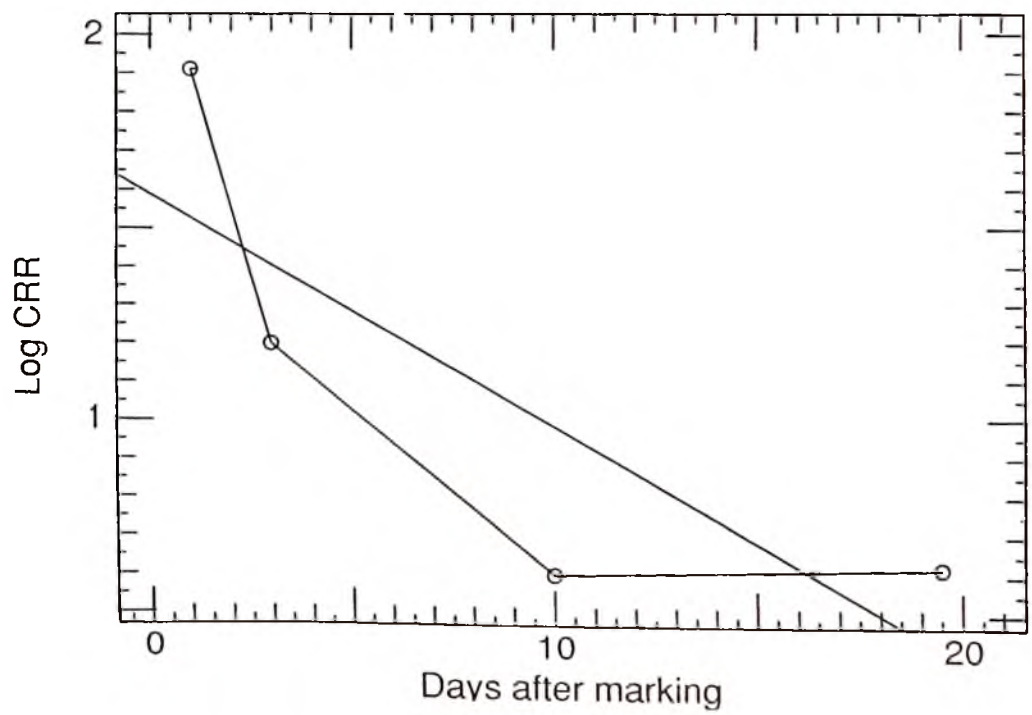


Figure 8.4: Changes in the recapture rate of male *G. longipennis* with days after marking.(June - October 1987) , Regression: Y = 1.59 - 0.060X; r = - 0.82, P< 0.001 dilution rate = 12.9%.

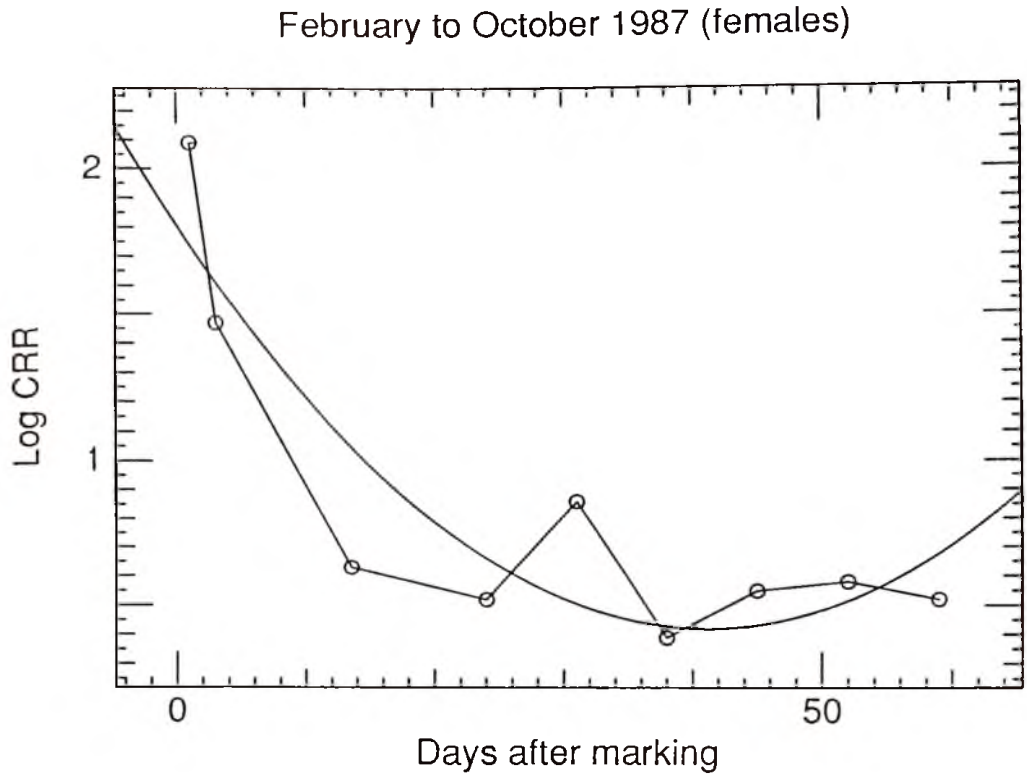


Figure 8.5: Changes in the recapture rate of female *G. longipennis* with days after marking.(February - October 1987) , Regression: $Y = 1.43 - 0.045X + 0.0005X^2$; r = - 0.83, P< 0.001, dilution rate = 9.8%.

8.3.2. *Seven-day marking experiment.*

Data for the seven-day marking experiment (grouped into the four marking occasions) are given in Tables 8.5 and 8.6 for males and females respectively. The average daily recapture rates were calculated up to 25 days for males and up to 29 days for females. The plots of recapture rates against days after marking with the fitted regression lines are given in Fig.8.6 for males and Fig. 8.7 for females.

Both sexes showed a decline in the daily recapture rate with time with damped fluctuations at more or less regular intervals. For males, the first increase in recapture rate occurred on day 3 with subsequent ones at 4-5 day intervals. On the females a peak was also recorded on day 3 after marking but more regular increases occurred at 9-10 day intervals.

Population estimates were carried out in the same way as before by extrapolating the regression line to day 0 and reading off the corrected recapture rate. The populations at the beginning of marking (late January 1987) were estimated at 15,848 males with a dilution rate of 8.2% per day and 14,125 females with a dilution rate of 6.7% per day. This would give a female percentage in the population of 47%.

Recaptures made over 4 weeks were used in estimating population sizes by the Jackson's positive method. The data are given below in Tables 8.7 and 8.8 (for males and females respectively) showing the number of recaptures per week, the proportion of marked flies in the weekly samples, and

Table 8.5: Numbers of marked male G. *longipennis* released in successive marking occasions, numbers recaptured and total numbers caught on subsequent days after marking from 28th January to 3rd February, 1987.

PERIOD (i)	NO. RELEASED (C_0)	NO. CAUGHT (C_n)	PERIOD AFTER MARKING(n=1-17) (Recaptures)													
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	231	281	3	7	0	2	1	2	0	0	1	1	0	0	0	0	0
2	165	184	2	2	2	5	1	2	1	0	0	0	1	0	0	1	1
3	105	107	2	4	0	0	0	0	0	0	0	0	1	0	0	0	0
4	31	383	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
5		209															
6		290															
7		166															
8		186															
9		158															
10		236															
11		62															
12		132															
13		141															
14		134															
15		220															
16		133															
17		173															

Average corrected recapture rates(CRR)

	Days after marking														
	1	2	5	7	9	11	13	15	17	19	21	23	25	27	29
Σ Rn	7	13	3	7	2	4	1	0	1	1	2	0	0	0	0
CRR	59.1	123.4	26.1	46.2	17.8	35.3	11.3	0	12.6	12.9	39.3	0	0	12.6	11.1

Table 8.6: Numbers of marked female *G. longipennis* released in successive marking occasions, numbers recaptured and total numbers caught on subsequent days after marking from 28th January to 3rd February, 1987.

PERIOD (i)	NO. RELEASED (C_o)	NO. CAUGHT (C_n)	PERIOD AFTER MARKING(n=1-17) (Recaptures)															
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	198	326	3	4	2	0	4	4	1	2	0	0	0	0	1	0	1	0	2
2	216	219	1	7	2	1	2	1	2	1	1	1	1	0	0	0	0	0	0
3	136	146	4	5	0	1	2	1	1	0	0	0	0	0	0	0	0	0	0
4	24	197	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
5		212																	
6		318																	
7		116																	
8		308																	
9		141																	
10		240																	
11		61																	
12		134																	
13		137																	
14		104																	
15		184																	
16		91																	
17		130																	

Average corrected recapture rates(CRR)

	Days after marking														
	1	2	5	7	9	11	13	15	17	19	21	23	25	27	2
ΣRn	8	16	4	2	8	7	4	3	1	1	1	0	1	0	1
CRR	58.6	152.1	38.7	16.2	62.8	56.5	37.7	26.3	12.0	13.2	17.7	0	14.4	0	14.

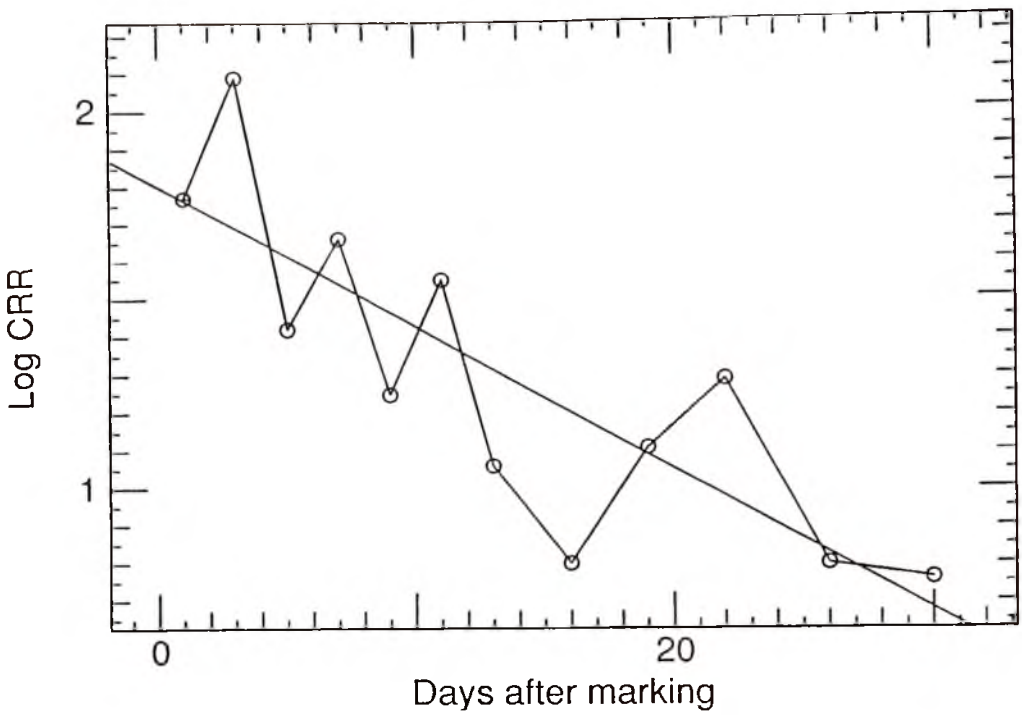


Figure 8.6: Changes in the recapture rate of males with days after marking. (28th January - 3rd February 1987). Regression: Y = 1.80 - 0.37X; r=0.83, P<0.001, dilution rate = 8.3%.

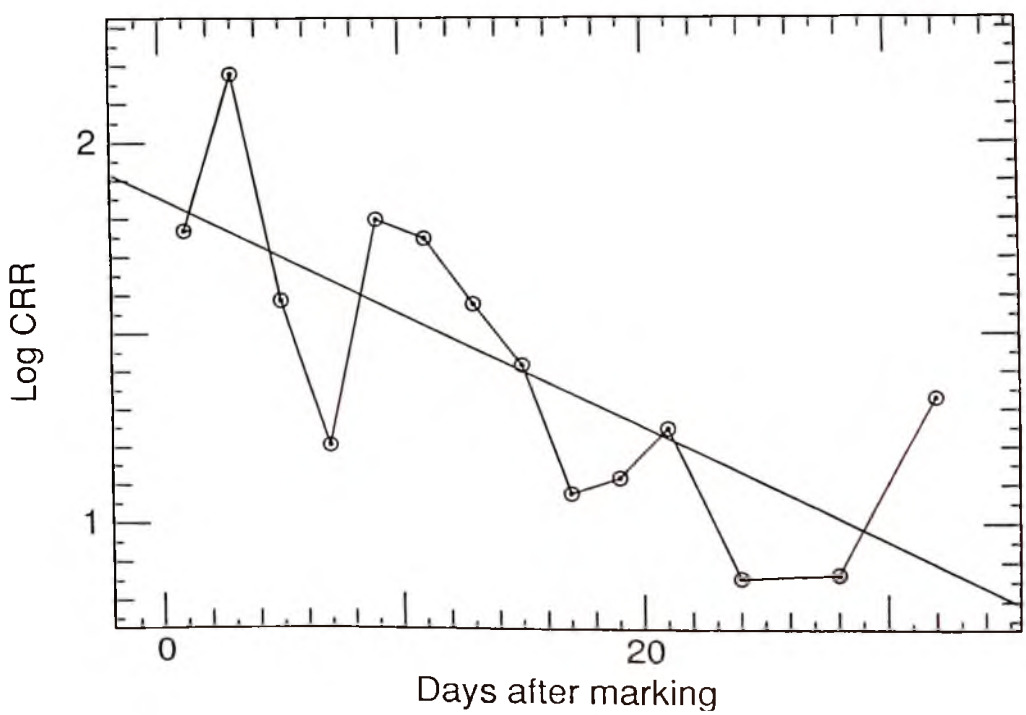


Figure 8.7: Changes in the recapture rate of females with days after marking. (28th January - 3rd February 1987). Regression: Y = 1.85 - 0.30X; r=0.74, P<0.001, dilution rate = 6.7%.

estimates of the population size and gain rate (b). Population size estimates were very close to those made by Parker's method.

Table 8.7: Weekly recaptures of male *G. longipennis* marked from the 23rd January-3rd February 1987

Week(i)	0	1	2	3	4
r_i	510				
No. caught(n_i)		754	580	501	560
No. recaptured(m_i)		16	3	1	2
q_i (m_i/n_i)		0.0212	0.0052	0.0020	0.0036
$\ln q_i$		-3.853	-5.264	-6.217	-5.635

$b = 0.554$ $\hat{N} = 13,421$

Table 8.8: Weekly recaptures of female *G. longipennis* marked from the 28th January to 3rd February.

Week(i)	0	1	2	3	4
r_i	647				
n_i		671	568	454	413
m_i		18	7	3	3
q_i (m_i/n_i)		0.0268	0.0123	0.0660	0.0073
$\ln q_i$		-3.518	-4.396	-5.019	-4.925

$b = 0.416$ $\hat{N} = 15,081$

Table 8.8: Weekly recaptures of female *G. longipennis* marked from the 28th January to 3rd February.

Week(i)	0	1	2	3	4
r_i	647				
n_i		671	568	454	413
m_i		18	7	3	3
$q_i\,(m_i/n_i)$		0.0268	0.0123	0.0660	0.0073
$\ln q_i$		-3.518	-4.396	-5.019	-4.925

$b = 0.416$ $\hat{N} = 15,081$

8.3.3. Relationship between relative and absolute population estimates

Table 8.9 shows the apparent and absolute population size estimates for the same periods. Relative densities are the averages over the same months for which the average absolute population size was also estimated.

There does appear to be quite a good correlation between relative and absolute population estimates although more data would be required to establish this statistically.

Table 8.9: Relative and absolute population estimates for G. longipennis.

	Relative estimate		Absolute estimate	
Month(s)	males	females	males	females
Feb. 1986-Jan. 1987	4.0	4.4	-	20,892
Jan. 1987	3.7	2.1	15,848	14,125
Feb. 1987-May 1987	2.5	2.2	10,471	-
Jun. 1987-Oct. 1987	5.2	5.9	25,703	-
Feb. 1987-Oct. 1987	4.0	4.2	17,340	15,848

8.3.4. The assessment of fly movement between Transect 1 and Transect 4 areas.

The monthly marking experiments on transect 4 yielded widely scattered recaptures which were considered inadequate for population size estimates. The data were however useful for assessing fly movement between the two transects. Only data from the monthly marking occasions from February 1987 onwards were used for assessing fly movement between the two areas, because during these months there was more continuity in the sampling between marking occasions than before.

To quantify the movement of flies between the two areas the methods proposed by Randolph and Rogers (1984) were adopted. According to these authors the exchange of flies between two areas can be quantified in two different ways.

a) by calculating the probability of capturing a marked fly either at the site of marking (Rn_{site1}/Cn_{site1}) or after transfer to the other site (Rn_{site1}/Cn_{site2}) or

b) by calculating the percentage of the total number of recaptured flies marked at one site that have moved to the other site before recapture ($Rn_{site2} \times 100/Rn_{site1} + Rn_{site2}$

Estimates of fly movement by the two methods are given in Table 8.10. By the first method, the probability of capturing marked flies on transect 4 was generally higher than it was on transect 1 and this included the capture of flies that crossed over from one transect to the other. By the second method, estimated percentage cross-overs were: 31.6% of the marked and recaptured transect 4 males and 42.9% of the females moved

Table 8.10: The assessment of movement of *G. longipennis* between Transect 1 (TR1) and Transect 4 (TR4) from February 1987-September 1987.

Site Marked	Site Caught	Co	Cn	Rn	Rn/Cn	$Rn_{site\,2} \times 100 / Rn_{site\,1} + Rn_{site\,2}$	
Males							
TR1	TR1	698	16182	42	0.003		
TR1	TR4	698	1849	2	0.001	4.54	
TR4	TR4	630	1849	13	0.004		$X^2 = 48.11^{***}$
TR4	TR1	630	16182	6	0.0004	31.58	
Females							
TR1	TR1	675	17090	46	0.004		
TR1	TR4	675	1465	3	0.002	6.12	
TR4	TR4	719	1465	24	0.011		$X^2 = 39.53^{***}$
TR4	TR1	719	17090	18	0.001	42.86	

Co=total number marked and released
Cn=total number of flies captured
Rn=total number of flies recaptured
***P<0.001

into transect 1 over the period whilst only 4.5% and 5.8% females moved in the reverse direction. A chi-square analysis showed that these differences were highly significant (X^2=8.25, P<0.01 for the males and 17.20, P<0.001 for the females).

8.4. DISCUSSION

The expression recapture rate is often used loosely to refer to the percentage of marked flies that have been recaptured. The value of this is dependent mainly on the efficiency of the sampling system and the behaviour of the flies after release. The corrected recapture rate proposed by Jackson (1948), on the other hand, is dependent on the size of the total fly population as well as on the other factors mentioned above. In this study, the corrected recapture rates appeared to be generally low which is most likely due to a high dispersal rate. Inferring from the rate of fly movement in the transect 4 direction alone, it appears that *G. longipennis* actually moved freely within a much larger habitat than was covered by the trap sampling arrangement, so that marked flies appeared to move out of the sampling area 1-3 days after they were released. They may then return into the sampling area after some time. This seems to explain the tendency to a curvilinear decline in recapture rate with time, i.e. high recapture rates in the first few days after marking dropping to very low rates soon after.

Phelps and Vale (1978) also obtained low percentage recaptures of marked *G. pallidipes* in Zimbabwe which they attributed to several factors including high mortality rate of marked flies caused by handling and/or starvation. In the present study, flies were trapped (most of them unfed) on the evening of the marking occasion at about 1845h, detained over night and released the following morning at about 0530h (if

marked the previous night) or at 0900hr after marking. Such interruption with the feeding activity of the flies could possibly lead to increased mortality compared to unmarked individuals. Another factor could be their failure to find suitable daytime resting sites when released outside their normal activity periods. The latter factor was circumvented in the 7-day marking experiments by releasing flies at dawn.

Periodic increases in activity, as indicated by increased corrected recapture rate, are associated with the feeding interval (Glasgow, 1961; Rogers, 1977; Randolph and Rogers, 1978 and Rogers and Randolph, 1986). However, the latter authors have pointed out, as earlier observed by Glasgow (1961), that the activity of female tsetse appears to be more influenced by the 9-10-day pregnancy cycle in which case one would require more than 5 sampling days after marking to detect such periodicity. However, the curve on the male recapture rate suggested a 2-3 day feeding cycle and this was supported by the data from the 7-day marking experiment which were collected over a longer period after marking. The 7-day experiment also provided much better data on the females and peak recapture rates did indeed occur at 9-10 days intervals after an initial peak on day three.

The above values are comparable to those reported by a number of workers for other *Glossina spp.* Jackson (1933) recorded increased activity of marked *G. m. morsitans* and *G. swynnertoni* at 4-5 days intervals. Glasgow (1961) showed that the feeding interval of male *G. swynnertoni* averaged 3.5-4.5

days. Rogers (1977) found a 4-day periodicity in the recapture rates of male *G. fuscipes* which he thought reflected the feeding cycle. In a more detailed analysis using autocorrelations and spectral analysis on long term recapture data on *G. p. palpalis*, Rogers and Randolph (1986) found mean periodicities of 4 days and 7 days in two different villages in Cote d'Ivoire for males and a 9-10 day periodicity for females. Turner (1987) also reported a 4-day feeding cycle in male *G. pallidipes* in the Lambwe Valley, Kenya and detected a 3-day feeding cycle for females which he thought occurred at specific stages of the developing larva. The results in this study strongly support the idea that the female activity cycle is mainly influenced by a 9-10-day pregnancy cycle and that of the males purely by the hunger cycle.

There are no previously published reports on the feeding intervals of *G. longipennis*. The only mark release recapture experiment ever carried out on the species was done by Power (1964) on males only near Lake Jipe, Kenya.
He did not analyze the data for the detection of feeding cycles. The data have been re-analyzed here for comparative purposes. Table 8.11 shows the daily recaptures for the various marking occasions, the numbers of flies released and caught in subsequent samples. The average corrected daily recapture rates over all the marking occasions (now calculated) are shown at the bottom of the table.

Table 8.11: Recaptures of male *G. longipennis* marked and released near Lake Jipe, Kenya (1964).

No. Caught	No. Released	Days after marking (recaptures) 0	1	2	3	4	5	6	7	8
66	66	0								
89	86	0	3							
54	49	0	0	5						
83	77	1	2	2	1					
108	92	4	7	1	3	1				
42	39	0	1	1	0	0	1			
0	0	0	0	0	0	0	0	0		
48	47	0	0	0	1	0	0	0	0	
152	140	2	1	0	1	1	2	2	1	2

Average corrected daily recapture rates(CRR)

Days after marking	0	1	2	3	4	5	6	7	8
Avg.CRR	1.7	4.1	4.6	2.2	0.7	1.8	1.7	0.6	1.2

Starting from day 0, peak recapture rates were observed on days 2, 5 and 8. These suggest a 2-3- day feeding interval, as was also observed in the present study.

On the estimates of population sizes from the monthly marking experiments, the values obtained are subject to large errors, first because of the very low recapture rates and secondly because the data have been pooled over several months with very varied conditions. Those from the 7-day marking experiment appear to be more reliable as they show a smoother decline in the recapture rate with time. Even the pooled estimates may be of value since there is some degree of agreement between:

a) the estimates made by the two different methods (Parker's and Jackson's positive)

b) the estimates made for the same period using the monthly marking data and those made using the 7-day marking data and

c) the trend of population changes, as shown by the absolute estimates at different periods and by the apparent densities (catch/trap/day) for the same periods.

The results on fly movement indicate that the probability of capturing a marked fly was higher on TR4 than it was on TR1, which is surprising because there were fewer traps on TR4 and hence it should be a less efficient trapping system. Randolph and Rogers (1984) pointed out that this probability in one area or the other is much influenced by the samples released and/or subsequently caught in the two areas. In this case the numbers released were about the same on both

transects for both sexes but the samples (Cn) taken on transect 1 were about 10 times larger than those taken on transect 4.

One explanation is that the large number of traps for suppression on TR1 were causing a higher mortality rate of marked flies than on TR4, hence the lower recapture rates over a period of time. The results also show that there is a greater movement of flies from TR4 to TR1 than in the reverse direction. If this movement into TR1 indicates a general higher immigration rate (which brings in unmarked flies), then marks on this transect will get more diluted than those on TR4. This could also explain the lower probability of capturing marked flies on TR1.

But what should cause a higher movement of flies into TR1? If the data were taken from a single marking occasion, it could be that TR1 offered more suitable micro-habitat at the time. Since these data cover a period of over a year, an explanation must be sought elsewhere. The fly population on TR1 was being reduced by the trapping (although this is not apparent from the MRR estimates because the periods chosen included times of re-invasion - see Chapter 9) The apparent densities shown by the NG2B and biconical traps on the two transects (Figs. 6.1-6.7) indicate trends of general decline on TR1 but of increase on TR4. The movement of flies into TR1 could, therefore,be in response to the vacant niche being created on this transect. Such movement of tsetse has

also been suggested by Turner and Brightwell (1986),for *G. pallidipes* between an adjacent coniferous forest and a thicket in the Lambwe Valley, Kenya, after the latter habitat underwent insecticidal spraying.

Transects 1 and 4 are about 7km apart, taken from the points of release in the two areas. Movement of flies from one transect to the other could take as short as one day. For instance, a female fly marked on transect 4 at about 0900h on the 7th of June 1987 was captured in the next morning's trap collections made on transect 1 at about 0700h about 8km away from transect 4. No vehicle moved between these areas during this period. Considering that this fly was released during the inactive period, it probably made the 8-kilometre journey during the evening activity period which lasts for about one hour. Although this might have been an exceptional case, many flies were observed to move up to 2 km in one evening and most flies took 2-3 days to make the crossover.

For future marking experiments on *G. longipennis* the recapture rates could be improved by marking and releasing flies in the same evening that they were caught (as was done on the seven day marking experiment) so as to minimize interruption with the feeding activity. Secondly, for a habitat such as Nguruman where the physical boundaries of the population are difficult to define, one needs to mark

very many flies and extend the trapping arrangement to cover as wide an area as possible.

CHAPTER NINE

SUPPRESSION OF A *G. LONGIPENNIS* POPULATION WITH BAITED NG2B TRAPS

9.1. INTRODUCTION

In the past decade, research has been intensified to develop tsetse control methods that are less dependent on the use of insecticides. Considerable progress has been made in using traps as a means of controlling tsetse populations rather than being just sampling tools. Insecticide impregnated targets have also been developed. The identification of odour baits that can be used to greatly increase catches has increased the potential of traps and targets for controlling tsetse populations.

An account has already been given in Chapter 2 (section 2.5.7) of the trial deployment of traps in some parts of Africa to reduce tsetse populations to very low levels. This started with the use of insecticide-impregnated biconical traps and cloth targets against populations of *G. palpalis* and *G. tachinoides* in Cote d'Ivoire (Laveissière, 1980; Laveissière and Couret, 1981). More research has since been carried out in the same country to improve the effectiveness of the targets and the methods of insecticide application (Laveissière *et al.*, 1988). Vale *et al.* (1988) also deployed insecticide-impregnated targets to reduce populations of *G. pallidipes* in Zimbabwe.

Research work at Nguruman was aimed at developing improved methods of trypanosomiasis control through a better understanding of tsetse population dynamics and development of more appropriate control technologies. By February 1987, it was considered that an appropriate stage was reached for a trial deployment of odour baited NG2B traps to suppress the local *G. pallidipes* population both to improve understanding of the system and to test out the new control technology. Unlike the trials carried out in the above mentioned cases, no insecticide was to be used in this operation. The effect of this exercise on the population of *G. longipennis* is reported in this chapter.

9.2. MATERIALS AND METHODS

One major factor that was considered in this operation was the cost involved. Efforts were therefore made to reduce the cost of the trap and the odour bait to as low a level as possible without reducing the efficiency of the trap. Brightwell *et al.* (1987) describe the initial experiments leading to the development of the NG2B prototype trap. Brightwell *et al.* (in press) give an account of experiments that were conducted to transform the NG2B prototype into a operational control version and to identify the optimum dose rates of the odour baits. The optimum dose rate of acetone was found to be 150 mg/h dispensed from a medicine bottle with a 0.2 cm diameter hole punched in the cap. Cow urine was dispensed from a 1 kg used cooking fat tin with the opening

covered with polythene and a 2 x 4 cm slot cut below the rim; this was found to give a dose rate of about 1000 mg/h.

The operation was limited to the main study area which includes transect 1 and covers about 100 km² (see Fig. 3.3). Although not completely isolated from other tsetse infested areas, it was hoped that immigration could be reduced by setting up barrier traps along the invasion routes.

Based on information on the natural mortality rates and estimates of the population size of *G. pallidipes* it was estimated that an average trap density of one trap/km² would increase the mortality rate enough to reduce the population to very low levels. It should be pointed out here that most of the operation was based on studies on the *G. pallidipes* population as there were only limited data on *G. longipennis*. Prior to trap deployment, a network of tracks were cut within the area with the help of the local community. To further involve the community, a training session on making the trap was given in each homestead (manyatta). Within two weeks the required number of 100 traps had been made by the community and were ready for deployment.

The month of February was chosen for the deployment of the traps because this was normally within the hot dry season when natural mortalities were highest for both *G. pallidipes* and *G. longipennis*. It was therefore hoped that a greater initial impact on the population could be achieved if the trap mortality was added at this time. Furthermore, it is known that the flies concentrate in the thicker part of the woodland

during this season thus giving the opportunity to place most traps in the thicker woodland to maximize the effect.

The traps were deployed over several days in the first week of February. Each trap was placed in a moderately shaded area to avoid direct exposure to sunlight which can cause rapid destruction of the nylon netting of the trap. The sites were cleared of surrounding vegetation to improve visibility of the trap to flies. To the north of the area, a higher density of traps was placed along the narrow strip of vegetation leading to transect 4 which was considered to be one of the main sources of immigration. To the south of the area lay more open woodland except for a narrow neck of thicker vegetation along the banks of the Oloibototo river within which several traps were set at 1 km intervals.

The odour baits were placed 30 cm behind each trap and firmly tied with wire to thick wooden pegs hammered into the ground. This was to prevent the baits from being knocked over by animals.

Out of the 100 traps, 20 of them were selected to be sampled regularly to monitor changes in the population. The selection was made in such a manner that each section of the area covered by the operation was represented and the number of traps sampled from each section was proportional to the density of the traps in the area. Catches from these traps were collected at least every 3 days and once every week the polythene bag cages were replaced by net cages to collect samples for ovarian age dissection. Grease was put around trap

supports to prevent ants from damaging samples from these traps.

Initially, trap servicing was carried out every two weeks on all hundred traps. This involved visiting each trap in turn to ensure that it was functioning. The trap was carefully inspected for holes, odour baits checked and topped up if necessary and all damage and their possible causes were recorded. For logistical reasons the frequency of this exercise was soon reduced to monthly intervals.

The impact of the suppression exercise was also monitored at monthly intervals with the biconical traps previously described (Chapter 4, sect 4.2). Since these extended outside of the suppression zone, an estimate could be made of percentage reduction taking into account seasonal changes.

9.3. RESULTS

The changes in the population levels of male and female G. *longipennis* from February to December 1987 as indicated by the monitoring NG2B traps are shown in Figures 9.1A and 9.1B respectively. Averages of all the monitoring traps, except trap 18, were taken over every 8 days. Trap 18, which was the outermost trap in the southern barrier, was catching virtually no tsetse flies and had to be moved to a different site; hence its omission from the analysis.

Population levels of both males and females rapidly declined over the first 2 months with some fluctuations from the general trend. Within this period trap catches declined

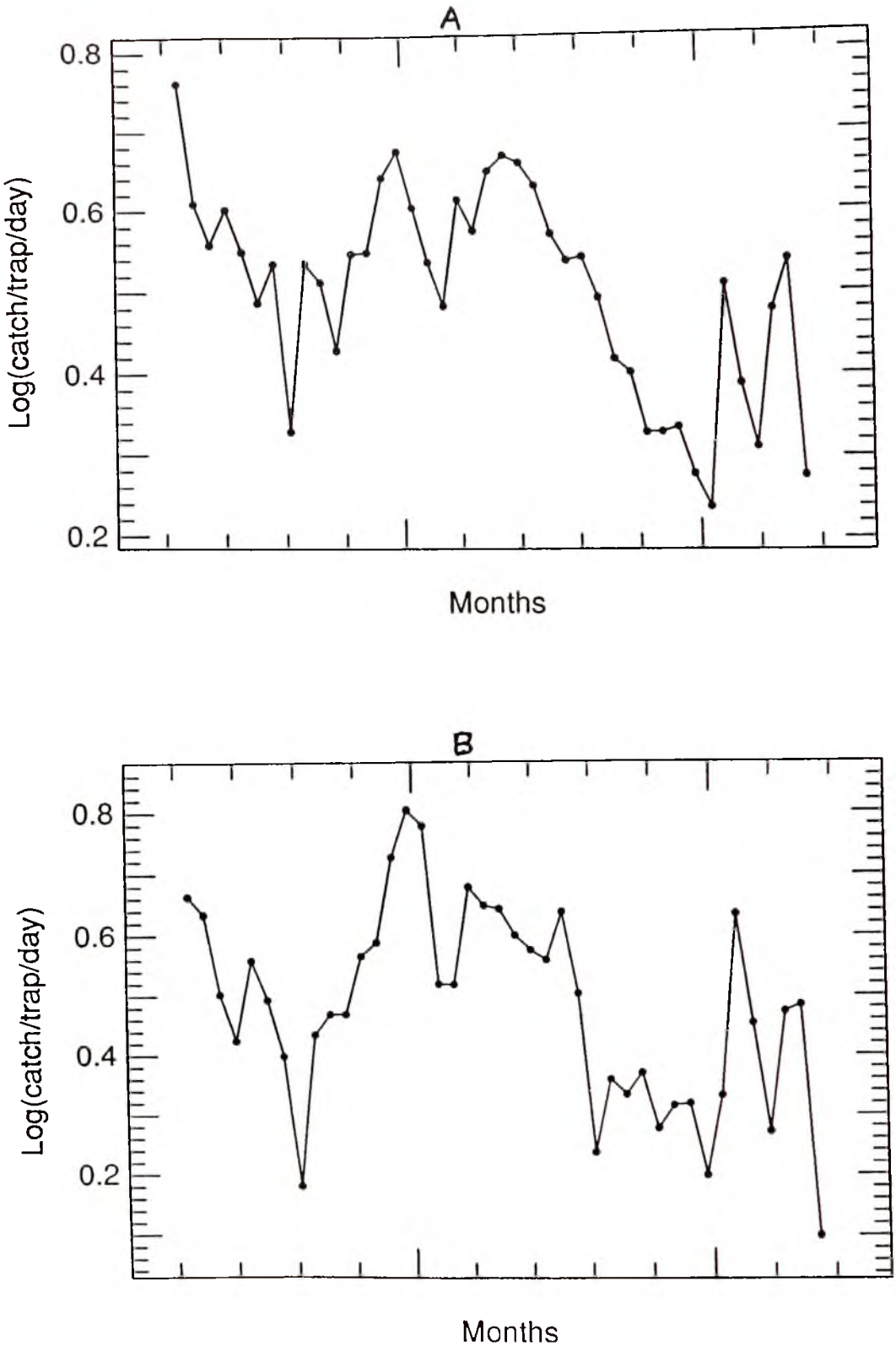
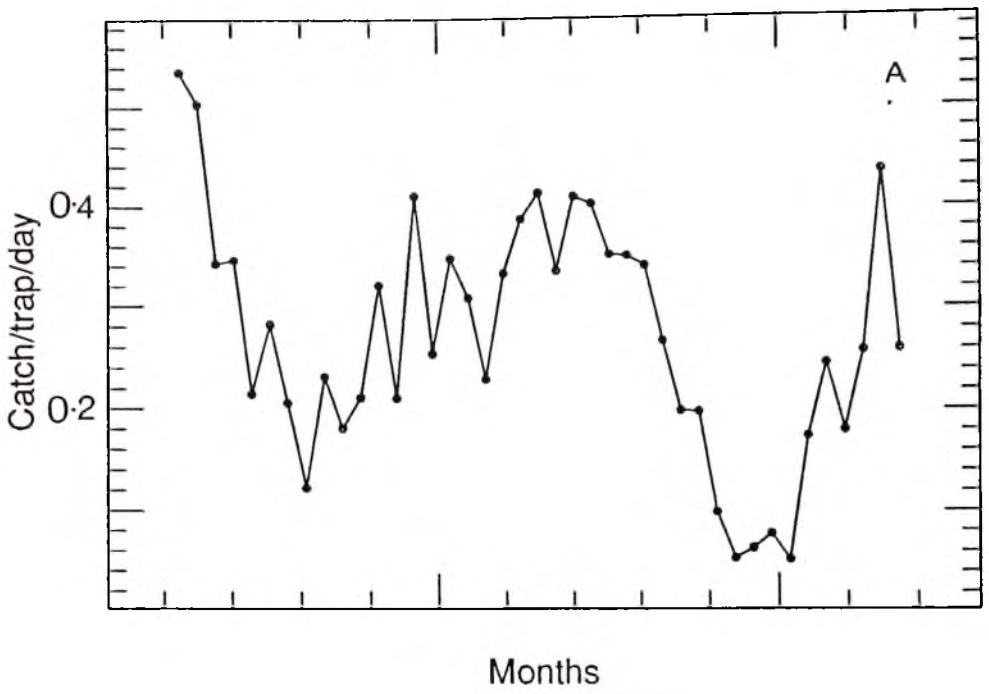


Figure 9.1: Changes in apparent densities of male G. *longipennis* in monitoring NG2B traps: A: Excluding barrier traps and B : all traps except trap 18.

from about 5.8 males and 4.6 females/trap/day to about 2.1 males and 1.5 females/trap/day giving a 64% reduction on the males and 67.4% on the females. With the onset of the rains, the numbers of both sexes increased and by the end of May the population levels were back to almost where they had started. In fact the female population reached a higher level (6.3 flies/trap/day) whilst that of the male was just below its starting level (4.8 flies/trap/day). A rapid decline followed over the next month to about 3.4 flies/trap for both sexes, increasing again to about 4.8 flies/trap on the average by the end of July. From then on there was a steady decline with some oscillation in the female population and by the end of October the traps were recording about 1.6 flies/trap for each sex. Rapid fluctuations were observed in November and December but the fly numbers were down to averages of 1.9 males and 1.3 females/trap /day by the end of December 1987. Thus over the 11 months the male population had fallen by 67.2% whilst that of the females was down by 73.9%.

Average catches from the barrier traps alone are shown in Figures 9.2A and 9.2B for males and females respectively. Catches in these traps generally follow the same trends as described above for all traps. The levels of population reduction shown in these traps are about the same as those shown in the general area (77% for males and 64% for females after the first two months). Similar increases were also observed in May-June and November-December except that the increases in the latter months were much greater in the



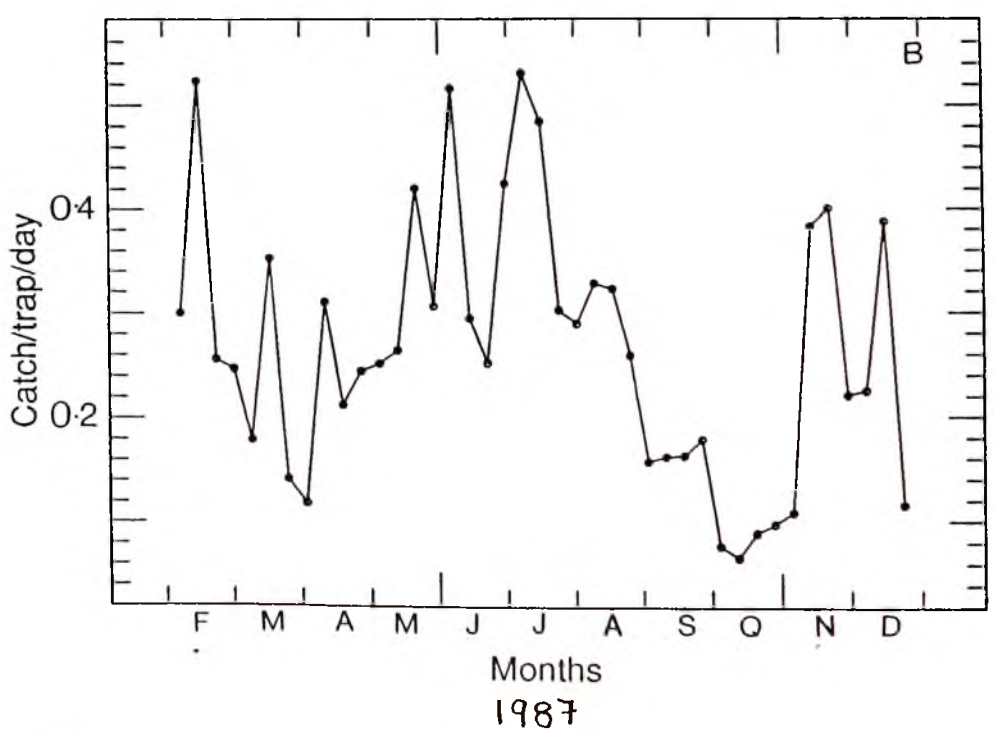


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Figure 9.2: Changes in apparent densities of male (A) and female (B) *G. longipennis* in 7 of the monitoring NG2B traps in the barrier.

barrier traps than those shown in the general area. By the end of December the reduction levels in the barrier traps were 51.8% for males and 60% for females.

Figure 9.3 shows the population reduction levels estimated from the biconical trap catches within the suppression area relative to those outside the area. Levels of population change were similar to those shown by the NG2B monitoring traps. Thus, there was an average 64% reduction of both sexes in the first two months with populations bouncing back to almost initial levels in June-July. By December-January reduction levels were about 60% for males and 90% for females.

The monthly age distributions and the estimated mortality rates from them are shown in Figure 9.4. Attention should be drawn to the fact that the mortality rate estimated from the ovarian age of flies caught in any month actually reflects the effects of mortality factors operating in the previous month. Moreover, if there is a steady decline in population size, the mortality rate must be corrected (Van Sickle and Phelps, 1988). The corrected mortalities are shown in the figure for those months in which a steady decline in population was observed. High mortality rates were observed in the first two months which then decreased over the next three and rose again in the following months. The overall mortality rate in February-March was the same (4.2%) as it was in July to September. The monthly age structure clearly reflects the corresponding levels in mortality rates i.e. there is a higher

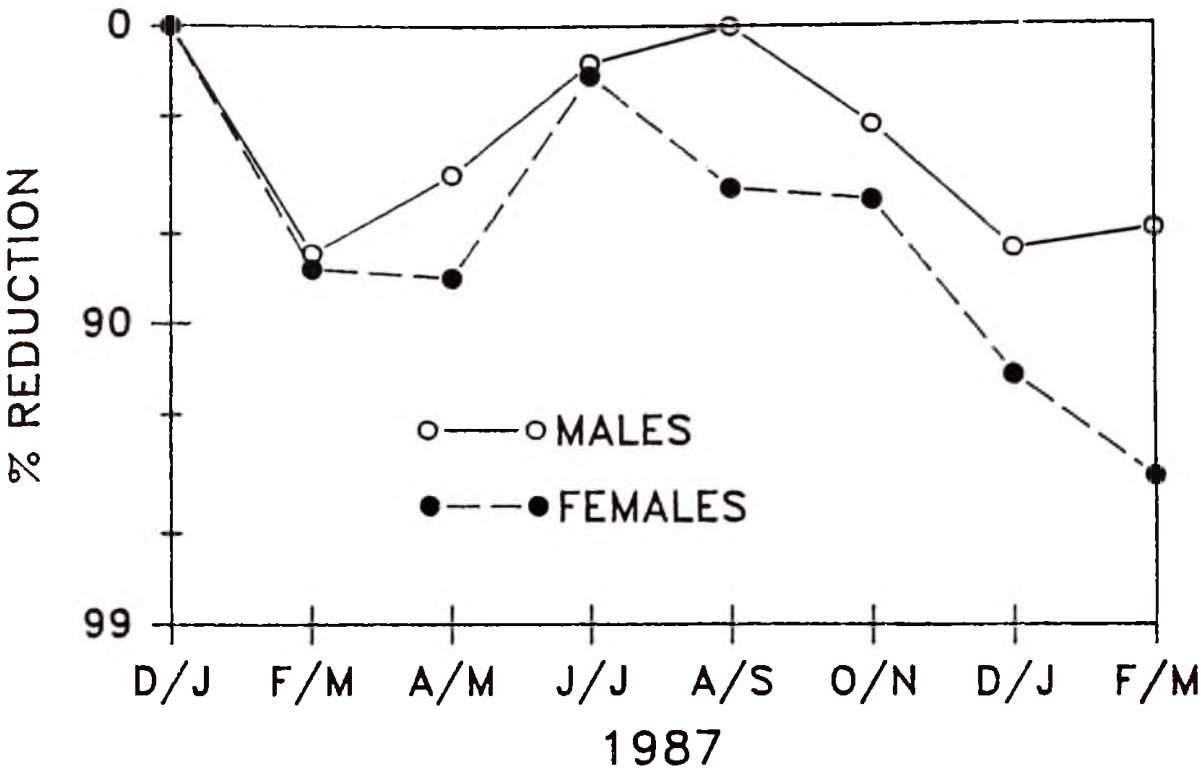

Figure 9.3: Bimonthly percentage reduction in the population levels of male and female *G. longipennis* estimated from apparent densities from the river biconical traps operating within and outside the suppression zone.

proportion of young flies when mortality rates are high (February to March and July to September).

4. DISCUSSION

It is obvious that there is a considerable seasonal variation in the degree of suppression of the *G. longipennis* population which is linked to climatic conditions. The impact of trapping on the population was very great in the dry seasons (February-March and July-September) whilst in the rainy season it had little or no effect on the population, and numbers increased to their former level.

Three factors probably contribute to the rapid decline in the dry seasons. First there is an increase in the natural mortality rate with increasing temperature and decreasing relative humidity as has already been established in Chapter 6 This however can only account for a very small part of the decline in 1987 since there was a considerable percentage reduction in the suppression zone relative to populations outside the zone which experienced similar climatic conditions.

Secondly there was a decrease in the efficiency of the suppression traps during the rainy seasons. It was also shown in Chapter 6 that flies spread out to open areas during the rainy season and concentrate in the thicker woodland during the dry season. Since there was a higher concentration of the suppression traps in the thicker woodland the impact of the

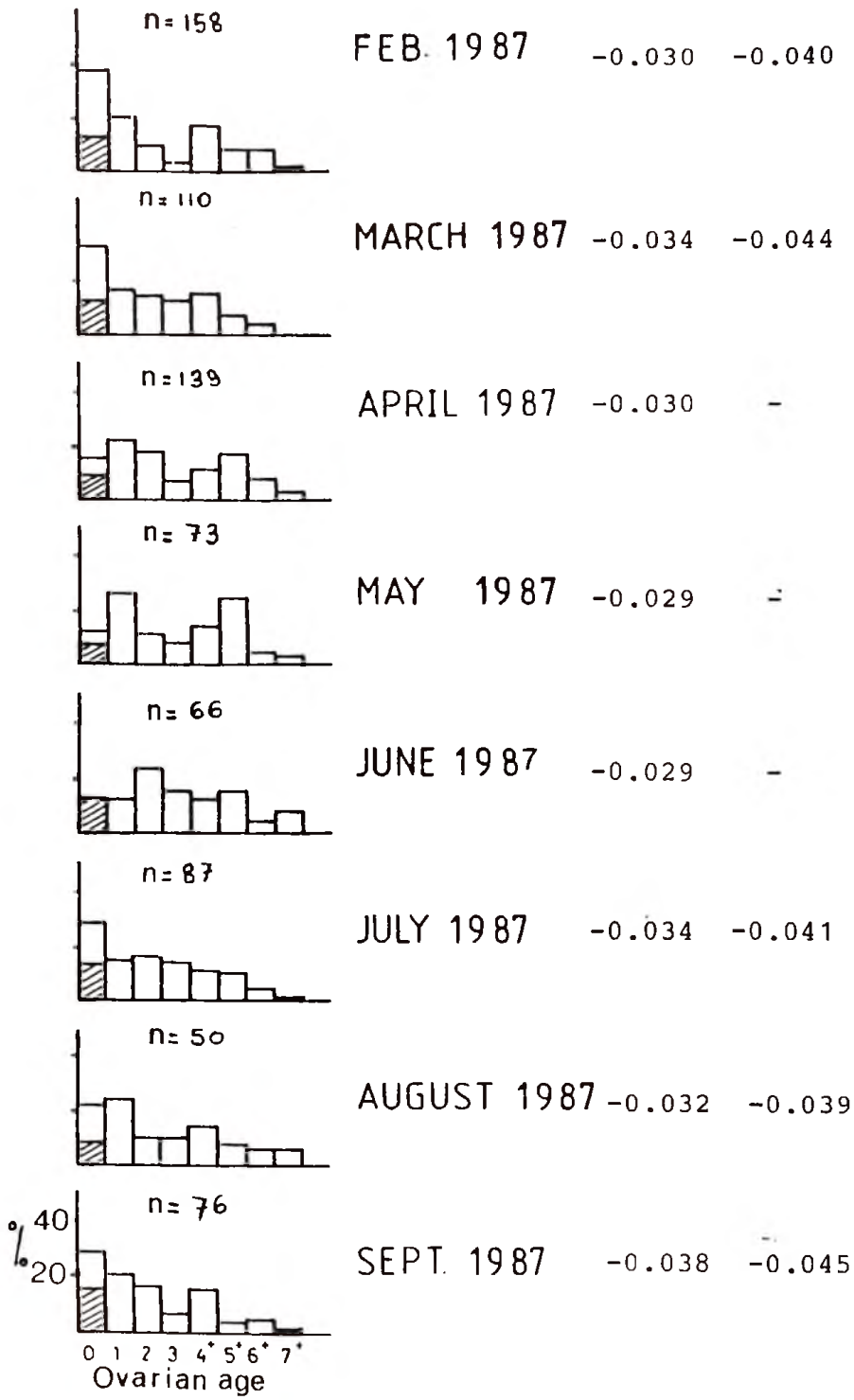

Figure 9.4: The age distribution and mortality rate estimates of *G. longipennis* caught in the monitoring traps during population suppression operation.

traps was greater during the time the flies are within this vegetation type.

The third and possibly most important factor influencing the whole operation is the seasonal immigration of flies into the area which was observed to be closely linked with climatic conditions. Although barrier traps were set up to reduce immigration, the barriers become less effective in the rainy season because the increased dispersal of the flies took them into very open vegetation types where there were few or no barrier traps. The increases in population levels in the rainy seasons are probably therefore mainly due to an increase in the immigration rate owing to a breakdown of the barrier. The relatively higher peaks observed in the barrier traps during the rains is strong evidence for immigration during these periods. Further evidence of immigration is the sudden rise in the percentage of older flies which could not have been derived from just the young flies of the previous months.

Therefore, the traps did have an effect on the population of *G. longipennis* but to a lesser extent than they had on the population of *G. pallidipes*. This is because firstly, the trap and odour baits are less effective for *G. longipennis* and secondly *G. longipennis* appear to occupy more open areas than *G. pallidipes*. This means that the trap densities in these areas are insufficient for *G. longipennis*. For the same reason it is more difficult to set up effective barriers for this species because barrier traps limited to only the thicker woodland would only be effective for very short periods.

The problem of immigration which applies to the population of *G. pallidipes* as well has also been experienced by other workers who have carried out trial deployment of traps to control tsetse populations (viz. Laveissière *et al.*, 1988; Vale *et al.*, 1988). It thus appears that success in this technology in a very small area relies on how well isolated it is from other infested areas. In the absence of sufficient isolation the alternative is to cover as much of the infested area as possible and thereby lessen the immigration pressure.

CHAPTER TEN

GENERAL DISCUSSION

There is increasing awareness that sustained control of tsetse and trypanosomiasis is dependent on acquiring a sound knowledge of the vector/trypanosome complex. Progress in the past decade on the development of better control strategies for the vector has been the result of intensive research work on their behaviour and ecology and there is every indication that with a proper understanding of vector populations their control is possible.

There is, however, the problem that in many localities where different tsetse species occur together, attention is still only being directed at the so-called main vector species. In most cases, the position of these main vectors were established by previous workers who may have laid down background information on methods of studying them. Therefore, they probably are more amenable to study than species which have been worked on less or not at all. As a result of this bias there remains lack of knowledge on 'minor vectors' such that in most cases, there is no evidence for their non-involvement in disease transmission. In view of this, if the move for vector control is to achieve its goal it is vital that proper knowledge be obtained on all tsetse species in any given system.

Glossina longipennis, one of the supposed minor vectors was found to be infected with trypanosomes at Nguruman. Further studies on the species were limited by the lack of an effective sampling device. In such a situation it would be unsafe to carry out a control programme without taking this species into consideration. The need for more information about *G. longipennis* was therefore vital for the development of a control strategy that would be effective for the system as a whole. The development of a sampling trap which was achieved in this project and the subsequent study on some aspects of the population dynamics of the species therefore provide a working base for developing such a control strategy.

The difference between the apparent densities recorded by the biconical traps and those recorded by the NG2B trap emphasizes the difference between the sampling efficiency of the two traps. This underlines the point that populations could remain undetected, especially at very low levels, if an ineffective sampling device is used. By the time field work on this project was completed, it was evident that the efficiency of the NG2B trap could be increased through further modification on the design and the use of more effective odour baits. The NG2F ('winged NG2B'), a modification from the original design, proved to be an improvement. On odour baits, the addition of octenol to the cow urine/acetone bait system showed a potential to increase catches but the treatment effect was not significant because of the generally low

numbers of flies that were caught. Brightwell *et al.* (in press) have since conducted further experiments to show that the use of octenol does indeed increase the catches of *G. longipennis* by 2-4 times.

For population studies the present trap/odour bait system was considered adequate for obtaining basic information on the population dynamics of *G. longipennis*. The observed trends in population change over the study period were similar to those observed by Dransfield *et al.* (pers. comm.) for *G. pallidipes* in the same habitat. Basically, both species attained peak population levels towards the end of the short and long rains and declined to low levels in the dry seasons. This indicates that both populations are probably responding to the same environmental factors. It was shown that high ambient temperatures and environmental dryness have adverse effects on the survival rate of both species. However, it is clear from the apparent densities of the two populations, supported by absolute population estimates, that the population levels of *G. longipennis* were always much lower than those of *G. pallidipes*.

The immediate question is what maintains the difference in population equilibrium levels in favour of *G. pallidipes*. Two factors could be maintaining the lower population of *G. longipennis*. Firstly, it could be that *G. longipennis* is less adapted to the environment than *G. pallidipes*. Secondly, or as a consequence of the first, *G. longipennis* is probably being out-competed by *G. pallidipes* for some essential environmental

resource(s). If *G. longipennis* was forcibly isolated by geographical barriers from a forest dwelling habitat as proposed by Machado (1959) and Evens (1953), there is the likelihood that it is less adapted to savannah conditions than most savannah species. If the two species are in competition, the most likely place where this occurs would be at the host. Vale (1974) showed that defence mechanisms when a host is being bitten by flies, such as skin rippling and general agitation,, can reduce the feeding success of tsetse. Being a larger species than *G. pallidipes*, *G. longipennis* would require a larger blood meal for larval development, in which case it might have more difficulty getting adequate feeds. The problem would be worse if they are feeding on the same host at the same time and using the same feeding sites on the host.

Some behavioral characteristics of *G. longipennis* appear to be adaptive efforts towards increasing the chances of survival under the conditions speculated above. Firstly, the crepuscular behaviour could be a move to both avoid adverse climatic conditions (high temperatures and low relative humidities) and to isolate itself temporally from *G. pallidipes*. Secondly, the high dispersal rate of *G. longipennis* suggests an active hunting life to increase its chances of encountering a host. Thirdly, the high insemination rate of young flies (Oa and Ob) is probably an adaptation to increase the chances of larval production.

From the high abortion rates, it appears that feeding success is an important limiting factor on the population size of *G. longipennis*. Abortion rates were observed to be particularly high in the hot and dry seasons probably because fly movement is more restricted during these periods, and hence there are fewer chances of getting adequate feeds. Furthermore, although the crepuscular behaviour may be a move to avoid competition and the rigors of climatic conditions, the rather short period does not offer the best chances for feeding success. Abortions may therefore be playing an important role in maintaining the low population levels of *G. longipennis* as was also suggested for *G. palpalis* in Nigeria by Jordan (1962b).

From the point of view of tsetse control operations, it would be important to establish whether competition is an important factor in determining the population levels of sympatric tsetse species. It is essential to know if the population levels of *G. longipennis* in the same habitat could rise to any higher levels in the absence of *G. pallidipes*. Could selective control of *G. pallidipes* lead to a replacement by *G. longipennis*?. Evidence for the possibility of such a phenomenon occurring has already been reported on some West African tsetse species by Laveissiere *et al.* (1988) in experimental control operations (see literature review 4.6 for details). Therefore, more information on this would be useful to tsetse control technology in general.

The results of the 11 months of population suppression showed that the system was more effective for *G. pallidipes* than it was for *G. longipennis*. Evidence from marking experiments with both species from within and outside the suppression zone showed that the trap barriers (at least the northern one) were more effective for *G. pallidipes* than they were for G. *longipennis*. Therefore, it is difficult to judge whether the lesser reduction in the population of *G. longipennis* was due to invasion or due to trap inefficiency. Whatever the case, the solutions to both problems are vital for the effective suppression of *G. longipennis* populations.

This would require a further improvement on the present system and the coverage of more area. However, at this stage the question of cost-effectiveness has to be considered. It was for this reason that the research into trap design and odour attractants concentrated as much as possible on the use of cheap and/or locally available materials and odour baits, such as locally produced cotton and cow urine. Chemicals like acetone, octenol, etc. although imported, were normally dispensed at very low dose rates so that very small quantities were required.

The trap/odour bait system which was developed turned out to be quite cheap requiring only 2 metres of blue cloth, 1 metre of black and 0.75 metres of netting. An inexhaustible supply of cow urine was available at no cost whilst acetone was required at only 150mg/day. The recent addition of an additional metre of blue cloth and octenol to the population

suppression traps was more for the population of *G. longipennis* and in terms of trap material and odour baits the system now costs about US$9 per trap per year. It is impossible to tell how much more material and/or odour bait would be required to develop a more efficient system. The coverage of more area would require more traps as well as increase the cost of trap servicing.

At this point the question arises as to whether the baited trap is the best tool for effective control of *G. longipennis*. Are there other already developed methods of tsetse control that are worth considering? The results from the electric screen test for trap efficiency indicated that a lot more flies come to the trap than actually get caught. Furthermore, it was a common observation that quite a number of flies landed and stayed on the outside of the trap for a considerable length of time before taking off again although many of such flies may eventually get caught.

In view of the above, insecticide impregnated traps and/or targets are worthy of consideration. However, the present trap/odour bait system is a standard against which any alternative approaches must be weighed in terms of cost. Ideally, a decision for any change or addition should be based on comparing the increase in efficiency over the present system and the extra cost involved. However, assuming that *G. longipennis* is as susceptible to insecticides as other tsetse species then impregnated targets may be more economical than traps because of the reduction in material cost. The target

principle was implied when the effect of cloth and no cloth was tested on the catch of an odour baited electric screen (Chapter 5). It was shown that although the black or blue cloth does not have the shape of the trap it caused a significant (3x) increase in catch over the odour bait alone. Targets of the Zimbabwe design have been tested against *G. longipennis* at Galana Ranch, Kenya, but as with traps they appear to be having a lesser effect than on *G. pallidipes* (Dransfield, pers. comm.).

Apart from the cost involved certain, other points should be considered before using insecticide impregnated targets in place of traps. Firstly, despite the controlled use of insecticides are used on targets, traps are still environmental safer. This point is especially important in a place like Nguruman where wild life is still abundant and Masai children roam the bushes with their cattle. Secondly, traps are self-monitoring and the effect of control can be closely followed without having to set up a separate sampling method as would be necessary with targets. Furthermore, the need to involve local communities is important for long term control campaigns as intended for the Nguruman project. In view of this, trap catches, which serve as convincing evidence of the possibility to control tsetse, play a significant role in getting co-operation from the community. However, targets are simple to construct and set up and require less servicing than traps do. It would therefore be easier to deploy targets over a larger area than traps.

In view of the pros and cons for traps and targets, the following approach is suggested for the control of G. *longipennis*. Since the traps presently being used are quite effective in the dry season, when fly movement is restricted to the thick woodland and taking into account the foreign exchange requirement of insecticides, a combination of traps and targets could be the most cost-effective approach to the control of the species. The currently baited modified NG2B trap can be concentrated in the thicker woodland and invasion routes whilst similarly baited targets should be placed in the more open woodland which forms the largest part of the habitat. Considering the high mobility of the species, targets could be effective at very low densities so that it may not require very many of them to cover a large area. The traps can be used to monitor population changes and detect routes of invasion. It may be necessary to increase the density of targets during the rains. Given the already low population levels which is apparently maintained by unfavourable environmental conditions, the suggested approach could keep the population below any significant levels.

SUMMARY

1. Investigations were carried out at Nguruman to develop an effective trap/ odour bait system that could be used for sampling populations of *Glossina longipennis* Corti. The trap was then used to carry out studies on the population dynamics of this species. Lastly, traps were deployed over about 100 km^2 in an attempt to suppress the population.

2. Acetone dispensed together with cow urine or buffalo urine increased biconical trap catches by about 4-6X over unbaited traps. The two chemicals appeared to act in a synergistic way since neither chemical on its own produced a significant increase in catch. Use of odour attractants did not affect the age distribution of flies caught in the trap.

3. The Zimbabwe F3 trap was found to be more effective than the biconical trap, especially for females. Several new traps were developed at Nguruman (NGU traps) and tested for *G. longipennis*. The best of these,the NG2B, was comparable with the F3 and, in view of material cost and ease of construction, was identified as the best sampling trap for this species. The NG2B caught a higher proportion of older flies than the biconical trap.

4. The crepuscular activity pattern of *G. longipennis* was critically investigated using an odour baited target adjacent to an electric screen. Morning peak catches were recorded from 0600-0615 hours, shortly before sunrise at 0630 hours. Evening catches were greater with males active before females. For males the peak was from 1815 - 1845 hours whilst for females it was from 1830 - 1845 hours. No flies were caught after 0700 hours in the morning and after 1900 hours in the evening. Light intensity was the main factor affecting flight activity.

5. The population dynamics of *G. longipennis* were studied through regular sampling with the biconical and NG2B traps. Trends in apparent densities showed two annual peaks, a major peak in June-July following the end of the long rains and a minor one during the short rains in November-December. Flies were observed to spread out into all vegetation types during the rainy seasons but were concentrated within the thick woodland during the dry seasons.

6. Daily mortality rates estimated from ovarian age structure were highest during the hot, dry seasons. They showed a positive correlation with maximum temperature and a negative correlation with minimum relative humidity.

7. The insemination rates of young female *G. longipennis* were very high throughout the sampling period being 100% in non-teneral nulliparous flies and over 80% in teneral flies.

8. An average abortion rate of 6% was recorded over the study period with a range of 0% in the rainy season to 60% in the dry season. Abortion rates showed a significant negative correlation with minimum relative humidity.

9. A significant relationship was established between adult fly size, as indicated by a measure of the wing vein length, and minimum relative humidity two months previously.

10. The absolute population size of *G. longipennis* in the study area was estimated using mark-release-recapture at an average of 17,300 males and 16900 females. Dilution rates were high indicating constant movement of flies into and out of the sampling area. Absolute population estimates at different times of year followed similar trends to apparent densities from trap catches.

12. Changes in the recapture rate of marked male flies indicated that they fed at 2-3 days intervals whilst the recapture rate of females showed 9-10 days intervals reflecting the pregnancy cycle.

13. A trial tsetse population suppression operation with odour baited NG2B traps carried out in the study area revealed that the system is more effective for *G. pallidipes* than it is for *G. longipennis*. Even so, the *G. longipennis* population was reduced by 60 -90% relative to populations outside the suppression zone during the dry season.

14. Barrier traps are less effective for this species due to its high mobility and wide distribution in more open vegetation types. Effective control of this species will probably require use of traps over a much larger area or the integration of insecticide impregnated targets with the traps.

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